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Understanding the evolution of native pinewoods in Scotland will benefit their future management and conservation

Summary

Scots pine (*Pinus sylvestris* L.) is a foundation species in Scottish highland forests and a national icon. Due to heavy exploitation, the current native pinewood coverage represents a small fraction of the postglacial maximum. To reverse this decline, various schemes have been initiated to promote planting of new and expansion of old pinewoods. This includes the designation of seed zones for control of the remaining genetic resources. The zoning was based mainly on biochemical similarity among pinewoods but, by definition, neutral molecular markers do not reflect local phenotypic adaptation. Environmental variation within Scotland is substantial and it is not yet clear to what extent this has shaped patterns of adaptive differentiation among Scottish populations. Systematic, rangewide common-environment trials can provide insights into the evolution of the native pinewoods, indicating how environment has influenced phenotypic variation and how variation is maintained. Careful design of such experiments can also provide data on the history and connectivity among populations, by molecular marker analysis. Together, phenotypic and molecular datasets from such trials can provide a robust basis for refining seed transfer guidelines for Scots pine in Scotland and should form the scientific basis for conservation action on this nationally important habitat.

Introduction

Scots pine (*Pinus sylvestris* L.) is a national icon in Scotland and a foundation species in the Caledonian forest. Currently, 84 woodlands of different sizes of Scots pine woodland in Scotland are recognized as native (Anonymous, 1998). In total these constitute less than 1% of the maximum postglacial range and represent the only recognised UK resource for this habitat, Caledonian pinewood, which receives protection under the EC Habitats directive. These pinewoods represent the north-western extreme of the species' distribution, which is one of the widest of all conifers, extending from northern Finland to Turkey and from western Spain to eastern Siberia (Critchfield and Little, 1965), covering a huge range of environments. In many places Scots pine is also a commercially important timber species, its wood being used for construction, furniture and other products. In Scotland, native trees of commercially desirable form persist in the relatively large populations of e.g. Abernethy, Rothiemurchus and Glen Tanar (Mason et al., 2004).

Recognition of the biological, cultural and recreational value of the species to Scotland has resulted in initiation of replanting programmes, and the commercial prospects for native pine are currently being re-evaluated, e.g. in ‘Developing the Scots Pine Resource’ project in collaboration with institutes from the Nordic Countries (Macdonald et al., 2008).

Adaptation to local climatic conditions through genetic differentiation is a widespread feature of forest tree species (Howe et al., 2003; Savolainen et al., 2007). This characteristic is of high importance for strategies focused on conservation of genetic resources, especially under changing environments. The use of maladapted planting stock or the uncontrolled translocation of non-local provenances may lead to losses in productivity or dilution of local gene pools, impacts to which highly reduced or fragmented populations may be especially vulnerable (McKay *et al.*, 2005). Despite the many unique characteristics of Scottish pinewoods, the extent of possible local adaptation has not been studied in detail.. The aims of this paper are to review current knowledge about the evolution of pinewoods in Scotland and to demonstrate how understanding the species’ history and evolution could provide valuable information with which to refine current guidance on the conservation and expansion of the existing pinewood resources. This is particularly timely given the Scottish government’s aim of increasing forest land cover from 17.1 to 25% (*Scottish Forestry Policy 2006*, 2006).

Re-colonisation and history of pinewoods in Scotland

The last glaciation has strongly influenced the distributions of numerous species in Europe as, during the last glacial maximum 23 000 – 18 000 years ago, ice covered the majority of northern Europe (Svendsen et al., 1999). Pine survived through the ice age in the Iberian, Italian and Balkan peninsulas (Bennett et al., 1991), but macrofossil evidence for refugia have also been found in central parts of Europe (Birks and Willis, 2008; Willis *et al.*, 2000; Willis and van Andel, 2004). Climate modelling suggests that these areas would have been suitable for pine at that time (Cheddadi et al., 2006). Populations from the Iberian and Apennine Peninsulas harbour unique seed-transmitted mitochondrial DNA (mtDNA) variation that is not found elsewhere in Europe (Cheddadi *et al.*, 2006; Pyhäjärvi *et al.*, 2008; Sinclair *et al.*, 1999; Soranzo *et al.*, 2000), and the Iberian pinewoods have also been found to differ from other continental populations for monoterpene and allozyme variation (Prus-Glowacki and Stephan, 1994; Tobolski and Hanover, 1971). These patterns support the view that more northern pine populations originate from refugia located north of the southern peninsulas and south of permafrost.

