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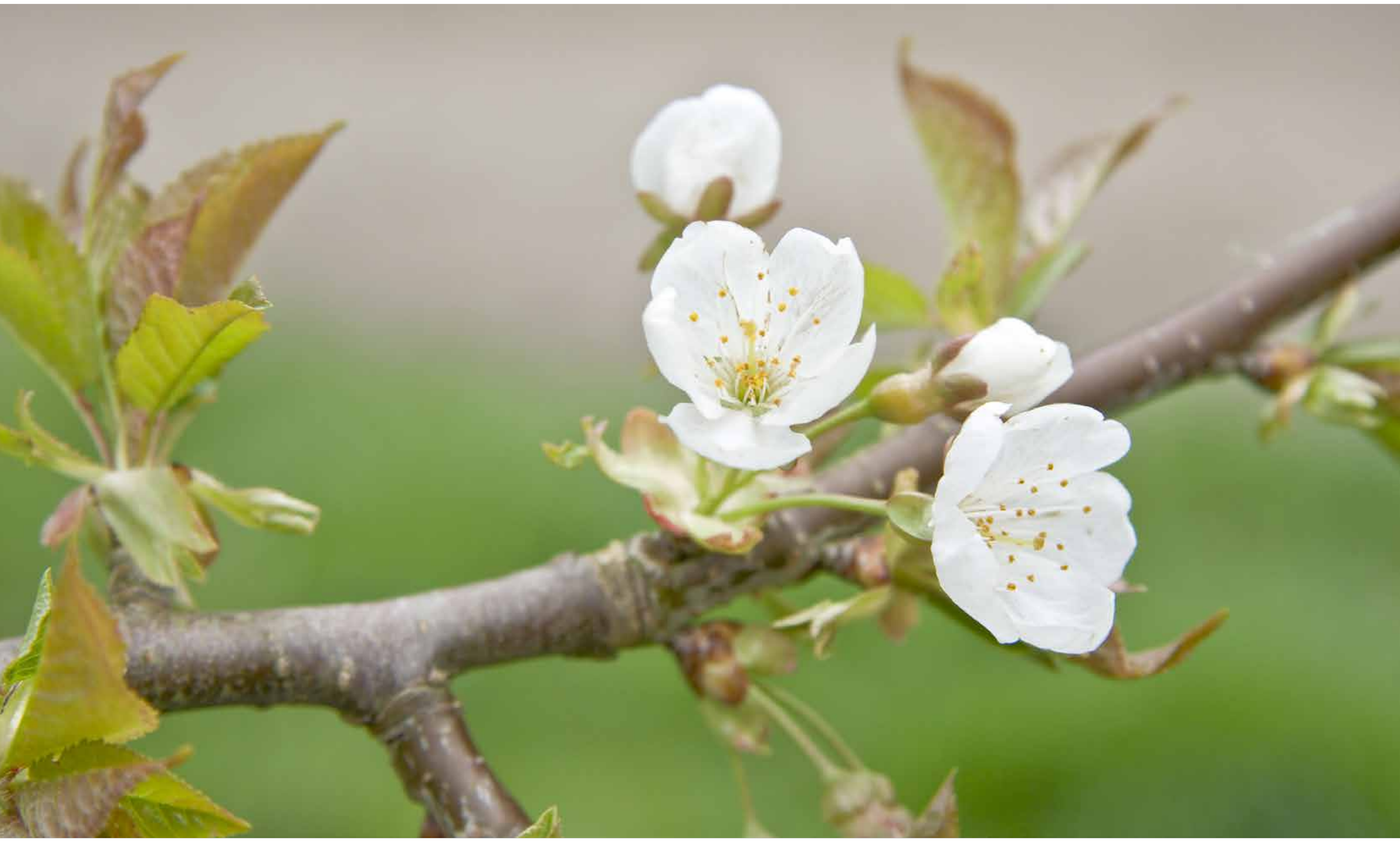

Research Report

Genetic considerations for provenance choice of native trees under climate change in England

Forest Research

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Genetic considerations for provenance choice of native trees under climate change in England

Richard Whittet, Stephen Cavers,
Richard Ennos and Joan Cottrell

Forestry Commission: Edinburgh

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Foreword

The UK Government, conservation bodies and the commercial forestry sector are committed to protecting, enhancing and expanding the resource of woods, trees and forests for the multiple benefits they provide, and doing so under conditions of a changing climate and increasing pest and disease threats. For a considerable time now the Forestry Commission has advocated 'the right tree in the right place' as a standard philosophy for tree planting, but how should this be interpreted when adapting to future environmental and climatic conditions?

A variety of views were expressed upon discussion of this topic, particularly in regard to appropriate provenance selection for native woodland planting. A lack of knowledge of the evidence base underpinning those views became apparent, and as a response we commissioned this report to answer the research question: What is the evidence around provenance choice and adaptation to climate change?

This report identifies, collates and analyses the available evidence to determine if using different provenances of native tree planting stock confers an adaptive advantage. This will help to influence and inform tree planting strategies, and the advice subsequently given to land managers. A clear and concise explanation of tree genetics and adaptation, as presented in this report, provides clarity of understanding of the evidence and highlights particular areas requiring further research.

However, this report only indirectly addresses the related issue of whether new native woods and trees should be established by planting or by natural regeneration to confer greater adaptive advantage. Natural England, The Woodland Trust and other conservation bodies frequently promote natural regeneration as the preferred mechanism for establishment, wherever feasible. This report does not compare the adaptive qualities of planted material with natural regeneration; rather, its explicit focus is upon planting material, and contrasting adaptation to projected climate change of more southerly provenance with local provenance. In addition, the evidence available is drawn from tree provenance performance in different situations and does not extend to a consideration of the ecosystem impacts of alternative provenance choices.

The Forestry Commission, Natural England and The Woodland Trust will use this body of evidence to shape policies and inform guidance on suitable actions for those seeking to build resilience to climate change into their woods and other tree planting situations.

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Steering Group

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Executive summary

Ongoing climate change and the increasing prevalence of native and exotic pests and diseases are generating considerable uncertainty regarding the choice of planting stock for new woodland establishment in England.

The first step in selecting stock for planting is to identify species which are well-suited to the environment of the planting site. Once species have been identified, it is important to decide which seed source (provenance) or sources of the species will be used. The assumption that locally sourced material provides the most appropriate option is increasingly being called into question because the environment to which trees are adapted is changing rapidly.

A strategy which has been proposed to help forests keep up with the rate of change is to source seeds from warmer areas further south, as they are expected to be better adapted to the future climate of the planting site on the basis of current climate projections. Although terminology for this approach varies, we describe this as assisted migration for convenience. The scientific rationale for assisted migration is introduced in the section 'Seed sourcing in an era of uncertainty' on page 4.

To explore factors of importance in deciding whether to formally advocate and adopt assisted migration, we first need to consider the range of objectives for the woodland, evaluate the likely changes in climate and their impacts on forests, and understand the processes and time frames governing local adaptation.

While we recognise that provenance decision-making may have ecosystem-wide consequences, the scope of this study is limited to considerations for trees alone, as keystone species within new native woodlands. Evidence of ecological impacts of assisted migration of provenances within species is severely limited and therefore further research is needed to ensure that there are not unforeseen consequences for other species already under stress from climate change and other environmental factors.

Annual average temperatures are projected to continue to rise throughout England at all times of year and by up to 4°C by the end of the century. This is an unprecedented rate of increase and may pose challenges for natural systems. Average summer precipitation totals are projected to decrease and average winter precipitation totals to increase, leading to an increased risk of summer drought and winter flooding. Climate change is unlikely to kill trees directly. Although reports of drought-induced mortality are increasing in southern Europe, tree mortality by extreme droughts over several consecutive years in England are unlikely outside of the southeast, although increased exposure to drought under hotter and drier summer conditions will increase physiological stress endured by drought-sensitive species. In areas where trees will not be moisture-limited, warmer temperatures will improve tree growth and productivity. Climate-related impacts on survival are more likely to arise due to the projected increased frequency and severity of extreme events and interactions between climate change and pests and diseases. Contemporary analogues for the climate projected for southern England exist in western France (in terms of average temperature and precipitation), but it is important to note that other aspects of the environment, including soils, pathogens, herbivores and mutualists, photoperiod and solar radiation, are very different. It is also important to note that drought-adapted trees sought from regions with a history of more frequent drought episodes would also have to be able to tolerate flooded conditions in winter and that earlier flushing trees from further south will be more exposed to late frosts.

Despite long generation times and immobility, trees possess a particular suite of evolutionary characteristics which can enable an efficient adaptive response. Levels of within-population genetic variation in trees are very high, which provides the raw material for evolutionary adaptation. Genetic variation is maintained by large population sizes, very high reproductive output and extensive gene flow. Due to their immobility, trees have also evolved to exhibit high levels of phenotypic plasticity in order to tolerate change *in situ*. Phenotypic plasticity will enable individuals and populations to tolerate the climatic changes projected over the coming century. While phenotypic plasticity can incur physiological costs, it will allow a buffer for trees while genetic adaptation through natural selection occurs during generational turnover.

Despite these inherent capabilities, the rate of change anticipated will mean that trees will lag behind a directionally moving optimum. In circumstances in which multiple sources of stress are simultaneous (e.g. heat and drought stress), trees may become predisposed to higher levels of pressure by pests and pathogens. Gaining an understanding of levels and patterns of genetic variation within species to help predict responses to an uncertain future is therefore a priority.

Understanding levels and patterns of adaptive genetic variation within and among tree populations requires measurement of trait variation in provenance tests. Provenance tests are experiments in which seed collected from many different locations are grown in a common environment or environments. An individual's phenotype (full complement of observable characteristics) is the product of its genetic make-up (genotype) and its interaction with the environment. Therefore, in a provenance test, where the environment is common, differences among provenances can be inferred to be due to their genotype. Results of provenance tests are used to help guide decisions about deployment of seed sources to planting sites.

To understand how populations of trees used in English forestry vary across their ranges, we have assessed results of provenance tests (n = 44) of trees which are native to or naturalised in England. We have focused on studies which were located in or near England. Although the evidence base is of mixed quality, relevance and comprehensiveness, and it is especially hard to generalise across species, some common, repeated findings emerged.

Overall findings from the review of provenance variation show that:

- Genetic variation in populations of trees is very high, typically exceeding the variation between populations.
- Different populations within a species show adaptive differences as a result of generations of spatially variable natural selection. Factors causing adaptive differentiation can include temperature and precipitation regimes, and local pest and pathogen pressures.
- The geographical pattern of adaptive variation varies among species and among traits within species.
- In multi-site trials, the proportion of phenotypic variation explained by the site is usually greater than the variation among provenances. This reflects phenotypic plasticity, the ability of trees to modify their phenotype *in situ*.
- Statistically significant provenance x site interactions are common although not ubiquitous and often small. This means that normally the ranking among provenances is relatively stable across sites.
- Provenances transferred from warmer to colder environments often show greater early vigour than local provenances although survival and stem form can be compromised if the transfer distance is too large or if transfer is made from an area with a continental climate.
- Local provenances often show average growth due to conservative adaptation to the local growing season and as a consequence can be hardier than those transferred from warmer environments.
- Stressful growing environments can reveal results which contrast with expectation, exposing cryptic genetic variation. This is when individuals and populations which do not differ greatly in the absence of stress produce very different phenotypes under conditions of stress.

Therefore, the success of any seed-sourcing strategy will be highly context-dependent. The relative risk of and need for changing from the status quo of sourcing seed which is putatively currently adapted (local) to sourcing seed from further south (assisted migration) can be influenced by the following factors, which are not independent of one another:

- **Management objectives.** Seed sourced from further south can show higher growth rates and may be desirable for production-oriented planting schemes, provided the risk of frost damage is considered acceptable.
- **The type and configuration of the landscape.** Upland environments are more topographically complex than lowland environments, with colder and windier conditions. In these circumstances, climatic conditions are more difficult to predict, adding uncertainty to selection of non-local seed. In harsh conditions, a conservative approach to seed sourcing is advisable, at least in the short term. In lowland planting schemes on agricultural soils, conditions will be more amenable to tree growth in general and so deployment of seed from further south entails less risk.
- **The temporal scale of the planting scheme.** In schemes where the intention is to create a forest which will regenerate naturally rather than being harvested, the period of exposure to rare but extreme events (e.g. frosts) is greater and therefore a conservative approach may provide the best chance of maintaining the large population size necessary for regeneration. On the other hand, the probability of exposure to new extremes (e.g. droughts) is also higher although there is no evidence that alternative seed-sourcing strategies can help manage for this. In any case, the risks of maladaptation over the short term have to be weighed against the risks of later stage maladaptation due to directional climate change. Over shorter rotations, exploiting past adaptation to longer growing seasons from southerly seed sources may be worth the risk where production is the primary objective.
- **The spatial scale, location and level of ongoing management anticipated in the planting scheme.** If forest-tending is sufficiently frequent to enable regular monitoring, aftercare and replacement of individual trees, the risks of sourcing seed from further south will be lower than otherwise. It is worth noting that monitoring of stands based on local seed will also be very important, especially in extreme years (e.g. heatwaves and droughts).

- **Aspects of species biology.** If provenance variation in the focal species has been shown to be very low, there may be no obvious advantage in sourcing local seed, and thus sourcing seed from further south could be seen as a precautionary measure, provided risk from other factors is also low.
- **The type of base material (i.e. improved versus unimproved) used.** Where sourcing seed from further south is considered desirable, improved seed sources ought to be favoured as they should have shown some evidence of genetic worth. There is a clear role for tree improvement in climate change adaptation, which is discussed in the section 'The role of tree improvement in climate change adaptation' on page 38.

We conclude this report by providing a summary of the major knowledge gaps which have been exposed in preparation of this report. In particular, gaining an understanding of geographical patterns of genetic variation in resilience to extreme events and identification of non-climatic (e.g. edaphic and biotic) factors involved in local adaptation are priorities. We stress the value of long-term field provenance tests and emphasise that further research into local adaptation will become increasingly important under rapid environmental change.

Introduction

Seed sourcing in an era of uncertainty

Current threats to forests call for a reappraisal of the way in which forest genetic resources are managed and deployed. Traditional approaches to sourcing seed to raise seedlings for woodland establishment have been built around the assumption that populations of trees show local adaptation to a stable climate. Rapidly changing environmental conditions undermine this assumption and the validity of local seed sourcing has been called into question domestically (Broadmeadow, Ray and Samuel, 2005; Forestry Commission England, 2010; Natural England and RSPB, 2014) and internationally (Ledig and Kitzmiller, 1992; Broadhurst *et al*., 2008; Aitken and Bemmels, 2016). One option that has been put forward to account for environmental change in seed sourcing is to identify populations already experiencing some of the environmental conditions forecast for the planting site and to source seed for planting from those populations, an activity broadly known as assisted migration (Box 1).

The ongoing international discourse surrounding assisted migration and allied strategies has been rich and nuanced during the last decade (Hällfors *et al*., 2014; Dumroese *et al*., 2015). However, the debate has remained mostly theoretical, with a large body of opinion papers and literature reviews (Broadhurst *et al*., 2008; Crowe and Parker, 2008; Kreyling *et al*., 2011; Sgrò, Lowe and Hoffmann, 2011; Weeks *et al*., 2011; Pedlar *et al*., 2012; Aitken and Whitlock, 2013; Breed *et al*., 2013; Jones, 2013; Williams and Dumroese, 2013; Havens *et al*., 2015; Kelly and Phillips, 2015; Sansilvestri, Frascaria-Lacoste and Fernández-Manjarrés, 2015; Aitken and Bemmels, 2016; Whittet *et al*., 2016a; McLachlan, Hellmann and Schwartz, 2017). Since its proposal as a climate change adaptation strategy is relatively recent, there has not yet been the opportunity to generate substantial evidence of its long-term effectiveness (Sansilvestri, Frascaria-Lacoste and Fernández-Manjarrés, 2015; Bucharova, 2017; Park and Talbot, 2018).

The scientific rationale for assisted migration of trees is based on the following arguments:

- Tree populations are adapted to climatic conditions.
- The climate is changing at an unprecedented rate and therefore trees adapted to the current or recent climate will encounter radically changed conditions to which they are not optimally adapted, which will bring about conditions of physiological stress.
- Species distribution models show that trees cannot migrate quickly enough to track their moving climatic optimum in space.
- Tree populations cannot adapt quickly enough to cope with changed conditions *in situ*.
- Analogous climates to those anticipated for a planting site can be found elsewhere in the species range (e.g. in warmer locations), and seed sourced from these locations will have a better chance of tolerating change than seed from local populations.
- Seed translocated northwards shows greater height growth which reflects higher potential productivity alongside greater competitive ability and dispersal capabilities (the hare wins the race).

Counter-arguments to the above points are:

- Even through tree populations are adapted to climatic conditions, there remains very high levels of genetic variation within populations, exceeding the variation found between populations. Local adaptation is multifarious in nature and it's drivers and manifestation are difficult to predict in time and space.
- Although there is long-term change in average conditions, high inter-annual variation and extreme weather events pose more immediate and serious threats to tree populations, such that responses are very difficult to predict.
- Species distribution models tend to ignore genetic variation and the possibility of adaptive responses, treating a whole species as genetically and ecologically homogeneous.
- Tree populations can tolerate change *in situ* through phenotypic plasticity and adapt in the long term via the action of natural selection upon genetic variation.
- The ideology of assisted migration is too strongly dependent on long-term changes in average temperature, which are the easiest changes to predict. This neglects variation in other aspects of the environment. Since some aspects of the environment will not change (e.g. photoperiod), future climates have no current analogues. The rationale for assisted migration completely neglects biotic interactions and soil characteristics.
- Superior height growth of seed translocated northwards does not necessarily imply higher fitness, and indeed can be considered an indicator of maladaptation to the local growing season. Conservative growth is likely to be better for long-term survival (the tortoise wins the race).

Box 1 – Terminology of assisted migration

The term assisted migration is used throughout this report because it is well understood by British foresters. The term assisted migration was initially put forward to describe climate change-motivated translocations of species in conservation biology for the purposes of extinction prevention or facilitated expansion into new areas to enable survival (Whitlock and Milspaugh, 2001; Hällfors *et al.*, 2014). Assisted migration *sensu stricto* is synonymous with assisted colonisation (Holmes, 2007) and managed relocation (Richardson *et al.*, 2009).

The meaning of assisted migration in our report is the sourcing of seed (or other sources of forest reproductive material) from populations experiencing thermal regimes predicted for planting sites into the future and deploying them in various mixtures with other non-local or local sources of seed. Since England is in the northern hemisphere, this practice would involve sourcing seed from further south, and we also use this more explicit description in some places, particularly in the Discussion section. The most likely donor populations for this practice in southern England would be from western France and northern England, and would involve populations from southern England.

The strategy is more similar to assisted gene flow (Aitken and Whitlock, 2013), composite provenancing (Broadhurst *et al.*, 2008), seed portfolio (Crowe and Parker, 2008), predictive provenancing (Breed *et al.*, 2013), ecosystem-oriented assisted migration (Sansilvestri, Frascaria-Lacoste and Fernández-Manjarrés, 2015), climate-based seed transfer (O'Neill and Ukrainetz, 2008), forestry assisted migration (Pedlar *et al.*, 2012), assisted range expansion, assisted population migration (Ste-Marie *et al.*, 2011), targeted gene flow (Kelly and Phillips, 2015), climate-adjusted provenancing (Prober *et al.*, 2015) and within-species assisted migration (Bucharova, 2017).

Alongside biological arguments, the debate around assisted migration is strongly influenced by emotions, belief systems and environmental ethics (Minteer and Collins, 2010; Maier and Simberloff, 2016). Subjectivity, lack of recognition of nuance within the discourse, and uncertainty about the future have created major sources of contention, complicating decision-making at policy level. For these reasons, Neff and Larson (2014) describe assisted migration as a 'wicked problem' which is 'trans-scientific' in nature, unlikely to be resolved by scientific evidence alone.

In recognition of the trans-scientific nature of assisted migration and deep uncertainty regarding the future of environmental change, we cannot and do not provide any assessment of the potential effectiveness of assisted migration, nor do we form strong conclusions or recommendations. Instead, we summarise evidence gained from experiments in trees from different environments which have been grown together under common conditions (provenance trials) involving species which are native to or naturalised in England. These data will be used to explore how genetic variation within and among populations of trees is arranged across the British landscape and how provenances from mainland Europe have performed in British provenance trials. This information is then interpreted to identify common findings to highlight a series of considerations for managers to take into account in their provenance decision-making.

Structure of the report

We begin the report by describing three major modes of anticipated environmental change and their impacts on forests in England: (i) directional change in mean values of some climatic variables; (ii) increasing frequency and severity of extreme events; and (iii) interactions between climate change and pests and diseases.

We then provide an overview of fundamental evolutionary principles to develop a picture of how genetic variation is generated, maintained and organised within and among populations of trees. The relevance of these processes to forest management is then discussed and is followed by an account of how adaptive genetic variation can be measured and described in experimental trials.

The main body of the report is a summary of published knowledge of the adaptive genetic resources of British tree species. This is arranged by taxon, and every study identified as sufficient to address the question at hand has been summarised in tables which contain details of both its experimental configuration, and brief statements summarising its key findings.

The evidence base is currently limited and the review is broad in scope, so it is not our intention to provide a meta-analysis *sensu* Boshier *et al*. (2015), which estimates the effect size of very specific actions. This is justified because the small sample size could not be used to produce meaningful, general results, and also it is especially difficult to generalise across species and geographical contexts to provide relevant guidance for site-scale decisions (Hubert and Cundall, 2006). In addition, we recognise that the motivation for assisted migration will very much depend on the management objectives and so it is impossible to choose a single, measurable indicator of suitability. Therefore, instead of any type of comparative quantitative analysis, the summary of evidence is synthesised, drawing attention to significant findings and phenomena to build statements regarding the possible effectiveness of certain actions.

Having pointed out the areas of uncertainty and variability, a series of tools designed to aid decision-making is provided, which will help to discover whether certain strategies are more or less risky given a set of conditions. These decision-making tools have been designed to point out how the relative risk and uncertainty associated with any given approach may change according to the context of the planting scheme and subsequent choices.

Technical terms used throughout the Report are defined in Box 2.

Box 2 – Glossary of terms

Common garden experiment. Various types of experiments in which plants from different populations are grown together. Used interchangeably with **provenance trial**.

Gene flow. The process by which genetic variation is exchanged between populations. Effective gene flow involves migration/dispersal, sex and birth.

Genetic drift. Random loss of genetic variation from a population.

Genotype. The genetic constitution of an individual organism.

Genotype X environment interaction. When different genotypes respond to environmental variation in different ways, that is, the effect of the environment upon phenotypes depends on the genotype. In the context of this report, **provenance x site interaction** would be more accurate.

Local adaptation. The syndrome by which a local population has adapted to its local environment via the process of natural selection. This ought to mean that individuals will possess components of trait variation which increase fitness in its home environment when compared to non-local individuals.

Mating system. The predominant manner in which sex takes place within and among individuals, for example, **outcrossing** (mating with other individuals) and **selfing** (when an individual mates with itself).

Mutation. A permanent change in the nucleotide sequence of a gene or chromosome. Occurs spontaneously.

Natural selection. The process by which individuals within a population are removed on the basis that they are not sufficiently fit to survive and reproduce. The process in turn ensures that fit individuals are retained and that the population as a whole has a better chance of adaptation.

Origin. The geographic location of the naturally regenerated, autochthonous population from which seed originates.

Phenotype. The full set of observable characteristics of an individual organism resulting from the interaction of its genotype (G) with the environment (E), $P = G + E$.

Phenotypic plasticity. The ability of an individual genotype to modify its phenotype *in situ* without genetic change.

Population. A group of individuals of the same species whose members may interbreed. Often population implies that the group of individuals are in a more or less contiguous geographical area.

Provenance. Often used interchangeably with origin. Refers to the geographic location from which seed was collected, regardless of whether the population was autochthonous.

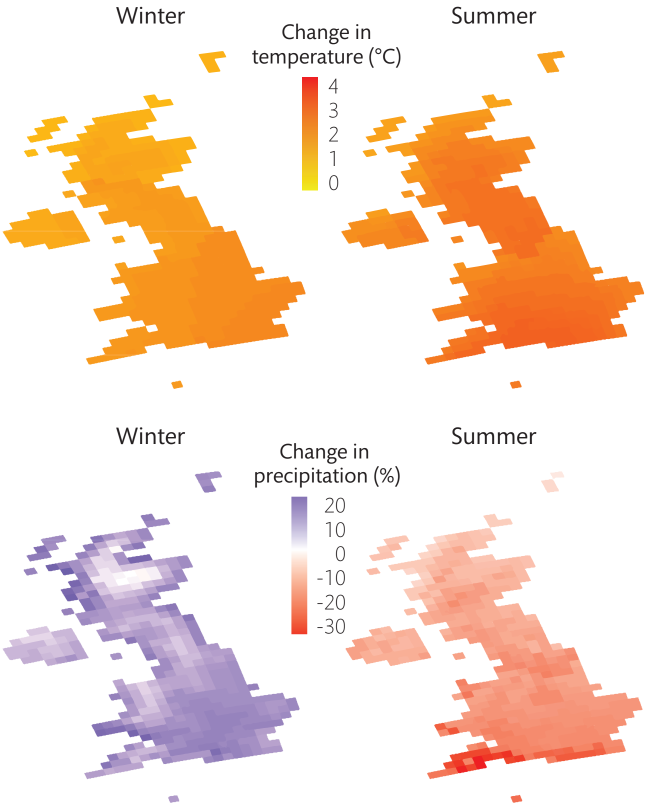
Environmental change and England's woodlands

Recent trends in meteorological variables indicate that the surface temperature of Great Britain has increased by 0.8–1°C since the 1980s, with the consequence of increasing growing seasons by 29 days throughout much of the country (Morison and Mathews, 2016). Annual precipitation sums have increased in Scotland in the last 45 years and, although long-term trends in England and Wales are less clear, all parts of Great Britain have experienced an increased contribution towards annual precipitation sums from heavy precipitation events in winter, and most regions have experienced drier summers in the last 50 years (Jenkins, Perry and Prior, 2008). The North Atlantic Oscillation (NAO), which can greatly influence winter weather conditions (Stenseth *et al*., 2002), has been particularly variable since 1990, and there has been an increase in the frequency of storms, although these have not been of greater frequency or magnitude than in the 1920s, another period in which the NAO exhibited great variability (Jenkins, Perry and Prior, 2008). It is therefore difficult to determine whether there has been or will be any overall change in average wind conditions.

Climate models indicate an increasing warming trend, with average temperatures expected to rise everywhere and at all times of year. Average summer temperatures are expected to increase by up to 4°C in parts of the country by the 2050s (Morison and Matthews, 2016; Figure 1). Annual precipitation totals are not predicted to change; however, seasonal patterns of precipitation are expected to continue to change, with lower precipitation expected in summer and more precipitation expected in winter, with a larger relative contribution of winter precipitation arriving in extreme episodes (Morison and Matthews, 2016; Figure 1). Warmer, drier summers will increase the risk of drought in the south and east of the country. Wetter winters, with high-intensity rainfall events, will increase the risk of flooding (Morison and Matthews, 2016).

All else being equal, higher temperatures and increased concentrations of CO_2 would be advantageous for tree growth in areas which are not water-limited (Saxe *et al*., 2001; Boisvenue and Running, 2006). Major climate change-induced challenges to forests are most likely to arise from interactions with changes to moisture regimes (e.g. flooding and drought), altered disturbance regimes and interactions with pests and diseases (Dale *et al*., 2001; Lindner *et al*., 2010).

Figure 1 Projected seasonal changes in average temperature (upper panel) and precipitation (lower panel). Projections are based on a central estimate, high-emissions scenario for the 2050s.



Data source: UK Climate Projections 09.

Alongside directional change in mean values of some variables, increases in the frequency and severity of extreme events are predicted for the future (IPCC, 2013). Such extreme episodes may include droughts, flooding, storms and fires. While directional change in the values of mean climatic variables will generate a long-term adaptive lag, extreme events pose greater immediate selective pressure on tree populations.

Extreme simultaneous drought and heat stress may kill trees through hydraulic failure through xylem cavitation, whereby pockets of air in the xylem prevent movement of water in the stem (McDowell *et al*., 2008). Also, prolonged exposure to drought conditions may lead to carbon starvation, whereby closure of stomata to prevent desiccation compromises metabolic processes (McDowell *et al*., 2008). For either of these two hypothesised mechanisms of drought-induced mortality to directly kill trees, drought would have to be very severe. As with other reports of drought-induced mortality in Europe (Allen *et al*., 2010), a more likely mechanism is via altered biotic interactions with antagonists or latent antagonists (Desprez-Loustau et al., 2006; Allen *et al*., 2010).

Intense precipitation events in winter are expected to increase in frequency, which enhances the possibility of flooding. While trees can play an active role in the interception of floodwater (Calder *et al*., 2003; Stratford *et al*., 2017), this is less efficient during winter when trees are not in active growth. The mechanical load and anaerobic conditions caused by waterlogging can lead to fine root death which results in poorer stability (Ray and Nicoll, 1998).

Climate change may interact with tree pests and diseases in many ways. Generalisations of impacts are difficult to make because effects will vary widely depending on the ecology and evolutionary history of the pathosystem (Sturrock *et al*., 2011; Ennos, 2015; Desprez-Loustau *et al*., 2016). The most important climate-related impacts on pest and pathogen outbreaks in England are likely to arise from stress and mechanical problems caused by drought and waterlogging, increased levels of injury during storms and higher minimum temperatures in winter changing the activity of pests and pathogens.

Some examples of possible interactions between climate change and pests and diseases are:

- Higher winter minimum temperatures would increase the active season for some species, for example, pine processionary moth (Battisti *et al*., 2005) and *Phytophthora cinnamomi* (Bergot *et al*., 2004), meaning greater exposure of trees to attack and potential range expansion of some pests and diseases.
- Warmer autumns may extend the asynchronous dormancy period, that is, the period between trees and insect pests entering dormancy (trees typically have higher minimum temperature requirements for entering dormancy). Damage caused by relatively weak dormant-season pathogens could increase if such pathogens have a larger opportunity to overcome host resistance (Van Vloten, 1952; Lonsdale and Gibbs, 2002).
- Flooding events in winter which lead to waterlogging of soils which kill or prevent formation of fine roots (Ray and Nicoll, 1998), coupled with root invasions of pathogens which require moisture for dispersal (e.g. *Phytophthora*), could be devastating for susceptible trees (Brasier, 1996).
- Humid spring conditions, favouring dispersal of some bacterial, fungal or fungus-like pathogens (Woods, Coates and Hamann, 2005; Brown and Webber, 2008).
- Trees may be predisposed to attack by facultative or non-aggressive pathogens although they can exhibit resistance when not under physiological stress, for example, drought stress (Schoeneweiss, 1975; Desprez-Loustau *et al*., 2006).
- Breakdown of competitive interactions among pathogens with different drought sensitivities causing a reduction of antagonism upon one species which then becomes aggressive (Redfern and Stenlid, 1998).

Increased pathogen pressure will occur simultaneously with ongoing human-mediated dispersal of pathogens on live plants and forest products as a result of international trade in live plants (Brasier, 2008). Therefore, forests will not only have to cope with higher levels of virulence or aggressiveness in native pests and pathogens but will also encounter exotic pests and pathogens to which they are not currently adapted (Ennos, 2015).

Evolutionary concepts and their application to forest management

Origins and organisation of genetic variation in trees

The origin of genetic variation within a species is derived from the process of mutation. Mutations are random changes to the DNA sequence which occur at low frequencies due to errors in the process of DNA replication when cells divide during tissue specialisation or reproduction. Mutations occur at a very low frequency, at a rate of around 10^{-7} per allele per generation in the model plant species *Arabidopsis thaliana* (Schultz, Lynch and Willis, 1999; Hoffman *et al*., 2004; Ossowski *et al*., 2010), and so mutation generates variation slowly. In animals there is a clear distinction between germline and somatic mutations whereby only the mutations which occur in cells related to reproduction (gametes) can be inherited. However, in plants, which have modular growth from multiple meristems, this distinction is less clear, and so heritable genetic variation can arise, even within an individual organism (Sutherland and Watkinson, 1986). Many tree species have very large genomes and live for long periods of time, so the absolute number of mutations accumulated by a single tree is high compared with other organisms (Petit and Hampe, 2006).

The majority of mutations can be considered neutral in the sense that they have no direct effect on the phenotype (the full complement of observable characteristics) of the individual. It is this selectively neutral variation which is identified by studies employing molecular markers to make inferences about historical migration routes and the genetic structure of populations (Ennos *et al*., 2000). The small number of mutations which do directly influence the phenotype are more likely to be deleterious (i.e. have a negative, usually lethal effect) than beneficial. A very rare example of a single deleterious mutation in trees can be found in albinistic coast redwood *Seqouia sempervirens* trees (White, Adams and Neale, 2007). The needles of albino redwood trees lack chlorophyll and are therefore unable to perform photosynthesis. They cannot reproduce sexually and so the mutation dies with the individual, remaining absent from the population until albinism spontaneously arises through mutation in another individual. Therefore, when a deleterious mutation arises and leads to death or fertility of the individual possessing the mutation, it is not passed on to subsequent generations.

However, adaptively significant phenotypic traits in trees tend not to vary in this binary (expresses trait/does not express trait) fashion and are seldom regulated by the action of very specific genes or gene regions (McKay and Latta, 2002; Le Corre and Kremer, 2012; Savolainen, Lascoux and Merilä, 2013). Instead, the majority of traits of interest in forestry vary continuously among individuals, for example, height, timing of bud burst, and diameter. Variations in these adaptive traits, also known as quantitative or polygenic traits, arise via the action of many genes (in the order of thousands) at positions across the genome, each of which makes a very small contribution to the total phenotypic variation.

In plants, reproduction can be sexual or asexual. When reproduction is asexual (e.g. by vegetative propagation), all offspring are genetically identical to one another and to the parent from which they are derived, save the occurrence of rare mutations during vegetative cell division. There is an array of means of asexual reproduction in British trees, for example by root suckers in the case of aspen and wild cherry, or by apomixis (asexual reproduction through seed) in some of the rare whitebeam species. However, no tree species is known to be exclusively asexual (Petit and Hampe, 2006) and so sexual reproduction is of much greater interest in evolutionary ecology as it gives rise to a greater diversity of individuals. It is also more relevant to this report since seed represents by far the largest proportion of forest reproductive material used in the raising of tree planting stock, therefore our major focus will be on sexual reproduction.

In the process of sexual reproduction, the genetic variation generated by mutation over long periods of time is reorganised, firstly during recombination in meiosis (gamete production) and then during fertilisation. Meiosis is the process by which single diploid (2n) parent cells containing two copies of each chromosome divide to produce four haploid (n) gametes (pollen or eggs) which contain half the number of chromosomes of the parent cell. During this process, recombination occurs which involves the physical crossing over of chromosomes which in highly outcrossing organisms such as trees, results in the exchange of genetic information between homologous chromosomes so that the resulting four gametes are non-identical. During subsequent fertilisation, two non-identical haploid (n) gametes fuse to form a diploid (2n) zygote which contains a unique combination of genetic material from each parent. In this way, a single tree receiving pollen from a range of near and distant fathers can regularly produce a highly diverse crop of seed on which natural selection can operate.

The mating system of trees is an important determinant of the quantities and patterns of genetic variation seen within and among populations of trees. Trees are predominantly outcrossing, meaning that mating tends to occur between different individuals (i.e. not self-pollinated), and those which are not closely related (Hamrick and Godt, 1996). Outcrossing is maintained via a series of barriers such as self-incompatibility, very strong and early acting inbreeding depression, which results in very poor survival, or abortion of selfed seed (Petit and Hampe, 2006). Monoecious trees are often dichogamous, which means that male and female flowers on the same tree are not reproductively active at the same time. Trees may also exhibit dioecy (e.g. willows and poplars), which means that male and female flowers are formed on different individuals, effectively ruling out self-pollination (Vamosi and Vamosi, 2004). In addition to predominance of outcrossing, trees are often highly fecund, producing large quantities of genetically variable pollen and seed. Although trees are immobile, gene dispersal in trees is substantial (Savolainen, Pyhäjärvi and Knürr, 2007; Kremer et al., 2012). Distance dispersal of genes is aided by trees' large stature which 'makes the world smaller for them' (Petit and Hampe, 2006). Wind dispersal of pollen, which is common in temperate and boreal trees, can occasionally be transported over very large distances, for example, 600 km in *Pinus sylvestris* in Finland (Varis *et al*., 2009). The bird-dispersed seed of the rosaceous trees, for example, *Sorbus aucuparia*, may also be transported over large distances, enabling efficient transfer of genetic variation among populations. The exchange of genetic variation among populations via pollen and seed is known as gene flow (Box 2).

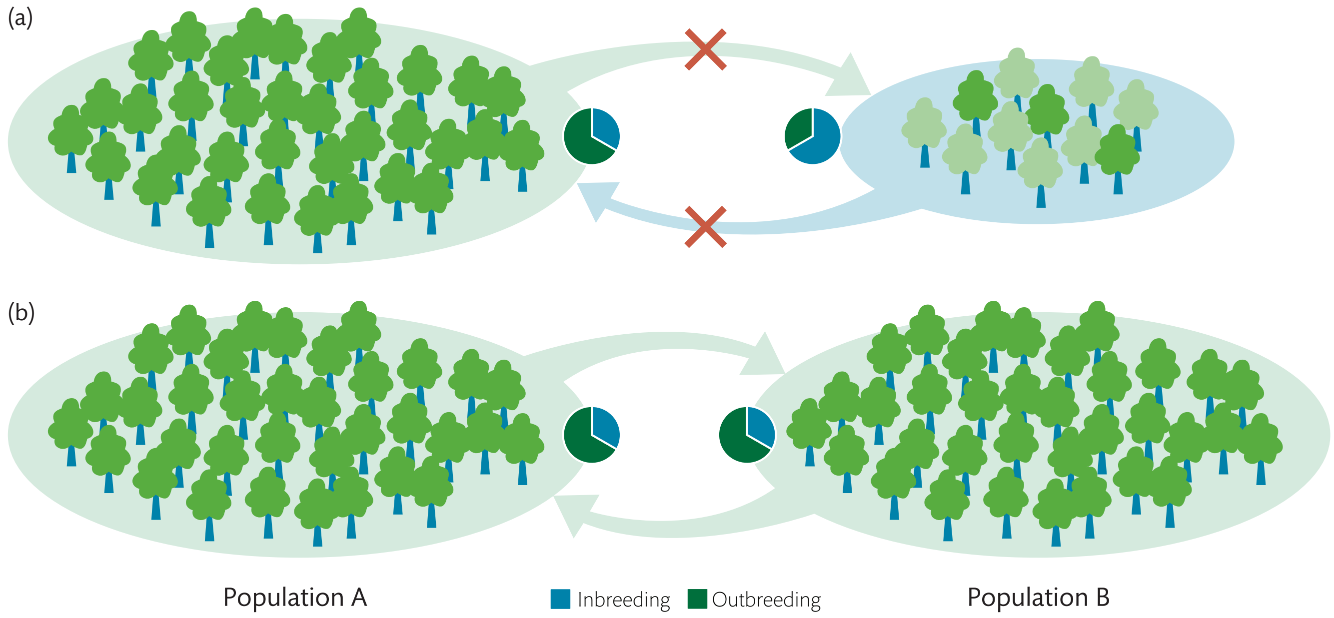
Gene flow reduces the differentiation between populations as constant exchange of genetic variation will act to homogenise the gene pool. However, it simultaneously increases the variation within a single population by delivering alleles from elsewhere. Constantly acting against gene flow is the process of genetic drift, which is the random fluctuation of allele frequencies from one generation to the next. This takes place whenever individuals possessing unique combinations of genetic variation die, or certain alleles are not passed on to the next generation by chance. Although genetic drift is a constant process removing genetic variation from populations, the variation is constantly replaced by that introduced by gene flow, providing donor populations and the conditions for effective gene flow exist. Genetic drift can become important when populations are very small and isolated for long periods of time, which would lead to increased differentiation between populations, a reduction in the available genetic diversity, and an increase in inbreeding which would give rise to a higher frequency of deleterious recessive genes within a population. However, there is good evidence that, even in very small populations of fewer than 10 trees in fragmented landscapes, it is possible for the maintenance of high levels of genetic variation and no fitness decrease in offspring even with rather infrequent gene flow events (Bacles, Lowe and Ennos, 2004, 2006; Hampe, Pemonge and Petit, 2013).

The action of mutation, sex, gene flow and genetic drift are responsible for determining the patterns of selectively neutral genetic variation present in any given population (Figure 2), and the amount will depend on population size, which is typically large in ecologically and silviculturally important trees due to their dominance within ecosystems (Petit and Hampe, 2006; Cavers and Cottrell, 2015) (Box 3). The process which determines the pattern and quantities of adaptive genetic variation, which is of most interest in reforestation, is natural selection, which will be the main focus of the next section.

Box 3 – Factors contributing to the high levels of genetic variation maintained by tree populations, adapted from Petit and Hampe (2006)

- Trees can produce very large quantities of pollen and seed many times in their lives.
- The gametes of a single individual are non-identical.
- Trees have many flowers, meaning that a single individual can mate with many different individuals each year.
- Trees are large, which helps dispersal/pollen catching.
- Trees are often dominant within their ecosystem, and so have large population sizes.
- Pre-zygotic mechanisms for avoidance of inbreeding (e.g. dichogamy and dioecy).
- Inbreeding depression is strong and acts early: selfed/inbred seed will typically be aborted, fail to germinate, die very young or fail to reproduce.
- Trees live for a long time, meaning that polymorphisms can persist for a long time in a mixed-age population.

Figure 2 Factors influencing genetic differentiation among tree populations, adapted from White, Adams and Neale (2007). In (a), populations will show a trend toward dissimilarity due to divergent natural selection, the absence of gene flow, differences in population size and mating systems. Population B undergoing high levels of inbreeding will experience stronger harmful effects of genetic drift than population A. In (b), the two large, outbreeding populations experiencing similar environmental conditions will tend towards similarity.



Adaptive pattern and process in trees

Natural selection

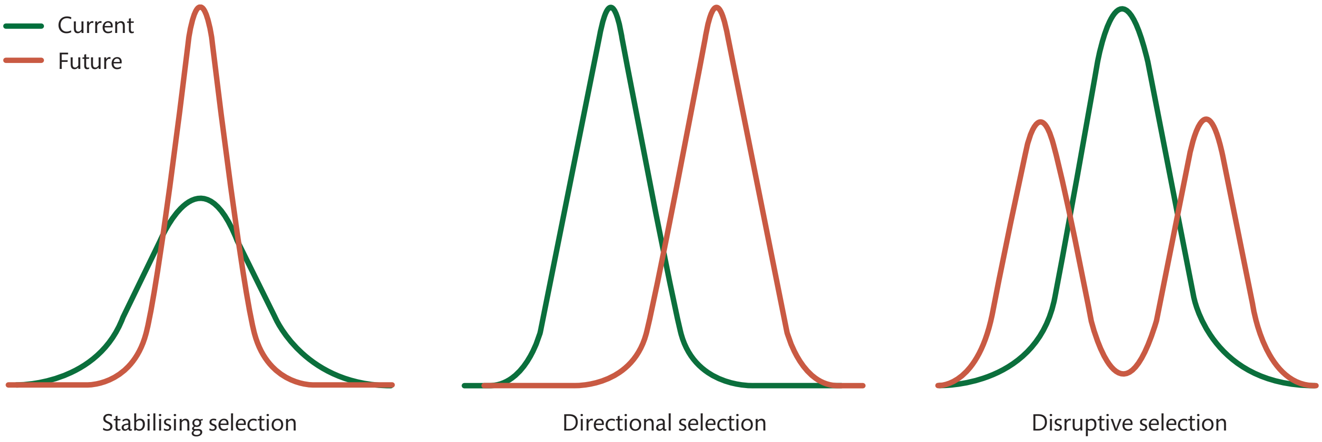
Natural selection operates upon the pool of genetic variation in a standing population by removing individuals which are not adapted to their environment, thus favouring the reproduction of individuals which are sufficiently fit to compete with siblings and other neighbouring trees, and sufficiently tolerant of stress to survive conditions which kill other individuals. Natural selection therefore removes genetic variation from a population but ensures that the variation which remains is suited to conditions prevailing at the time.

Natural selection acts on phenotypic variation in tree seedlings from an early age and is typically very strong at early life stages when trees are particularly sensitive to stress. Tree seed crops can be very large and highly variable and, typically, only a small proportion of the total offspring will survive to maturity (Persson and Ståhl, 1990; Petit and Hampe, 2006; Amm *et al*., 2012).

When different populations of the same species experience environmental conditions which differ spatially, natural selection causes populations to become adaptively different from one another (Kawecki and Ebert, 2004; Hereford, 2009), a process which can take place even in the absence of strong neutral genetic differentiation. This situation of local adaptation is common in trees (Savolainen, Pyhäjärvi and Knürr, 2007), but not ubiquitous (Leimu and Fischer, 2008), and has been demonstrated in many studies. Local adaptation is stronger in situations where selection pressures are intense, population sizes are large, and where populations have been present in a given location for many generations (Savolainen, Pyhäjärvi and Knürr, 2007).

Forces that impose natural selection can change over time as well as space. Over many generations of stable environment, natural selection will act against the extreme phenotypes within a population, meaning that the mean phenotypes are favoured. This is known as stabilising or balancing selection (Figure 3). When natural selection changes directly (e.g. due to rising temperatures), selection will act against one extreme in the population and there will be a steady shift towards the other extreme (directional selection). A rarer form of natural selection is disruptive selection. In this case, selection acts against the mean phenotype, favouring values at either phenotypic extreme. This may take place due to differential resource use within a population or non-random (assortative) mating and is one factor which may, over many generations, lead to reproductive isolation, and eventually separation into two or more species (Figure 3).

Figure 3 Hypothetical current and future distributions of phenotypic variation in a population undergoing different modes of natural selection.



Phenotypic plasticity

In the absence of generational turnover and natural selection, trees may respond to climate change through acclimation within their own lifetimes. The process by which individuals can alter their phenotype is known as phenotypic plasticity, which involves non-heritable change in an individual's physiology or morphology in the absence of changes in their genetic constitution (Nicotra *et al.*, 2010; Reich *et al.*, 2016).

Since trees cannot move and have long lifespans which include exposure to a wide range of conditions, plastic responses are highly developed in trees (Jump and Peñuelas, 2005; Alberto *et al.*, 2013; Chevin, Collins and Lefèvre, 2013). Highly variable environments are likely to select for phenotypic plasticity across a range of traits and so plastic responses to contemporary environmental change will be crucial (Jump and Peñuelas, 2005; Botero *et al.*, 2015). However, plastic responses are often associated with ontogenic costs, or trade-offs among traits (DeWitt, Sih and Wilson, 1998; Valladares, Gianoli and Gómez, 2007; Richter *et al.*, 2012), and selection for plasticity may conceal adaptive genetic responses to directional change, although phenotypic plasticity ought to be considered as an adaptive trait in itself (Jump and Peñuelas, 2005). There are limits to acclimation responses and trees may die either directly or as a consequence of stress which compromises their herbivore and pathogen defences if conditions far exceed such limits (Telford *et al.*, 2015).

Why is adaptive genetic variation relevant to forest management?

Adaptive genetic variation is relevant to forest management because the components of this variation held by an individual determine the capability of that individual to survive at a planting site. Patterns of geographic variation in trees have long been recognised and, for this reason, foresters have conducted provenance research for centuries, to identify which seed sources to use at planting sites (Langlet, 1971). A more complete account of the conduct of studies into provenance variation will be provided in the following sections. However, before doing so, it is worth introducing several key concepts of geographical variation which will be referred to throughout the text, and to highlight the rationale for considering adaptive genetic variation in forest management.

An understanding of the term phenotype, which was defined in the previous section as the full complement of observable characteristics in an organism, is essential. An individual's phenotype is the product of its genotype and the environment in which it grows (Figure 4).

A consequence of this is that identical genotypes will not necessarily produce identical phenotypes when exposed to different environmental conditions and thus the performance of any seed source will vary from site to site. If we consider a situation in which three distinct genotypes (provenances) are grown at two different sites, several different patterns may emerge (Figure 5). First, it may be the case that there are differences among genotypes, but no effect of the environment; in this case, the phenotype is not influenced by the environment. Second, it may be the case that, again, there are differences among genotypes at both sites, but the overall ranking is identical. Finally, a provenance x site (genotype x environment) interaction may emerge. In this case the effect of genotype and environment interact, which means that the different genotypes do not perform consistently across sites. In practical terms, this would mean that the best seed source will vary from site to site. In order to justify choice of seed sources for planting sites, it is very useful to identify whether such patterns exist.

Figure 4 Examples of genetic and environmental factors which will influence tree phenotypes.

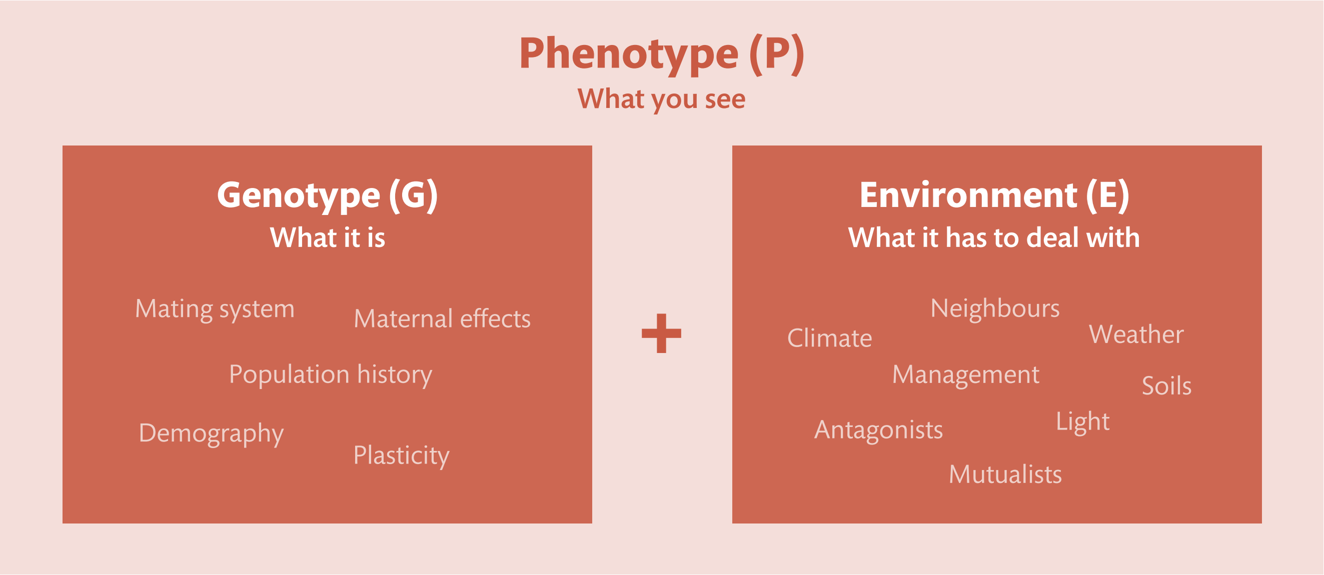
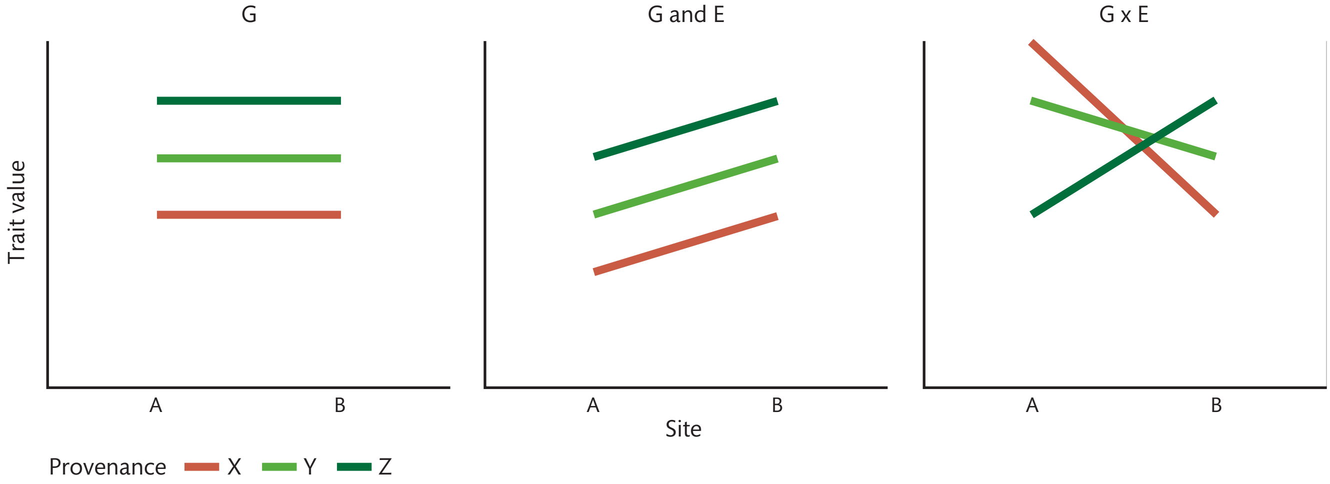


Figure 5 Types of reaction of a hypothetical trait for three genotypes (provenances) grown together in different environments (sites). In the G panel there is an effect of provenance, whereby the three provenances are uniformly different from one another at both sites but that the performance is identical at both sites. This means that performance is stable, and not varying by environment. In the G and E panel, there are uniformly different responses, although performance is better at site B. In the G x E panel, the effect of the trait value of each provenance depends on the site in which it is growing and there is thus a provenance x site, or, for convenience, a Genotype by Environment interaction.



Since natural selection acts on continuous or quantitative variation in phenotypic traits, and gene flow acts to increase genetic variation within populations but decrease variation among populations, there is often considerable overlap in phenotypic variation among populations. If a series of eight populations (a–g in Figure 6), for instance, situated along an environmental gradient in mean annual temperature which imposes a selection pressure, we expect to see a steady change in the average phenotype along the gradient (Figure 6). However, reliance on reporting the mean value alone ignores the very high levels of genetic variation that exist within populations (Box 3). This means that, between two or more populations, the phenotypes will not usually be completely different, implying an absence of any particular component of genetic variation. Rather, in the idealised case presented in Figure 6, they express variation clinally, but there will be overlap in their distributions (Figure 6b).

How can adaptive genetic variation be investigated?

Investigating adaptive genetic variation requires interpretation of the results from common garden experiments (Table 1). Common garden experiments involve growing plants raised from seed collected in different populations together in a common environment. Since the conditions under which the plants are grown are uniform, differences observed between plants can be inferred to be due to their genotype.

Figure 6 Idealised illustration of patterns of quantitative genetic variation among populations arranged along an environmental gradient, visualised in two ways: (a) population mean values increase with higher values of the environmental variable; however, in each population there is a large variation around the mean; (b) density of phenotypes in each population, illustrating the large overlap in phenotypic values among populations.

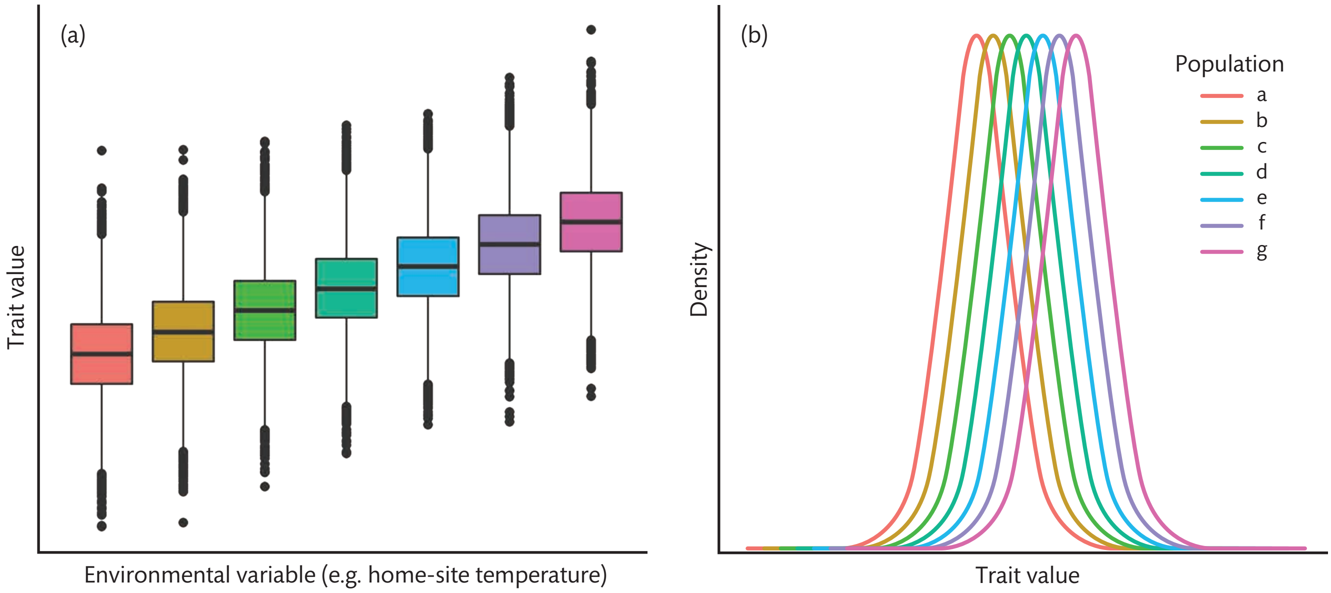


Table 1 A comparison of different types of common garden experiments.

Trial type	Advantages	Disadvantages
Short-term seedling test	• Rapid • Easy to control and minimise environmental variation • Can apply experimental treatments • Can identify clines and differences among populations	• Unrealistic • Short term • Difficult to replicate • Limited sample size
Long-term field provenance test	• Long term • Replicable across sites • Realistic • Large sample size possible • Can build response functions • Can act as sentinels • Can identify clines and differences among populations	• Resource-intensive • Very difficult to apply experimental treatments
Reciprocal transplant experiment	• Gold standard for identifying whether local-is-best in the strictest sense • Incorporates realistic edaphic and other biophysical properties of home sites	• Very resource-intensive • Difficult to establish • Large sample size difficult

There are several types of common garden experiment that are used in applied forest science. The types of questions that they can be used to address varies strongly according to the design of experiment, the size (number of individuals/populations/trial sites) and age of the trial, the reason for conducting the trial, the traits assessed, and the methods used to assess trait variation (White, Adams and Neale, 2007; Aitken *et al*., 2008; Fady *et al*., 2016; Gibson *et al*., 2016).

An important distinction in any kind of provenance test is whether the identity of parent trees of seedlings is retained throughout the investigation, so that the experiment has family structure. Maintaining family structure enables calculation of heritability values and levels of variation associated with families within populations. For these reasons, tests which maintain family structure provide the best information about adaptive capacity within populations, and are required if a provenance test will eventually be used as a source of material in an improvement programme.

Short-term seedling tests

Short-term seedling tests are usually experiments conducted in a single location involving containerised tree seedlings growing in artificial conditions (e.g. glasshouses and controlled environment growth chambers) for short periods. Short-term seedling tests are useful for identifying whether populations, or families within populations, show differentiation for adaptive characteristics relatively quickly. Since it is possible to exert a level of control over conditions, short-term seedling tests are useful for imposing experimental treatments, for example, drought (Arend *et al*., 2001; Anekonda *et al*., 2002; Matías, González-Díaz and Jump, 2014; Matías *et al*., 2016, 2017; Bustos Salazar *et al*., 2017), flooding (Donnelly *et al*., 2018; Bustos Salazar *et al*., 2017), exposure to pathogens (Elvira-Recuenco *et al*., 2014; Pliûra *et al*., 2015; Perry *et al*., 2016b) or extremes of temperature (Bower and Aitken, 2006; Matías, González-Díaz and Jump, 2014; Matías *et al*., 2016, 2017), and determining whether populations show differentiation in their responses to stress. An important disadvantage of performing the experiment in unrealistic conditions is that results are unlikely to reflect field performance (Gibson *et al*., 2016). While it may be possible to identify clinal trait variation by associating responses to environmental characteristics of the provenance home site, the sign and size of effects ought to be interpreted with caution as the plants are growing in unrealistic conditions. A further obvious shortcoming of such trials is that they are necessarily short-term, and so do not provide insights into survival.

Long-term field provenance tests

Long-term field provenance tests are common garden experiments in which trees are grown outdoors in field conditions for long periods, ideally up to at least one half of the rotation age (White, Adams and Neale, 2007). A major advantage of long-term field provenance tests is that they can be meaningfully replicated in multiple environments, which means that genotype x environment (or more accurately: provenance x site) interactions and phenotypic plasticity can be understood. Since the conditions are more likely to reflect realistic conditions of planting sites, field provenance tests can be used to guide decisions about deployment of adapted planting stock. Exposure to natural extreme events with long return rates (e.g. storms, flooding, drought, fire, extremes of temperature and outbreaks) allow networks of trials to act as sentinels to help understand the impact of extreme events, although they represent a largely untapped resource for this purpose. For these reasons, long-term field tests are more useful for identifying suitable seed sources than short-term seedling tests (Table 1).

With high levels of replication across sites, it may be possible to utilise results to predict responses in many environments, using population transfer functions (Rehfeldt *et al*., 1999) or population response functions to specific sets of environmental variables (Rehfeldt *et al*., 2002; St Clair, Mandel and Vance-Borland, 2005; Wang *et al*., 2006, Sáenz-Romero *et al*., 2017).

Reciprocal transplant experiments

A reciprocal transplant experiment involves collecting seed from multiple populations and raising seed from all of the populations sampled together at each collection site, ideally within the woodland itself to reflect growing conditions of the local parent trees as closely as possible. This design makes reciprocal transplant experiments the gold standard for investigating local adaptation as, if a home-site advantage exists, it can be observed directly. However, the complexity also means that they are difficult to scale and to establish and, consequently, fully reciprocal transplant experiments in trees are very rare (Latreille and Pichot, 2017). There are two examples in the domestic literature which come close to a reciprocal transplant design (Boshier and Stewart, 2005; Clark, 2013), although both had problems with establishment.

Traits

In many biological systems, fitness is measured as a function of reproductive output, or the genetic composition of subsequent generations, that is, Darwinian fitness (Orr, 2009). Trees are long-lived, take up large amounts of space and resources, and typically have delayed maturity, so measuring fitness in this manner is typically not feasible (Aitken and Bemmels, 2016). Instead, variation in a range of phenotypic traits can be assessed as proxies for fitness, each of which come with advantages and disadvantages (Table 2), and thus it is best to consider variation in multiple traits when considering adaptation to the environment.

Table 2 A summary of traits which can be assessed in provenance experiments as proxies for fitness with comments on their application, in terms of advantages and disadvantages.

Trait	Category	Comments
Survival	Performance	• Ultimately the most important trait • Very easy to measure, and can be done while assessing variation in other traits • Best measured after several seasons as maladaptation, which is usually evident early, can take longer to develop (Worrell *et al.*, 2000)
Height	Performance	• Most commonly reported trait • Reflects ability to compete, grow, and ultimately will enhance dispersal capabilities • Of clear silvicultural and selective importance • Can covary with flushing and forking meaning that it should not be considered in isolation (although it commonly is)
Stem form (forking)	Performance	• Stem forks form when a leading shoot is damaged by frost • Occurs when trees flush too early • Compromises timber quality and ease of processing • Provides indication of maladaptation
Other size traits (e.g. diameter and volume)	Performance	• Similar in principle to height • Combining with height to describe allometric relationships provides more meaningful size traits than height alone
Spring phenology (e.g. bud burst)	Phenology	• Time in spring when leaves emerge; measured/analysed in different ways • Indicates adaptation to growing season length, often under strong genetic control • Can indicate spring frost avoidance • Useful to investigate over multiple years to identify cues
Autumn phenology (e.g. bud set and leaf fall/ senescence)	Phenology	• Time in autumn when leaves form buds; measured/analysed in different ways • Indicates adaptation to growing season length • Can indicate autumn frost avoidance • Useful to investigate over multiple years to identify cues
Chlorophyll fluorescence (Fv: Fm ratio)	Ecophysiology	• Tests the efficiency of trees' light-harvesting apparatus • Used as an indicator of stress • Difficult to investigate in field conditions, best conducted in short-term seedling tests indoors
Stomatal traits (e.g. size/density)	Ecophysiology	• Stomata are pores on the surface of leaves • Differences in the size/density of stomata can indicate adaptation to moisture regimes
Leaf traits (e.g. size)	Ecophysiology	• Leaf size, shape and pilosity may indicate adaptation to various aspects of the environment, most notably moisture regimes • Measurements involve sampling leaves and measuring them either manually or with image-processing software
Disease/pest resistance (pathogens, herbivores and pests)	Biotic interactions	• Can be done by deliberately inoculating trees or following a local outbreak • Methods will be highly variable, depending on the disease (e.g. lesion size and dieback score)
Microbiome (e.g. associations with endophytes/ mycorrhizae)	Biotic interactions	• Typically uses molecular techniques (e.g. metabarcoding) to characterise microbiome • Can be complicated, a relatively young technique

Methods

In this report, we aimed to identify studies involving various types of common garden experiments of tree species which are native to or naturalised in England in order to create a set of general findings which could be applied to decision-making in forest management.

The initial step in the literature review was to examine previously compiled lists of published studies of provenance variation (Ennos *et al*., 2000; Cavers and Cottrell, 2015; Whittet, 2016; and references therein).

Further studies were identified using combinations of search terms in academic databases, principally Google Scholar (https://scholar.google.co.uk/). We did not follow a formal search strategy, although search terms included provenance, genetic, [species name], [Great] Britain/United Kingdom/ British/Engl[and/ish]/Wales[Welsh]/Scot[ish/land], adaptive, variation, experiment, tree, and population.

Overall, there was likely to have been some bias against older, harder-to-find, grey literature articles, unpublished details of experiments archived within institutional databases, and those studies not published in the English language. However, our method has identified most of the geographically relevant literature.

The articles were assessed against criteria for their geographical and topical relevance (Table 3). The main focus was on studies conducted in or near England, although some studies from elsewhere in Europe were included if they explicitly addressed latitudinal transfer of seed and fell within the first four groups of our geographical relevance criteria.

Types of studies which were not considered include:

- Purely ecophysiological studies of trait variation measured *in situ*.
- Any *in silico* or purely predictive studies which were not firmly grounded in measured trait variation (e.g. bioclimatic envelope/species distribution models; growth forecast models; and individual-based models).
- Taxonomic studies or any studies which aimed to describe variation which is not obviously of clear adaptive significance (e.g. flower colour/shape, bark characteristics, wood anatomy, cytology, and biochemistry).
- Landscape genomic/genetic studies which did not contain a strong phenotypic component.
- Results of species trials which were not organised by population/provenance.
- Laboratory studies of seed or embryo characteristics (e.g. germination and storage).

Furthermore, our review does not cover the exotic conifer species which are used in productive forestry as these are generally deployed from improved sources following research during the last century (Fletcher and Faulkner, 1972; Shelbourne, 1974; Lee, 2002, 2003; Lee and Connolly, 2004, 2010; Samuel, Fletcher and Lines, 2007; Fletcher and Samuel, 2010). Since these will not show naturally developed patterns of genetic variation, the question of assisted migration is not particularly salient.

This summary of evidence is not intended as a meta-analysis which aims to calculate the effect size of very specific actions (Boshier *et al*., 2015). Rather, our intention has been to provide an account of the extent of the current knowledge base regarding adaptive genetic variation in English trees.

Table 3 Ranked relevance, quality and comprehensiveness criteria. Comprehensiveness is not ranked. Instead, a list of indicators of comprehensiveness is provided.

Relevance	Quality	Comprehensiveness (unranked, all indicators of comprehensiveness)
1. England and Wales 2. Scotland 3. Ireland, Benelux (Belgium, Netherlands and Luxembourg), North or West France, North Germany and Denmark 4. Fennoscandia (Finland, Sweden, Norway) and Baltic (Lithuania, Latvia, Estonia).	1. Reciprocal transplant experiment 2. Multi-site long-term field provenance test 3. Short-term seedling test 4. Results from progeny trials/ breeding seed orchards	• High levels of replication at different sites (and blocks within site) • Maintenance of family structure • Many individuals and provenances from a range of environments • Number of traits measured • Age at which traits measured • Age of trial

The rationale for this rather more qualitative approach is that:

- The available information is of mixed relevance, quality and comprehensiveness.
- It is very difficult to generalise over species and generalised results would not provide meaningful results for local-scale decision-making in English forest management planning.
- The sample size would not permit robust statistical analyses, especially considering that it is unlikely to be legitimate to generalise results across species.
- The purpose of this evidence review is not to calculate the effect size of single, specific actions. Rather, we aim to represent the variability in responses of trees to environmental variation.

Caveats to consider when interpreting results from provenance trials are that:

- provenance trials are often located on relatively favourable sites;
- most studies only report variation in one or two traits;
- geographical coverage (sites and provenances) can be highly variable;
- publication bias is inevitable whereby only interesting/positive results are reported (others are not, and it has only recently become normal practice to publish or archive raw datasets);
- very large volumes of data are generated, therefore reporting tends to rely on summary values (e.g. mean values), often without reference to associated variances;
- different motivations for conducting research (e.g. tree improvement and understanding local adaptation) can influence reporting/interpretation.

We provide a brief account of findings from provenance experiments detailing (i) the type of experiment, (ii) the number of provenances represented, (iii) the number of sites the experiment was replicated on, (iv) the country the trial was conducted in, (v) traits investigated and (vi) a summary of key findings. The summaries of key findings have been edited to a few research highlights. Phenomena we were particularly interested in conveying were:

- Were trait values significantly different among populations?
- Was intra-population variation associated with aspects of the environment or geography?
- Where appropriate, were there significant differences in results among trial sites?
- Was the site effect greater than the population (provenance) effect?
- Were trait–trait correlations identified?

Because it was typically evident from an examination of titles and/or abstracts as to whether or not a study presented results from a provenance test, we did not keep a record of the number of articles that were screened. However, of the literature examined, 44 studies involving 10 species were retained for discussion (Table 4).

Table 4 Number of studies (A) per species and (B) per trait.

A. Species	Number of studies
Ash	9
Silver birch	9
Scots pine	7
Oaks	7
Downy birch	3
Alder	3
Hawthorn	2
Sycamore	2
Beech	1
Rowan	1
B. Trait	**Number of studies**
Survival	20
Height (< 10 years)	20
Spring phenology	17
Diameter	12
Height (> 10 years)	10
Stem form/habit	9
Autumn phenology	7
Ecophysiology	7
Resistance/health	6
Leaf traits	6
Other	4

Results: species summaries

Key to understand the summary tables (Tables 5–14).

Study: Each paper's citation.

Type: Abbreviations: BSO, breeding seed orchard; FPT, field provenance test; STST, short-term seedling test; SPT, single progeny test; RTE, reciprocal transplant experiment; (F) indicates that the experiment retained family structure.

Number of GB provenances: Maximum number of provenances represented in the experiment. The value in parentheses indicates the number of provenances which are from Great Britain (GB). A value is not always reported and is not relevant in situations involving improved progeny.

Number of sites: Number of sites which results were reported from. This does not necessarily imply that experiments were entirely balanced, with equal representation of provenances at all sites.

Trial country: ISO 3166-1 Alpha-3 country codes indicating the country or countries in which the experiment was conducted (BEL: Belgium; DNK: Denmark; FIN: Finland; FRA: France; IRL: Ireland; ITA: Italy; LTU: Lithuania; SWE: Sweden). Within the UK, the codes given are ENG: England; SCO: Scotland and WAL:Wales.

Traits: The traits listed broadly correspond to those described in Table 2. Where the measured trait is complex (e.g. for certain ecophysiological or morphological characteristics), then these are grouped under a more simple heading.

The darker blue shading of cells at the bottom of the table indicates studies conducted outside Great Britain.

Table 5 Alder (*Alnus glutinosa*).

Study	Type	No. of GB provenances	No. of sites	Trail country	Traits	Comments
Worrell (1992)	FPT	3 (1)	2	SCO	Survival Height (< 10 years)	• One Welsh (local), central German and one Polish provenance. • Higher 6-year survival of Welsh provenance • Relative height growth of continental provenance 53–72% on deep peat in Sutherland. • On mineral soils in southern Scotland, relative height growth of Polish provenance versus Welsh was 115%.
De Kort *et al.* (2014a)	~ RTE	3 (0)	3	BEL, DNK, ITA	Survival Diameter	• One RTE with Belgian only. • One RTE with Italian, Danish and Belgian. • Significant differences between provenances and sites but no G x E interaction in Belgium-only experiment. • At Belgian site, Belgian had largest diameter. • At Danish site, Danish had largest diameter but smaller difference between the two provenances than in Belgium. • Complete failure of a Tuscan trial site due to extreme drought.
De Kort *et al.* (2014b)	STST	21 (0)	1	BEL	Autumn phen Leaf traits	• Tuscan provenance set buds later and had larger leaves. • Danish provenance has smallest leaves and earliest budset. • Belgian provenances were intermediate and not significantly different from one another.

Table 6 Ash (*Fraxinus excelsior*).

Study	Type	No. of GB provenances	No. of sites	Trail country	Traits	Comments
Cundall, Cahalan and Connolly (2003)	FPT	22 (12)	6	ENG WAL	Survival Height (< 10 years) Diameter Stem form	• Uniformly high 4-year survival. • Site effect greater than provenance effect (60% and 24% variation in height, respectively). • No significant relationship between height and latitude. • Good performance of most French material. • British provenances highly variable. • Romanian, Czech and German material had poor form and vigour.
Boshier and Stewart (2005)	RTE	8 (8)	8	ENG WAL	Survival Height (< 10 years) Diameter	• Trees grown reciprocally in home soils. • Measurements were made after one year in a nursery. • No obvious geographical pattern in height growth variation. • Two best provenances tended to grow best under each treatment.
Mwase, Savill and Hemery (2008)	BSO	NA	1	ENG	Survival Height (< 10 years) Diameter Stem form	• Not a provenance trial but shows some important phenomena. • Age-age correlations for height were weak. • Height positively correlated with forking.
Clark (2013) (i)	~ RTE	10 (6)	5	ENG SCO FRA	Survival Height (< 10 years) Diameter	• Survival was poor due to problems with establishment. • Small provenance effect for height. • Greater differences in height growth at northern trial sites. • Locals usually showed average growth. • Large site effect. • No G x E interaction. • A French provenance showed greatest growth, even in northern Scotland. • Growth did not exceed 30 cm after 3 years.
Clark (2013) (ii)	FPT	22 (10)	2	ENG	Spring phen	• Significant differences among provenance associated with site and year. • Earlier flushing of continental provenances. • Same ranking of provenances across 2 years (no provenance x year interaction). • Significant provenance x site interaction. • Significant year x site interaction. • Flushing 4 days earlier in Oxfordshire than East Yorkshire on average.
Stocks, Buggs and Lee (2017)	FPT	14 (10)	2	ENG	Disease resistance *(Hymenoscyphus)*[1]	• Significant differences among populations in dieback levels. • No clear geographic pattern. • Central Scottish populations most resistant.
Rosique-Esplugas (2018)	FPT	42 (42)	2	ENG WAL	Survival Height (< 10 years) Diameter Stem form Spring phen Autumn phen Ecophysiology Leaf traits	• Southern trees tallest. • Southern trees flushed earliest. • Southern trees had most forks. • Provenance effect on forking stronger at a continental site. • Southern provenances had larger leaves. • Northern provenances had higher stomatal density. • Provenances from drier environments had lower density of larger stomata.
Baliuckas *et al.* (1999)	SPT (F)	3 (0)	1	SWE	Height (< 10 years) Stem form Spring phen Autumn phen	• At an early age, family variance component larger than population variance component. • After a severe frost, the population effect became larger. • Populations from north and eastern Sweden were shorter. • Strong correlation between early flushing and forking following frost event (R2 = 0.5).

Table 6 Continued.

Study	Type	No. of GB provenances	No. of sites	Trail country	Traits	Comments
Pliûra and Baliuckas (2007)	FPT (F)	24 (0)	3	LTU	Height Spring phen Health condition	• Large provenance effect for all traits. • Earlier flushing trees had better health condition. • Local (Lithuanian) trees were shorter than foreign provenances but had better health condition. • Trees from further west (ROI) flushed latest.

1. In recent years there have been a very large number of studies involving assessments of severity of ash dieback in provenance trials in other countries. We make no attempt to summarise these here as the task would require a full review. We only describe the first results of British ash.

Table 7 Beech (*Fagus sylvatica*).

Study	Type	No. of GB provenances	No. of sites	Trail country	Traits	Comments
Worrell (1992)	FPT	?	?	?	Survival Height Stem form	• Very little information provided about the experiments reviewed. • Northern French, Belgian and Dutch provenance taller than British provenance. • German, Czech and USSR provenances shorter than British. • Survival of British provenances was not obviously higher. • Differences in stem form were small.

Table 8 Birch (silver) (*Betula pendula*).

Study	Type	No. of GB provenances	No. of sites	Trail country	Traits	Comments
Billington and Pelham (1991)	SPT (F)	3 (3)	1	SCO	Spring phen	• Only three populations so geographic variation difficult to describe. • Significant heritability values. • Authors calculated a selection gradient based on predicted warming, concluding that additive variation alone would not enable an adaptive response.
Worrell (1992)	FPT	?[1]	7[2]	SCO ENG	Survival Height Stem form	• Lower height, survival and stem form of most continental origins (mostly Nordic). • Superior height growth of improved Finnish progenies compared to Scottish control (see below).
Worrell *et al.* (2000) (i)	FPT	? (1)[3]	2	SCO	Survival Height (> 10 years)	• Later visit to (1992) trial showed that select Finnish origins had suffered frost damage after a mild winter. • Relative survival and height of Finnish versus Scottish control poor (38–61% and 74–83%, respectively).
Worrell *et al.* (2000) (ii)	FPT	38 (38)	2	SCO	Survival Height (< 10 years) Spring phen	• Greater early (one year) height growth in southern and western provenances. • Earlier flushing in southern provenances.
Worrell *et al.* (2000) (iii)	FPT	9 (8)	1	SCO	Spring phen Autumn phen	• Differences among populations for autumn phenology larger than differences in spring phenology. • Much earlier flushing and senescence in the (one) Norwegian provenance.
De Silva (2007)	FPT	?	2	SCO	Disease resistance (*Anisogramma Virgultorum*)	• Provenance effect at one of the trials with large differences between provenances in presence of pathogen and levels of dieback. • No stated geographical pattern. • Disease affected by position in trial (i.e. proximity to inoculum source).

Table 8 Continued.

Study	Type	No. of GB provenances	No. of sites	Trail country	Traits	Comments
Lee *et al.* (2015) (i)	FPT	37 (37)	4	SCO IRL	Survival Height (< 10 years)	• Survival generally high (> 70%). • Lower survival was often of local provenances, although no significant association between latitude and height. • Local provenances showed approximately average height. • Stable rankings for height growth – G x E due to differences in ranking of average provenances. • Greater height growth from southern provenances at all sites. • Slow growth from northern provenances. • Large variation among proximal provenances.
Lee *et al.* (2015) (ii)	FPT	38 (33)	5	SCO ENG WAL	Survival Height (< 10 years)	
Rosique-Esplugas (2018)	FPT	37 (37)	4	SCO ENG WAL	Survival Height (< 10 years) Diameter Stem form Spring phen Autumn phen Ecophysiology Leaf traits	• Southern provenances are the tallest. • Significant differences in rates of survival among provenances. • Lower survival of southern provenances. • Significant provenance x site interaction for leaf size. • Southeast provenances had larger leaves. • Higher stomatal density of northern and western provenances. • Different ratio between height and DBH. At a northern site, trees were relatively broader and shorter, at a southern trial site, trees were relatively thinner and taller.
Viherä-Aarnio and Heikkilä (2006)	FPT	29 (2)	1	FIN	Ungulate browsing	• Moose preferentially browsed southern origin trees. • May be due to timing of growth initiation and cessation.
Viherä-Aarnio *et al.* (2013)	FPT	38 (2)	5	FIN	Survival Height (> 10 years) Stem form Stem volume	• Effect of seed transfer significant and curvilinear. • Best growth and yield at local or slightly more southern origins. • Best survival and stem form at local or slightly more northern origins. • Similar results found in another trial series (Viherä-Aarnio and Velling, 2008).
Viherä-Aarnio and Velling (2017)	FPT	22	2	FIN	Height (> 10 years) Diameter Wood density Bark thickness Wood defects	• Greatest height growth ~2° south of planting site but curvilinear. • No effect of latitude on wood density. • Southerly origins had thicker bark. • Incidence of darkened core wood increased with increasing seed origin latitude. • Frost cracks were most common in south Latvian origins grown in central Finland.

1. Unstated number of provenances
2. Article refers to seven experiments. It is unstated whether these were balanced replicates (Worrell, 1992).
3. Most of the material involved select progenies from Finland, so the term provenance is incorrect. They were compared with a local control.

Table 9 Birch (downy) (*Betula pubescens*).

Study	Type	No. of GB provenances	No. of sites	Trail country	Traits	Comments
Blackburn and Brown (1988)	SPT (F)	7 (7)	1	SCO	Survival Height (< 10 years)	• Most height variation held within provenances rather than between provenances. • Variation in crown dieback was explained by provenance. • No clear geographic signal.
Pelham *et al.* (1988)	SPT	26 (26)	1	SCO	Height (< 10 years) Diameter Leaf traits Presence of various fungi	• Growth negatively correlated with latitude and humidity. • Growth positively correlated with rain acidity, sunshine and temperature. • Plants from the north-west had smaller and hairier leaves. • Leaf shape (roundness) was associated with longitude. Plants which were distant from the east coast had less round leaves. • Plants from warmer environments had more pubescence on the lower surface of leaves.
Billington and Pelham (1991)	SPT (F)	7 (7)	1	SCO	Spring phen	• Significant differences among populations and among families within populations • Significant population x year interaction, suggesting variation in phenotypic plasticity among populations. • No family x year interaction. • Heritability positively correlated with latitude suggesting more efficient evolvability of northern populations. • Authors calculated a selection gradient based on predicted warming, concluding that additive variation alone would not enable an adaptive response.

Table 10 Hawthorn (*Crataegus monogyna*).

Study	Type	No. of GB provenances	No. of sites	Trail country	Traits	Comments
Jones, Hayes and Sackville Hamilton (2001)	FPT	9 (5)	2	WAL	Height (< 10 years) Diameter Spring phen Resistance (powdery mildew) Habit (thorniness, branchiness)	• Experimental hedge at top and bottom of a hill. • Large site effect. Plants in lowland site grew faster. Powdery mildew at lowland site was more severe. • A local ecotype was shortest in the lowland site but tallest in the upland site. • Local ecotype suffered least powdery mildew. • Local ecotype was thorniest, branchiest and flushed latest. • Local ecotype was the only provenance capable of adjusting its flushing time plastically. • Local ecotype showed the lowest loss of growth following removal of fencing (grazing tolerance).
Vander Mijnsbrugge, Onkelinx and De Cuyper (2015)	FPT	10 (1)	1	BEL	Height (< 10 years) Spring phen Flower phen	• Differences in height growth modest after four years. • The only provenance which was significantly shorter was from Great Britain. • Great Britain provenance similar to Flemish provenances for flushing. • Earlier flushing in Walloon, Hungarian and Italian provenances. • Flowering phenology more variable than vegetative phenology.

Table 11 Oaks (*Quercus petraea* and *Quercus robur*). Much more information is available for *Q. petraea* than for *Q. robur*. Hubert (2005) and Wilkinson, Eaton and Morison (2017) include small proportions of *Q. robur* within mixed experiments. In the latter experiment, there was no clear geographical trend for *Q. robur*. In the former experiment, results are presented together for the two species.

Study	Type	No. of GB provenances	No. of sites	Trail country	Traits	Comments
Worrell (1992)	FPT	?	?	?	Survival Height (< 10 years) Stem form	• Few details of experiments provided. • Relative height growth did not vary substantially. • British provenances generally showed better growth. • French provenances had better form.
Deans and Harvey (1995)	FPT	16 (1)	1	SCO	Survival Height (< 10 years) Spring phen Autumn phen	• No significant differences in height growth. • Earlier flushing in southerly and low altitude provenances. • Ranking of provenances did not change between years. • Higher levels of frost damage of French provenances.
Deans and Harvey (1996)	FPT	16 (1)	1	SCO	Ecophysiology	• Shoots harvested from trees and exposed to low temperatures in a freezer. • French, English and Austrian provenances more sensitive than German, Danish and Polish.
Hubert (2005) (i)	FPT	13 (4)	5	SCO ENG	Survival Height (< 10 years) Height (> 10 years)	• Large absolute differences among provenances. • Similar ranking across trial sites, tallest trees were tallest at most sites, shortest were shortest in most places. • Survival was so poor at a trial site in North Scotland that it had to be abandoned. • Survival of continental provenances at that site was particularly poor (~5%). • Lower than average growth of northern material transferred south but survival was higher. • In general, greatest height from select British seed sources.
Hubert (2005) (ii)	FPT	23 (7)	3	SCO ENG		
Wilkinson, Eaton and Morison (2017)	FPT	19 (4)	1	ENG	Spring phen	• Latitude linearly related to timing of bud burst – earlier flushing in southern provenances. • Differences in timing of bud burst among years. • Bud burst earlier in warmer years.
Sáenz-Romero *et al.* (2017)	FPT	116 (7)	23	MANY	Survival Height (> 10 years)	• Generated transfer functions from very large dataset. • Annual dryness index best predictor of survival – quadratic effect. • Survival expected to be highest in sites similar to seed source. • Growing season dryness index best predictor of height growth – quadratic effect. • For height, site effect much larger (60%) than provenance effect (1.4%).
Ducousso, Guyon and Kremer (1996)	FPT	50 (?)	4	FRA	Spring phen	• Earlier flushing in southern and low elevation provenances. • Higher frost damage in earlier flushing provenances.

Table 12 Rowan (*Sorbus aucuparia*).

Study	Type	No. of GB provenances	No. of sites	Trail country	Traits	Comments
Rosique-Esplugas (2018)	FPT	42 (42)	4	ENG SCO WAL	Survival Height (< 10 years) Spring phen Autumn phen Ecophysiology Leaf traits	• In southern trial sites, trees were taller. • Site effect larger than provenance effect for height. • Provenance effect on height greater in southern trials. • Earlier flushing of provenances from the east. • Significant provenance x site interaction for leaf size. • Provenances from drier environments had larger leaves. • Populations from the west had a higher density of smaller stomata, indicating adaptation to moisture regimes.

Table 13 Scots pine (*Pinus sylvestris*).

Study	Type	No. of GB provenances	No. of sites	Trail country	Traits	Comments
Perks and McKay (1997)	STST (F)	6 (5)	1	SCO	Height (< 10 years) Diameter Ecophysiology	• All measurements after one growing season. • No major differences among the four native populations. • Improved British (A70) material grew fastest, had largest root collar diameter and highest biomass. • It hardened later and had a lower root: shoot ratio. • Swedish provenance most frost hardy.
Perks and Ennos (1999)	FPT (F)	4 (4)	1	SCO	Survival Height (< 10 years) Spring phen	• Significant differences were found among provenances for most traits. • Too few provenances to describe geographic variation. • Heritability varied among populations.
Salmela *et al.* (2011)*	STST (F)	8 (8)	1	SCO	Ecophysiology Spring phen	• Stress response (Chlorophyll fluorescence) measured periodically during a cold winter. • At certain times, there were significant differences among populations. • Those from colder, high elevations were under lower stress than those from warmer environments.
Salmela *et al.* (2013)*	STST (F)	21 (21)	2	SCO	Spring phen	• Populations from the colder east flushed earlier. • Later flushing in Aberdeen than in Edinburgh. • Higher phenotypic variation found within populations from higher altitudes. • This pattern found to be the opposite of what happens *in situ* (Whittet *et al.*, 2017).
Donnelly *et al.* (2016)*	STST (F)	8 (8)	1	SCO	Leaf traits	• Generally more variation within than between populations. • Resin canal density positively correlated with longitude. • Stomatal row density negatively correlated with longitude. • Trends reflect moisture availability.
Perry *et al.* (2016a)*	STST (F)	6 (6)	1	SCO	Disease resistance (*Dothistroma*)	• Progeny artificially exposed to *Dothistroma*. • Most variation within rather than between populations. • Slight geographic trend showing more severe infection in pops from drier environments (east). • Progeny exposed to infected stands *in situ*. • Significant differences between populations. • Higher severity of infection in populations from drier environments (east).
Perry *et al.* (2016b)*	SPT (F)	8 (8)	1	SCO	Disease resistance (*Dothistroma*)	• Progeny exposed to infected stands *in situ*. • Significant differences between populations. • Higher severity of infection in populations from drier environments (east).

*All tests conducted on subsets of the same initial seed collection comprising maximally four open-pollinated families from each of 21 native populations. With the exception of Perry et al. (2016b), these were conducted in a glasshouse.

Since Scots pine is clearly a commercially important tree species in Great Britain and elsewhere, there is a rich literature encompassing tree improvement activities and larger provenance trials. However, we have chosen to overlook much of the tree improvement literature in Scots pine to focus on patterns of local adaptation expressed in populations native to Great Britain (Scotland).

Table 14 Sycamore (*Acer pseudoplatanus*).

Study	Type	No. of GB provenances	No. of sites	Trail country	Traits	Comments
Helliwell and Harrison (1978)	STST	6 (3)	1*	ENG	Height (< 10 years) Ecophysiology (root and shoot weight)	• Soil type explained most of the variation. • There were significant differences among seed sources. • Details of geographical variation not reported.
Cundall, Cahalan and Plowman (1998)	FPT	10 (6)	5	ENG WAL	Survival Height (< 10 years) Diameter	• Survival by fourth year > 86%. • No significant differences in height among provenances. • Larger differences were observed at more testing sites.

*One experiment site but seedlings were raised in 25 different soils.

Discussion

Summary of common findings

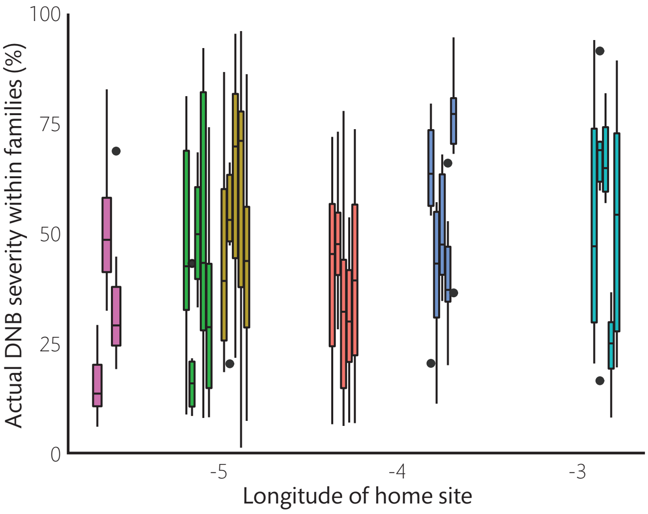
Adaptive trait variation within populations of trees is high, often exceeding the variation between populations, indicating a high capacity to adapt to change

In tests which adopted family structure, variance components associated with families-within-populations are often larger than among-population variance components (Blackburn and Brown, 1988; Billington and Pelham, 1991; Salmela *et al*., 2011; Donnelly *et al*., 2016; Perry *et al*., 2016b). Where studies did not retain family structure, it is less easy to determine the extent of within-population genetic variation, as reporting tends to rely on plot mean values. Nonetheless, when variance is reported, there is typically considerable overlap among provenances, despite differences in mean values. This is in keeping with theoretical expectations that large population size and extensive gene flow retain high levels of genetic variation within populations (Kremer *et al*., 2012). While natural selection sorts variation to lead to adaptive divergence within a population, selection pressures vary over time in any population and so different individuals within a population can exhibit different phenotypes (Kelly *et al*., 2003; Jump *et al*., 2008). High levels of genetic variation within populations suggest that there is potential to evolve to cope with change through the action of natural selection. A good example of substantial family-level variation can be found in the artificial inoculation trial described by Perry *et al*. (2016b). Progeny from several families within six Scots pine populations were exposed to *Dothistroma septosporum* in chambers and the severity of infection was subsequently measured. Results showed that, in each population, families had different levels of susceptibility, and that, considered together, a large range of susceptibility values was observed. There was a slight association with longitude, although total differences among provenances were not statistically significant as the distribution of phenotypes overlaps substantially (Figure 7).

Despite high variation within populations, adaptation to the environment has taken place among populations of trees, although the scale over which it takes place varies and different species can show different patterns

In most of the studies reviewed, some differences were found between populations for the traits measured, possibly indicating a response to natural selection in the past.

Figure 7 Severity of *Dothistroma* infection among families of Scots pine from six populations. The individual boxplots correspond to families and the colours correspond to populations, which are ordered along the horizontal axis by longitude. The range of susceptibility within populations is very large, indicating strong potential for natural selection to help populations adapt to *Dothistroma* (adapted from Perry *et al*., 2016b).



For example, many studies report lower, conservative growth of northern provenances when compared with southern provenances (Baliuckas *et al*., 1999; Worrell *et al*., 2000; Lee *et al*., 2015; Rosique-Esplugas, 2018). Other studies show that variation is associated with moisture regimes of home sites, for example, studies involving Scots pine in Scotland tend to find that variation is partitioned longitudinally, along a major gradient in continentality (Salmela *et al*., 2011, 2013; Donnelly *et al*., 2016; Perry et al., 2016a,b).

The spatial scale of local adaptation can vary depending on aspects of species biology and the heterogeneity of the landscape. For instance, Vitasse *et al*. (2009) observed opposing adaptive clines in the phenological response of beech (*Fagus sylvatica*) to those of ash (*Fraxinus excelsior*) and sessile oak (*Quercus petraea*) in the Pyrenees. In multiple common garden experiments established along an altitudinal cline, beech populations from a higher altitude were found to be the earliest to flush, whereas the opposite trend was recorded in ash and oak. Moreover, in the same trial it was shown that for three other species, sycamore (*Acer pseudoplatanus*), holly (*Ilex aquifolium*) and European silver fir (*Abies alba*), there was no evidence of adaptive differences in phenology in response to altitude (Vitasse *et al*., 2009). Frank *et al*. (2017) established a common garden experiment involving *A. alba*, *Fagus sylvatica* and *Picea abies*, and found a lack of major differentiation among populations of *A. alba* but differences among populations of *F. sylvatica* and *P. abies*, and considered the former to be an adaptive generalist, while the latter two were considered specialist.

Different traits within a species can also show contrasting patterns of variation. For example, longitude explained 48% of the variation in timing of bud burst of rowan at a trial in Llandovery, but latitude was found to be a better predictor of height growth, explaining 17% of the variation among the same provenances (Rosique-Esplugas, 2018).

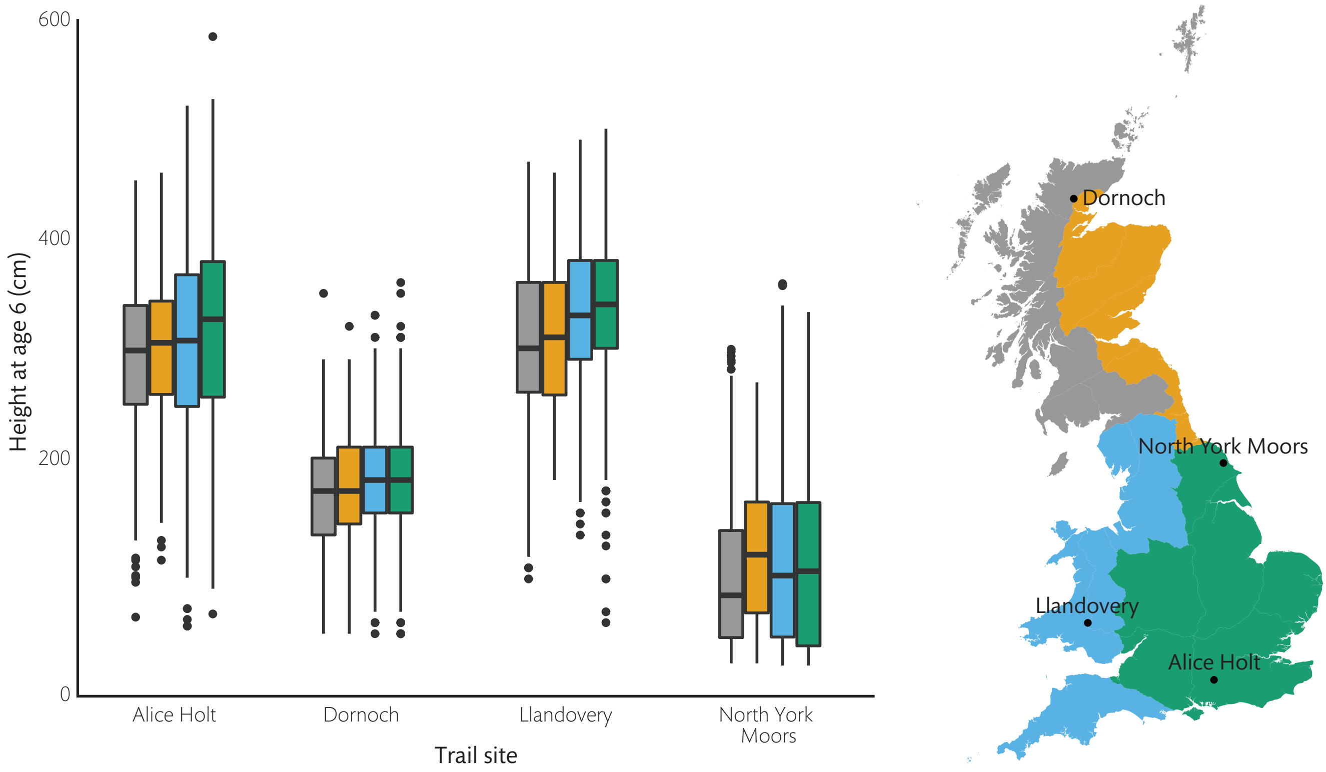
The effect of site is often larger than the effect of provenance, although statistically significant G x E interactions, though common, are usually small

In several of the studies here which included provenance tests established in multiple sites, it was possible to report the proportion of trait variance associated with site, provenance and the interaction between provenance and site. In many cases, the site effect is of larger magnitude than the provenance effect (Jones, Hayes and Sackville Hamilton, 2001; Cundall, Cahalan and Connolly, 2003; Clark, 2013; Sáenz-Romero *et al.*, 2017; Rosique-Esplugas, 2018). Figure 8 provides an example.

This reinforces the importance of paying close attention to site characteristics when deciding which species and provenances to plant, as results can vary substantially at local scale (Worrell *et al.*, 2000; Jones, Hayes and Sackville Hamilton, 2001). Refinement of systems such as ecological site classification (ESC) (Pyatt, Ray and Fletcher, 2001), or uptake of site-matching tools which extend to provenance, such as those that exist in North America (McKenney, Mackey and Joyce, 1999; Howe, St. Clair and Beloin, 2009; Doherty, Butterfield and Wood, 2017), offer opportunities to improve provenance decision-making.

Genotype x environment interactions for growth traits were found to be of generally small magnitude (Cundall, Cahalan and Connolly, 2003; Boshier and Stewart, 2005; Hubert, 2005; Clark, 2013; Lee *et al.*, 2015). Often, statistically significant genotype x environment interactions emerge solely from changed rankings of those provenances with average trait values among sites, rather than changes in the rank of provenances with high or low values. When genotype x environment interactions are very small or non-existent, it means that provenances which perform well in one environment may be well placed to perform well in terms of growth traits in other environments.

Figure 8 Example of a situation in which the site effect is of much greater magnitude than the provenance effect in multi-site trials involving > 40 provenances of rowan (Rosique-Esplugas, 2018). The boxplots group provenances within the four regions of provenance (ROP) and are coloured according to the region with the same colour on the map. At each site, differences among ROPs are non-significant although it shows that height growth is slightly greater from southern provenances. However, of much greater magnitude is the difference in height between sites. Height growth at Dornoch and North York Moors is clearly lower than at Llandovery and Alice Holt. The provenance effect is also larger at Llandovery and Alice Holt, where growth is much less limited than in the northern trail sites.



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Sourcing seed from currently warmer climates can increase values of growth traits but can also increase the risk of frost injury or other sources of maladaptation

Many of the studies described here demonstrate clinal variation in height growth, with taller trees being found from provenances located further south than the planting site (Baliuckas *et al*., 1999; Worrell *et al*., 2000; Lee *et al*., 2015; Rosique-Esplugas, 2018). Aitken and Bemmels (2016) gathered a series of 23 datasets and identified common clines in height growth, whereby height was linearly associated with the mean annual temperature of home site in virtually all cases. The theoretical basis for this is that height is under directional selection from one generation to another, as seedlings in a cohort which can grow well will have the best ability to compete with their siblings. Selection on timing of bud flushing and senescence is, however, under strong stabilising selection, and is dictated by the length of the growing season, as timing of such events is phased to minimise the risk of frost damage (Howe *et al*., 2003; Aitken *et al*., 2008). These selection pressures give rise to local adaptation, and typically moderate-to-high levels of quantitative genetic differentiation for these traits (Alberto et al., 2013). Since growing seasons are longer in warmer locations, trees moved towards the poles are likely to grow faster than locals, which are likely to have undergone selection to local extremes in the past and will therefore show more conservative (or average) growth (Gutschick and BassiriRad, 2003).

For example, improved Finnish sources of silver birch growing in trials in Scotland showed strong early growth (Worrell, 1992), exceeding that of a local control provenance, yet proved susceptible to frost damage at a later age (> 10 years), while locals were less affected (Worrell *et al*., 2000). A consequence of this was that, ultimately, relative height and survival of the improved Finnish progenies were lower than the Scottish control.

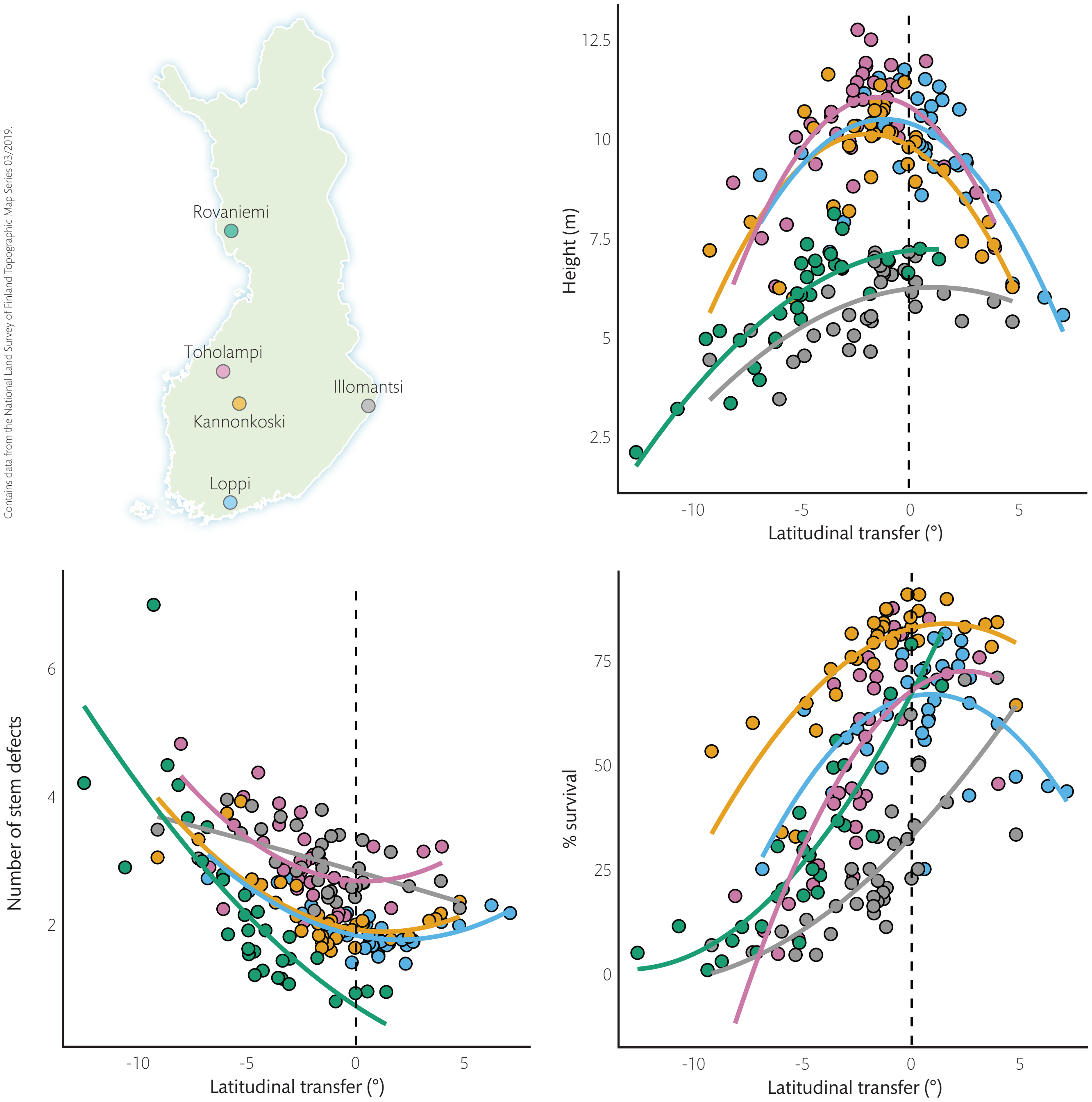
Also in silver birch, Viherä-Aarnio *et al*. (2013) showed that height growth could be increased by making modest translocations from the south to the north in multi-site provenance trials located in Finland which included material from a broad geographic base. However, these gains in height growth came at the cost of lower survival and a higher number of stem defects (Figure 9), with the severity of stem defects and mortality increasing substantially with longer distance translocations. This effect was not identified in British trials of silver birch by Lee *et al*. (2015), who showed a negative linear rather than a quadratic relationship between height growth and latitude, even over transfers of 7°, and found no significant differences among provenances for survival. This is corroborated by Rosique-Esplugas (2018), who showed that height and survival were not correlated, and that forking and height were only positively correlated in one-third of sites studied. Variation among provenances in survival was found to be explained by longitude, with significantly poorer survival of trees from eastern Britain (Rosique-Esplugas, 2018).

Analysis of results from provenance trials with ash in Great Britain revealed significant associations between latitude, height, spring phenology and flushing (Rosique-Esplugas, 2018). Provenances from further south generally showed greater height growth, ostensibly due to adaptation to longer growing seasons (as the timing of flushing was also earlier). However, as a consequence of early flushing, there was also a higher prevalence of stem forking in southerly origin material. It is worth noting that frost damage had not led to higher mortality, as differences among populations were not significant. The same result was found in a progeny trial conducted in Sweden, in which ash trees from northern and eastern Sweden were shortest, and those which flushed early had the greatest number of forks (Baliuckas *et al*., 1999).

A classic case in which poleward transfer of material resulted in widespread damage can be found in the introduction of Portuguese origins of *Pinus pinaster* into the Landes region of southwest France in the 1950s (Benito-Garzón *et al*., 2013). There was about a 3.5°C difference in mean annual temperature between source (Portugal) and planting (Landes) regions, and each region has a similar number of average frost days in January. However, Landes is prone to extreme frosts approximately every 10–20 years. Frosts in 1956 and 1963 caused notable damage in stands established from non-local seed, and a very severe frost in January 1985 with temperatures as low as -22°C led to damage to 30 000 ha of plantation. The stands of local origin were far less damaged during this frost episode (Benito-Garzón *et al*., 2013).

Despite a clearer warming trend, risks of frost injury have been predicted to remain the same, or worsen under climate change in Switzerland (Vitasse *et al*., 2018). This is because the average (plastic) advance in spring phenology during four decades of warming has been greater than advance in the date of the latest spring frost. It would be useful to analyse longitudinal trends in the date of the latest spring frost in different regions of England compared to advances in phenology. Even though the total number of frost days is expected to continue to reduce (Morison and Matthews, 2016), extreme late frosts will be problematic, especially if exposure is increased by earlier flushing.

Figure 9 Example of trade-offs between height growth, survival and stem form based on 19-year-old multi-site provenance trials of silver birch in Finland (adapted from Viherä-Aarnio *et al.*, 2013). In this case, provenances were derived from a broad geographical range. The horizontal axis represents latitudinal transfer to each of the trial sites whereby the dashed vertical line indicates a seed source from the same latitude as the experimental site. Populations with negative values on the horizontal axis are from further south than the experiment, and populations with positive values are those from further north. Greatest height growth tends to be from local sources or those up to 2° further south; however, northward transfers led to poor survival and a higher number of stem defects.



Contains data from the National Land Survey of Finland Topographic Map Series 03/2019.

Stressful growing environments can reveal results which contrast with expectation, exposing cryptic genetic variation

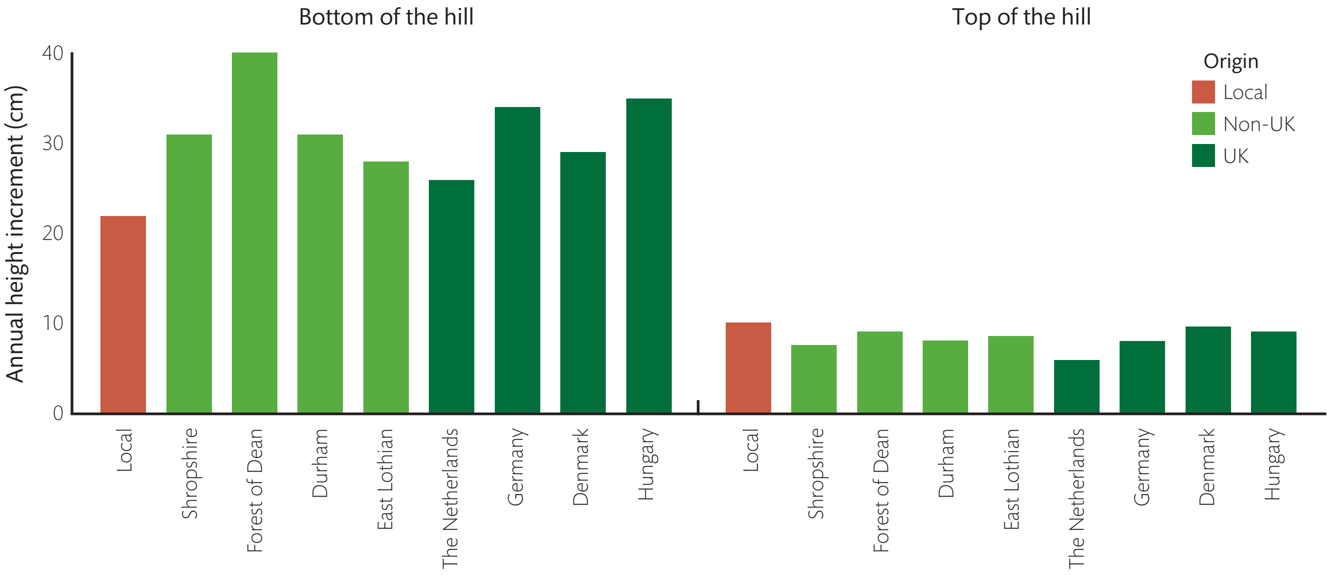
The study of hawthorn grown in two hedges in Wales showed that the adaptive differences among seed sources became much more apparent in the hedge planted at higher altitude in approximately the same location (Jones, Hayes and Sackville Hamilton, 2001). While the local ecotype was the shortest provenance at the bottom of the hill, it was actually the tallest under harsher conditions at the top of the hill (Figure 10). Not only was it the tallest under these circumstances, it also had the most thorns and branches, a far lower incidence of powdery mildew, and showed the lowest reduction in growth following exposure to grazing. For timing of bud burst, differences among populations, both in the upland and lowland hedge, were of a larger magnitude than differences among populations grown in an experiment in Belgium, despite the larger geographic range in the latter (Vander Mijnsbrugge, Onkelinx and De Cuyper, 2015). In sycamore, Cundall, Cahalan and Plowman (1998) noted that differences among provenances were also accentuated in more testing environments. Relative survival rates of improved Finnish silver birch origins were considerably lower at an exposed site in northern Scotland than they were at a more sheltered ex-agricultural site, despite separation of trial sites by only 7 km (Worrell *et al*., 2000). Oak raised from Scottish source-identified (collected from native stands not chosen for phenotypic superiority) seed grew poorly in England and Wales in comparison with selected origins, yet showed the best survival on a testing frost-prone site in northern Scotland by the age of 12 (Hubert and Cundall, 2006). Donnelly *et al*. (2018) showed that exposing progeny from different Scots pine populations to extended periods of waterlogging exposed cryptic genetic variation in some populations. Physiological responses to waterlogging were monitored by assessing chlorophyll fluorescence over the course of a year. Phenotypic variance increased during the treatment, with a smaller increase in variance for populations from western, flood-prone sites. In general, the reduction in chlorophyll fluorescence was of a larger magnitude for populations originating from drier, eastern sites. Baliuckas *et al*. (1999) observed that the majority of early variation in height growth in Swedish ash was held within, rather than between, populations. However, following a severe late frost, the variance component associated with population became larger than that of family, indicating that a selective event had exposed previously unrecognisable differences.

Considerations for deployment

Provenance in practice: How local is 'local'?

A major source of contention in the discourse around local adaptation and assisted migration is the choice of language used (McKay *et al*., 2005; Hällfors *et al*., 2014; Maier and Simberloff, 2016; Box 1). This is particularly the case when considering the meaning of the word 'local' as its interpretation varies widely across different jurisdictions (Broadhurst *et al*., 2008). A very stringent definition of local can be found in the Western Australian Forest Management Plan 2004–2014, which stipulated seed collection within 15 km of the planting site (Conservation Commission of Western Australia, 2004). To enable regeneration of rare species within ancient woodland sites in England, it is recommended that seed or cuttings are taken from trees within the same site (Forestry Commission England, 2010). However, most approaches to seed sourcing in forestry involve delineation of seed zones (Whittet *et al*., 2016a). Seed zones are fixed geographical regions with distinct boundaries. The purpose of seed zoning is to define regions in which seed can be transferred with minimal risk of maladaptation as well as to enable product description and administrative control of seedlots (Herbert, Samuel and Patterson, 1999; Ying and Yanchuk, 2006). Alía *et al*. (2009) document the range of approaches to seed zoning used across Europe. In Denmark, the Netherlands and the Republic of Ireland, there is no subdivision of land into seed zones and seed can be exchanged freely throughout these countries. Several countries operate different sets of seed zones for different species. For example, Spain has a default series of geographical seed

Figure 10 Average height increment growth of various provenances of hawthorn growing in replicated experimental hedges on the same site in mid-Wales (adapted from Jones, Hayes and Sackville Hamilton, 2001). The right-hand facet shows results from the top of the hill, where differences among provenances were small but the local ecotype was the tallest. At the bottom of the hill, differences among provenances were larger and the local ecotype was the shortest.



zones which can be applied to all species. However, for species in which more information has been gathered from genetic, demographic and ecological studies, customised seed zones have been defined (Alía *et al*., 2009). In North America, decision support tools which calculate climatic distance between seed source and planting site are used alongside fixed seed planning zones which are retained for administrative purposes (Ying and Yanchuk, 2006). These site-matching systems can be adjusted to take future conditions into account (Howe, St. Clair and Beloin, 2009).

The system of seed zoning in Great Britain divides land into four broad regions of provenance, which are further subdivided into a total of 24 seed zones. These are applied uniformly to all species (with the exception of the special case of native Scots pine, which has its own system of zones based on genetic markers). Delimitation of the common seed zones was not based on known patterns of genetic or ecological variation, but on major geographical landforms. It was recognised from its inception that the seed zone system for encouraging the use of currently adapted seed sources in Great Britain was no more than a first attempt which would require refinement as more knowledge became available (Herbert, Samuel and Patterson, 1999). A number of shortcomings in the system have since been recognised, the first of which is that the regions of provenance and seed zones do not accurately reflect geographic areas with uniform environmental conditions for tree survival and growth in Great Britain (Salmela *et al*., 2010; Whittet, 2016). In upland regions, geographically fixed seed zones may contain within them a high degree of climatic variation (Salmela *et al*., 2010). Therefore, adhering to local seed zones in a heterogeneous landscape does not necessarily guarantee a local fitness advantage, as plants from a geographically proximal location may be adapted to very different temperature, moisture and exposure regimes (Bischoff *et al*., 2006). On the other hand, in more topographically homogeneous lowland regions such as central and eastern England, seed zones could justifiably be enlarged. Seed zones which are smaller than necessary may make seed collection and stock management more laborious and complicated than necessary without any clear fitness advantage to planted stock (Hubert and Cottrell, 2007; O'Neill, Stoehr and Jaquish, 2014). An example of excessively conservative seed zoning has been found for alder (*Alnus glutinosa*) in Belgium, a relatively flat country, where assessment of patterns of molecular and adaptive variation demonstrated that material from each of the five seed zones could be exchanged with little risk of maladaptation (De Kort *et al*., 2014a). A further problem with geographically fixed seed zones which are applied across many species is that it discounts the possibility that different species can show different patterns of genetic variation, or are adapted at different spatial scales (Vitasse *et al*., 2009; Whittet *et al*., 2016a).

This background demonstrates the difficulties in understanding the concept of local when evidence of phenotypic variation is limited and when the reason for setting the boundaries of 'local' vary. In the following two sections, we make direct comparisons between assisted migration and the status quo option of sourcing local seed. For this, we require more explicit and precise definitions. We have adopted the following acronyms for use in the rest of the report:

- **Sourcing local or matched seed (SLMS):** sourcing local, climate-matched or putatively currently or recently adapted seed. We use the term local in a broad, regional sense (e.g. exchange throughout lowland region of provenance 40 as local). This may, for example involve modest northward transfers in situations where multiple aspects of the environment of seed source and planting site have been matched, especially return rates of extreme frosts. This represents the *status quo* option.
- **Sourcing seed from further south (SSFS):** deliberately sourcing seed from warmer locations further south (most likely France) in the expectation that it will be better adapted to current and future conditions. This represents the assisted migration option.

Provenance risk assessment

The benefits of SLMS are:

- Trees are most likely to be adapted to the variation in current or recent edaphoclimatic conditions, including adaptation to indigenous pests and pathogens, due to contact in recent evolutionary history.
- Due to greater tolerance of infrequent but severe climatic episodes (e.g. late frosts), higher survival of planted trees will ensure that newly established populations are large and genetically variable, providing the potential for ongoing adaptation to occur.

The drawbacks of SLMS are:

- The opportunity for gains in yield through adaptation to a longer growing season is foregone.
- The current system of SLMS does not guarantee that a currently adapted seed source will be found due to topographic complexity at narrow spatial scales in upland landscapes. It is not always possible to determine the scale at which local adaptation operates. However, more sophisticated approaches to ecological and climatic site-matching could be adopted rapidly.
- Standing trees are likely to have undergone strongest selection in a past climate, therefore seed collected now will already be lagging behind a phenotypic optimum. The average tree phenotypes in a population will lag further behind a moving

climatic optimum and may become increasingly stressed under radically changed conditions (e.g. drought), which may compromise defences against herbivores and pathogens.

The benefits of SSFS are:

- The opportunity for gains in yield through adaptation to a longer growing season is taken.
- Opportunities for inclusion of planting stock from tree improvement programmes on the near continent are available.
- Theoretically, genetic variation for drought resilience may be found elsewhere in the range (although evidence for this is lacking). Therefore, this approach has the most value in drought-prone sites.
- Trees from further south may be better adapted to pests and pathogens which are also undergoing northward range expansion due to a history of co-evolution.

The drawbacks of SSFS are:

- Trees may be poorly adapted to the current typical climate and its pattern of variability (e.g. frost damage), which together with other environmental factors at the planting site may lead to poor establishment, survival and form. The impact may not become apparent until many years after initial planting.
- Trees may also be poorly adapted to aspects of the future climate, as future climatic conditions at a given planting site are not analogous to current climates and conditions elsewhere. Although temperature can be projected with some accuracy, other climatic and non-climatic variables are much less certain.

There clearly exists a trade-off between minimising the risk of early maladaptation and intolerance of local extremes by using local seed, and that of minimising the risk of late-rotation maladaptation by using seed from warmer environments. Therefore, mitigation of the negative effects of predictable, directional change in average conditions and unpredictable extreme events appear to be opposed to one another. Attention should be paid to factors which will influence the relative risks and relative desirability or need of SSFS.

The relative risk and desirability of SLMS versus SSFS can be influenced by the following factors, although it is strongly emphasised that these considerations are not mutually exclusive, and trading off risk among factors is not appropriate:

- **Management objectives.** Since SSFS is likely to increase the risk of maladaptation in the short term, schemes which are principally financially motivated are more suitable, and managers can decide whether the need for improved/maintained yield is worth the risk of maladaptation and failure. For schemes in which the primary objectives are associated with restoration, conservation and amenity, and which are established in perpetuity, the risks of establishment failure will be higher in the short term. In the longer term, and because conservation-oriented planting schemes established in perpetuity tend not to set specific requirements on tree form (e.g. forking), it can be argued that the desirability of SSFS is higher than would otherwise be, as the environment will have changed substantially by the time trees reach maturity. However, it is unclear how SSFS may influence reproductive fitness and whether natural regeneration processes could be disrupted as a result of SSFS. Additionally, the high levels of genetic variation available from even a single tree population should mean that, if genetically sound seed collection practices are followed, tolerance of change via phenotypic plasticity and later adaptation by means of natural selection assisted by gene flow is a realistic expectation. The best opportunities for ongoing adaptation and resilience will be found in large populations.
- **Type and configuration of the landscape.** In harsh, exposed, upland environments which are cold, wet, windy and prone to frost, the risks of SSFS will be higher. In lowland sites which are not prone to frost and soils are relatively fertile, the risks will be lower. A proviso should be made for lowland drought-prone sites. If sites are expected to experience significant drought, the desirability of SSFS will be higher, although the risk may not necessarily be lower. On the other hand, on drought-prone sites, the risks of SLMS may also be high. In areas where severe and extended drought is unlikely (e.g. upland/oceanic areas), the need for SSFS is lower because warmer temperatures without moisture limitation are likely to be beneficial for tree growth (Saxe *et al*., 2001; Boisvenue and Running, 2006).
- **Spatial scale, location and management intensity.** If management of the site is regular and sufficiently intense such that monitoring and replacement of maladapted individual trees can take place, the desirability of SSFS will be higher than otherwise and the risk will be lower. In planting schemes involving very large numbers of trees planted in remote locations, a more conservative (SLMS) approach is advisable because opportunities to monitor survival, replace dead trees and perform other forest-tending activities in the short term will be fewer.
- **The intended temporal scale of the planting scheme.** An increase in the period of time trees are expected to grow on site increases the likelihood of exposure to extreme but infrequent climatic episodes to which local material has become conservatively adapted (Benito-Garzón *et al*., 2013). Therefore, the relative risk of SSFS will be lower in schemes which have a shorter intended rotation length (Aitken and Bemmels, 2016). However, the risk of early maladaptation should be weighed against the risk of late-stage maladaptation due to long-term climate change. Therefore, depending on other aspects of the planting site (especially drought risk), it can be argued that modest proportions of SSFS would be desirable in the long term.

- **Aspects of species biology.** If it is known that patterns of provenance variation in the species are modest, there may be no obvious advantage to SLMS, and SSFS could be taken as a precautionary measure. However, this is not the case in species typically used in English forestry, as evidence is rather limited for most species. If knowledge is severely limited, which is the case for most species without known high economic value, it may be safer to assume that local adaptation exists rather than assuming it does not (Aitken and Bemmels, 2016).
- **The type of base material used.** Provided the use of improved or selected material is contingent with other management objectives, the risk and desirability of incorporating proportions of SSFS will be lower because some indication of general genetic quality should be available.

With these considerations in mind, we propose a risk and desirability/need framework for the implementation of assisted migration in English woodland establishment (Figure 11). This is, of course, a rather crude representation of the realities of modern multi-purpose forest management, and so the examples listed on either side of the considerations should be seen as opposite ends of a spectrum. To address some possible nuance, we outline four hypothetical scenarios to explore how various considerations will influence the possible effects of SSFS (Table 15).

Figure 11 A simplified risk and desirability framework for implementing assisted migration decision-making indicating how different criteria may influence deployment strategies.

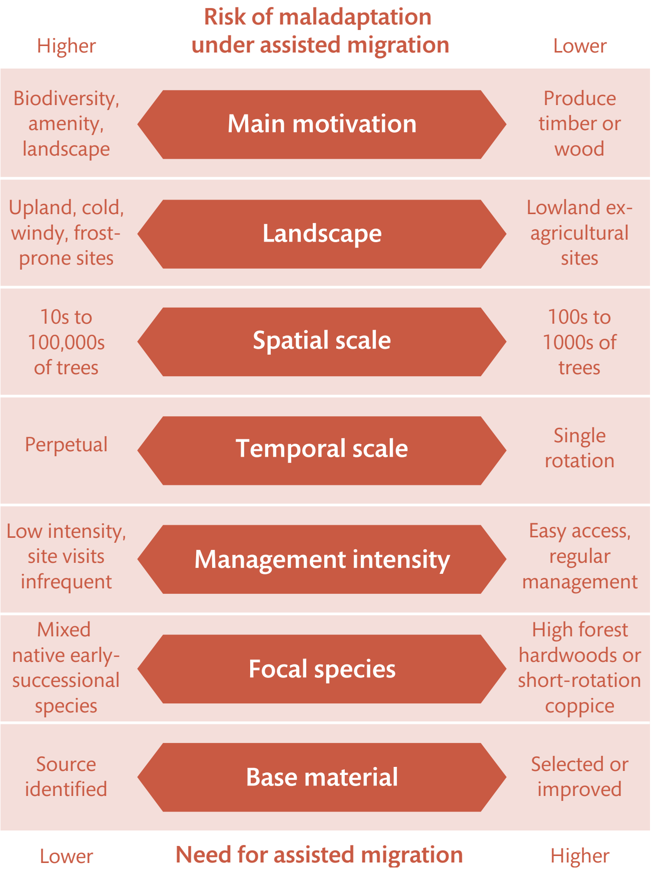


Table 15 Hypothetical planting schemes and the way they may influence thinking about provenance choice.

Consideration	Scheme 1	Scheme 2	Scheme 3	Scheme 4
Primary motivation	Establishment of self-perpetuating woodland (reforestation)	Expansion or maintenance of small, chronically fragmented populations which are not regenerating naturally, and where strong inbreeding depression has been identified	Production of quality hardwood timber	Short rotation coppice/biomass
Landscape	Upland rough grazing/ unimproved grassland	Any	Lowland ex-agricultural	Lowland agricultural
Spatial scale	Tens to hundreds of thousands of trees	Few trees: tens to hundreds	Thousands of trees	Hundreds to thousands of trees
Temporal scale	Perpetual	Perpetual	Long term but with periodic selective felling and some retention orcontinuous cover	Short rotation crop
Management access	Limited, beating up but little aftercare	Fairly regular	Regular	Regular
Focal species/ species groups	Mixed native early successional species	Rare species	High forest hardwood species (oak, beech, sycamore and cherry)	Fast growing coppice/ biomass crops
Type of base material	Genetically variable source-identified or selected seedlots	Genetically variable source-identified seedlots	Genetically variable selected or improved seed orchard material (but not full-sibling families or clones)	Clonal
Possible effect of SSFS	Risky, unlikely to be necessary, especially in areas which are not drought-prone	Risk remains but proportions of non-local material from ecologically similar sites may provide demographic support and increase genetic variation	Risk lower than in scheme 1; however, selected/improved local or regional may provide the same gain as selected from further south with lower risk (Hubert, 2005; Viherä-Aarnio and Velling, 2008; MacLachlan *et al.*, 2017)	Low risk; advantageous to use the fastest growing material available, regardless of origin

Mitigating and managing risk

If SSFS is deemed necessary following risk assessment, managers will then have to make decisions about how best to deploy seedlings on their establishment site to manage or mitigate the risk of early establishment failure due to maladaptation. One possible solution is to plant seedlings at much higher densities than usual (Lefèvre *et al*., 2014; Fady *et al*., 2016). Although this could dramatically increase the overall cost of purchasing plants, higher density will increase the strength of natural selection, removing individuals which are unable to cope. However, problems could arise in this scenario if provenances are mixed, and could be exacerbated if they are at very high initial densities. The rationale for high-density planting is that it will increase competition among neighbours. Since early vigour is often greater in plants originating from warmer locations, it is probable that unless there are unseasonal frosts in the first few years following establishment, translocated material will be at a competitive advantage and potentially outgrow conservatively adapted local material. Depending on the magnitude of this effect, this could result in a stand of purely translocated-origin trees, without the local, conservatively adapted component. A later unseasonal frost event to which the translocated trees eventually succumbed (Worrell *et al*., 2000; Benito-Garzón *et al*., 2013) would leave an absence of forest cover (Whittet *et al*., 2016a). Since age-age correlations in height growth tend to decay over time (Baliuckas *et al*., 1999; Mwase, Savill and Hemery, 2008), we can think of this situation rather like Aesop's tortoise and the hare, with tortoise SLMS genotypes and fast-growing hare SSFS genotypes. Therefore, where it is contingent with landscape priorities for the site, it may be safer to deploy mosaics of single-origin blocks or clumps within a planting site, rather than in intimate mixtures throughout. This has the advantage, not only of minimising the risk of a tortoise and hare scenario developing, but will also enable managers to monitor performance more closely over time and feedback results to the industry. Possible disadvantages of this approach is that it will require more sensitive stock control and handling, and may have detrimental aesthetic impacts if conducted on a large scale.

It is difficult to provide a rule-of-thumb to decide upon the relative proportions of different seed sources to be used if SSFS is considered necessary following risk assessment. Aitken and Whitlock (2013) suggest that the risk of outbreeding depression (reduction in fitness due to mating between very distantly related parents) will be very low if a non-local component remains below 25% of the mixed seedlot. Realistically, outbreeding depression is unlikely to occur among French and English origin trees but will be a greater risk if material from different glacial refugia (e.g. Balkan and Italian) (Petit *et al*., 2003) were to be mixed with native provenances. However, the poor performance of continental provenances in Great Britain should preclude this in any case. A rule-of-thumb proposed by O'Neill et al. (2017) is that, to account for climate change which has already happened, and to account for possible maladaptation at rotation age while minimising the risk of maladaptation at seedling stage, target climates should be those predicted for the planting site at one-quarter of the rotation age. This should be conducted for as many variables as are known to be relevant to local adaptation.

Management to facilitate adaptation in existing stands should endeavour to encourage natural regeneration, as natural selection under regeneration is many times more efficient than in planting schemes in which the density of seedlings are orders of magnitude smaller (Fady *et al*., 2016). Provided levels of herbivory and competition are sufficiently low or can be controlled, disturbances, thinning and selective felling should be considered to promote regeneration (Lefèvre *et al*., 2014; Cavers and Cottrell, 2015). Felling should aim to avoid dysgenic selection (e.g. avoid felling only trees with superior phenotypes, retaining trees with poorer phenotypes to contribute to the next generation). This has been suspected to have taken place in British oaks as a legacy of Palaeolithic clearance, selection of straight-stemmed trees for ship-building and, in particular, the tradition of open-grown coppice-with-standards management (Savill and Spilsbury, 1991).

Evidence gaps and opportunities for further research

Genetic differences in tolerance/responses to extreme events

A major challenge posed by climate change is the increase in the frequency and severity of extreme events (e.g. flooding, fires, drought, heatwaves and outbreaks). Some evidence from tree ring chronologies of beech trees growing *in situ* suggests that resilience to drought is higher in southeastern France and northern Spain than it is in southern England (Cavin and Jump, 2017). Although transfers of material over this distance would be precluded by other factors, it would be desirable to conduct experiments to directly test whether higher drought resistance in drought-sensitive species such as beech can be identified elsewhere.

To directly test whether populations are more or less adapted to such extremes, it will be necessary to establish experiments in which such extremes can be imposed upon trees. It may also be interesting to assess whether SSFS would produce populations capable of coping with compound extremes (e.g. flooding in winter, drought in summer, outbreaks). The introduction of genetic variation associated with drought tolerance is one of the main motivations for SSFS. However, since flooding is expected to increase in winter, it would be valuable to assess whether there are trade-offs between drought and flooding tolerance, which was found not to be the case in *Drimys winteri* seedlings in an experiment in Chile (Bustos-Salazar et al., 2017).

It may be valuable to identify pests and pathogens which are expanding their range due to climate change or international trade and to conduct provenance-progeny experiments in which trees are exposed to the pests and pathogens prior to their entry into England. While this would not reduce risk or exposure in the long term, it would help to quantify levels of susceptibility and increase the precision of anticipatory action or, ultimately, damage control.

An indirect test of responses to extreme events may be gained by examining tree rings of trees growing in long-established provenance trials, to determine whether populations show genetic differentiation for resistance or resilience to past extremes (e.g. droughts and late frosts) (Savva *et al*., 2002; McLane, Daniels and Aitken, 2011; Montwé, Spiecker and Hamann, 2015; Cavin and Jump, 2017). This will help to determine whether responses to extreme events are predictable across a species range and whether there is any advantage in sourcing seed which is adapted to predicted future extremes (e.g. drought). A major advantage of this approach is that it may be conducted without the need to establish expensive experiments.

Patterns of adaptation to non-climatic aspects of the environment

It is very well known that plant populations adapt to aspects of the environment other than climate, for instance, geology, soils and soil microbes (Ayres *et al*., 2009; Smith *et al*., 2012; Van der Putten, 2012; Gehring *et al*., 2017; Van Nuland, Bailey and Schweitzer, 2017; Lankau and Keymer, 2018), biotic interactions with mutualists, herbivores and pathogens (Linhart and Grant, 1996; Ennos, 2015; Grady *et al*., 2015; Kranabetter, Stoehr and O'Neill, 2015; Pickles *et al*., 2015), or purely abiotic factors such as photoperiod (Vitasse and Basler, 2013). These aspects of the environment are likely to vary in more patchy or complex spatial patterns and remain approximately the same over time, or change in different patterns to large-scale climatic changes (Frascaria-Lacoste and Fernández-Manjarrés, 2012; Aitken and Whitlock, 2013; Brown and Vellend, 2014; Bucharova *et al*., 2016). Very little work has been conducted on this phenomenon in Great Britain to date. Gaining an understanding of whether and how populations of trees in Great Britain have adapted to non-climatic aspects of the environment would be an important step in the risk assessment of SSFS.

Investigating such phenomena (especially biotic interactions) is likely to be complicated due to the potentially enormous number of variables involved. Plausible experiments could consist of growing a range of genotypes reciprocally in soils collected from their home sites in controlled conditions, with a control replicate involving growth in sterilised (boiled) soil (Smith *et al*., 2012; Lankau and Keymer, 2018). Interpretation of results is likely to be complicated by the choice of fitness measures, as traditional performance measures (growth traits) may reflect enemy release, rather than local adaptation or lack thereof (Dostál *et al*., 2013; Gundale *et al*., 2014). A sample of the biotic component of the different soils could be described using molecular approaches (e.g. metabarcoding) prior to sowing seed and at the end of the experiment to determine whether the different tree genotypes influence recruitment or turnover of different soil-dwelling species, or whether fitness is related to dissimilarity between the community composition of native and non-native soils (Kranabetter, Stoehr and O'Neill, 2015; Lankau and Keymer, 2018).

As a corollary, it is also important to ask whether SSFS would have consequences on other species, for instance across trophic levels (Bucharova *et al*., 2016). There is some evidence from Great Britain that tree genotype influences the abundance of associated species. For instance, the genetically determined timing of oak budburst was found to have consequences for abundance of different gall wasps (Sinclair *et al*., 2015). The composition of lichen epiphyte communities associated with aspen trees has been shown to depend on tree genotypes (Davies *et al*., 2014). The genetically determined chemical diversity (monoterpenes) of individual Scots pine trees was shown to influence species richness of ground vegetation (Iason *et al*., 2005). As previously mentioned, conducting such research is likely to be complex. However, insights may be gained by conducting detailed biodiversity surveys in existing provenance trials. It seems probable that the best provenancing strategy to sustain native biodiversity would be SLMS, which would maintain established species associations. A possible exception to this may be if consumer species with a faster life cycle are advancing their phenology in response to warming faster than trees are able to do so plastically, leading to trophic asynchrony. It is unclear whether SSFS would be necessary or effective in ameliorating this effect.

The role of tree improvement in climate change adaptation

Traditional tree selection and improvement programmes in Great Britain and elsewhere have tended to focus on commercially desirable traits such as yield, uniformity and stem form in a restricted number of species (Hubert *et al*., 2010; Fady *et al*., 2016). Under increasing environmental variability, tree breeding programmes which aim to minimise genetic variation (e.g. clonal forestry) may become increasingly risky if deployment of clonal origins takes place on a very large scale (Fady *et al*., 2016). Opportunities to 'infuse' (sensu Zobel and Talbert, 1984) seed collected from field-grown trees derived from breeding programmes into seed orchards should be taken to update the genetic resource. While this may come at the cost of reducing genetic gain statistics in the short term, it does take advantage of rapid adaptation that can take place within a single generation, especially for domesticated exotics (Bennuah, 1992). Sourcing seed from plus trees in these stands could also be favoured over direct importation from the origin, as adaptation to British conditions will have occurred, forming a 'land race'. This would provide a cheaper and faster way to make gains than incorporation into a formal breeding programme, and is advantageous for domestic biosecurity. Opportunities to select and breed for a wider range of traits would also be desirable, especially when a distinct threat is recognised (e.g. drought intolerance of beech or ash dieback). Technologies enabling genomic selection are constantly improving and provide options to reduce the length and cost of breeding cycles (El Kassaby and Lstibůrek, 2009; Boshier and Buggs, 2015).

Reproduction, competition and demography

This review has mainly discussed considerations for making decisions about seed sourcing for woodland establishment, and has therefore focused on adaptive variation in traits typically measured in provenance experiments, and thus making no more than this superficial mention of life history. However, an important consideration in existing stands is whether and how climate change will influence reproductive characteristics and regeneration of particular species.
An obvious situation in which the desirability of assisted migration is higher than otherwise is if reproduction is hindered in stands of conservation importance and other species are increasing in relative abundance. Changes in the relative abundance of species are more likely to be evident along altitudinal than latitudinal gradients because the environment varies at a narrower spatial scale (Jump, Mátyás and Peñuelas, 2009; Loarie *et al*., 2009). Monitoring, establishment of experimental plots and spatially explicit ecological modelling exercises incorporating a component of interspecific genetic variation could go some way towards determining the risks posed to threatened species by heightened competition, and help to quantify the permeability of the landscape for upslope migration.

Understudied species

Comprehensive data are not available for a large number of species. For silver birch, ash, Scots pine and oak, sufficient evidence is available to understand rather broad patterns of adaptive genetic diversity, which help to guide decisions about seed sourcing. However, for any other species, little or no evidence has been generated. For instance, no investigations into provenance variation among British populations of alder, aspen, elm, hazel, yew, willows, bird and wild cherry, juniper, limes or hornbeam, have been conducted. For minor species, a desirable approach may be to begin by setting out rather modest short-term seedling tests to understand whether populations show adaptive differences. For widely deployed understudied species and those which can play an important role in the provisioning of ecosystem services (e.g. alder, aspen, beech, wild cherry, hazel and juniper), long-term, multi-site field tests should be the ultimate goal to add to the evidence base. Embedding provenance trials or small experimental plots into larger planting schemes would provide a useful way to generate evidence and give practitioners greater ownership over research activities (Broadhurst *et al*., 2017).

A further advantage of establishing and maintaining a network of long-term field provenance tests is their latent capacity to act as sentinels for currently unknown future pressures (e.g. newly introduced or latent pathogens). For example, if a new pathogen emerged in England, existing provenance trials could rapidly be assayed to determine variation in susceptibility and potentially begin selection for tree improvement efforts.

Taking stock of existing experiments

The majority of provenance trials presented here are likely to have been established by the Forestry Commission. It would be desirable for details of existing trials to be made publicly available so that researchers and other interested parties could plan collaborative research to extend the knowledge of British forest genetic resources. It would be particularly valuable to revisit provenance trials that still exist to determine whether results, which are typically reported at an early age (Table 4), still stand.

Monitoring recent planting schemes and keeping records of new planting schemes

If SSFS is to be adopted on a large scale, it will be key to monitor the health and performance of translocated plants. Even where SLMS is continued, monitoring the health of newly established woodlands will be extremely important as the environment continues to change. Theoretically, when plants are delivered to site, the planter receives a supplier's document containing provenance details (master certificate number) in accordance with Forest Reproductive Material regulations. In reality, it is uncommon that particular provenances are specified by customers or the competent authority, and so precise details are rarely known (Whittet *et al*., 2016b). A system which enabled accurate recording of where different provenances were deployed would be highly desirable to provide an indication of success rates. Although findings could not be considered formal experiments due to a large number of uncontrollable variables (e.g. plant handling, seed year, seedling production and planting season), very large sample sizes, relating performance and health to the environmental distance between seed source and planting site, would be informative in the long term. Such a system would place a large additional responsibility upon nursery producers which would be difficult to keep up with (Whittet *et al*., 2016b). Therefore, it would be desirable for such infrastructure to be built into grant schemes and for the responsibility of recording and record-keeping to remain between the planter and the competent authority.

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Climate change and the increasing prevalence of pests and diseases are generating considerable uncertainty regarding the seed origin of planting stock for new woodland establishment in England. The assumption that locally sourced material provides the most appropriate option is increasingly being called into question because the environment to which trees are adapted is changing rapidly. It has been proposed that seed should be collected from warmer and drier environments than the planting site – a practice which can be termed 'assisted migration'. This Research Report provides a review of published results from provenance tests of relevance to English native trees to identify factors which may influence the risk, suitability and desirability of the use of local versus non-local seed under climate change.

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