According to pollen studies, pine reached Scotland about 8,000 years ago and, appeared first in the Wester Ross area in the northwest, and then shortly afterwards in the Cairngorms (Birks, 1989), the latter presumably having spread northwards through England (Bennett, 1995). Interpreting pollen data in species like pine can be challenging due to its abundance and long dispersal distances, and therefore macrofossil data are needed to verify presence of local populations (Birks, 2003). In fact, fossil stomata from two sites in the Highlands indicate that pine was locally present 1,600-600 years earlier than suggested by pollen data (Froyd, 2005). Contemporary populations from Wester Ross differ from those in the rest of Scotland in their allozyme and monoterpene frequencies, suggesting that the contemporary Scottish population derives from multiple refugia (Forrest, 1980; Forrest, 1982; Kinloch et al., 1986). For example, in contrast to the rest of the populations, the frequency of 3-carene in the northwest is very low (Forrest, 1980); biochemically, populations from this area seem more closely related to southern European populations than those from north-central Europe, which are similar to the rest of the Scottish pinewoods (Forrest, 1982). It is possible that the north-western trees originate from refugia near southwest Ireland or western France (Ballantyne and Harris, 1994; Bennett, 1995), but this has not yet been verified by analysis of Irish macrofossils or potentially native pinewood remnants. Alternatively natural selection or genetic drift (random loss of genetic diversity due to e.g. sudden decrease in population size) may account for the differences, as these populations are on the edge of the species' range and under strong oceanic influence. The wet, mild climate is markedly different from that in other parts of the range and provides potentially divergent selective pressures involving, for example, pathogen attack, which may have driven biochemical differentiation. Biochemical similarity between northwest Scotland and southern Europe may reflect the effects of adaptation in a similar direction. However, if variation was due to drift, this would imply lack of gene flow between populations in western Scotland and elsewhere. In their mtDNA study, Sinclair et al. (1999) found two molecular variants in Scotland, the less common type being found in the western part of Scotland. Such differentiation further supports the view of colonization from two directions. Similarly, multiple origins might be suggested by the presence of a unique, paternally-inherited chloroplast DNA (cpDNA) microsatellite allele that was found only in the Wester Ross area (Provan et al., 1998). However, this variant could also represent a recent mutation. Had it been an ancestral polymorphism it would have been surprising that the allele was restricted to the area, considering efficient pollen-mediated transmission of cpDNA. Currently, the low number of mtDNA haplotypes detected prevents precise definition of the colonisation routes of pine in Europe (Naydenov *et al.*, 2007; Pyhäjärvi *et al.*, 2008; Sinclair *et al.*, 1999), but further evidence for separate evolutionary origins of eastern and western pinewoods in Scotland has recently been found in candidate gene variation (Wachowiak *et al.*, 2010).

Current status of native Scottish pinewoods

During its history in Scotland, pine has fluctuated in abundance, sometimes very rapidly, due to various factors such as competition from deciduous tree species, decrease of deciduous forests, climate change and human activity (Bennett, 1995). Nowadays, the only natural pinewoods on the British Isles are patchily distributed in Scotland from latitude 55 ºN to 57 ºN and from longitude 3 ºW to 1 ºW at altitudes up to 600 metres (Mason et al., 2004). According to the most recent available estimate, the native pinewood area in Scotland covers 18,000 hectares in 84 separate pinewoods varying in size from less than one to over 2,000 ha (Anonymous, 1998); some populations are small and sparse consisting of little more than 100 trees at a density of less than one tree per hectare (e.g. Martin, 1995). A substantial number of the native populations were already identified and described in the influential book 'The Native Pinewoods of Scotland' by Steven and Carlisle (1959). Natural pinewood regeneration is often prevented by grazing of domestic livestock or wild deer, muir burning and planting of non-native trees (Anonymous, 1998), and many of the populations have been reduced to very small numbers due to human interference. Also, in the past, trees of poor growth form have often been left in the forests while those considered to be superior from the silvicultural perspective have been felled and extracted for timber (Mason *et al.*, 2004). In such cases, the surviving trees could negatively affect the quality of later generations if they contribute to mating (Ennos et al., 1998; Mason et al., 2004). However, the extent of such practices is not known. In addition, undocumented quantities of trees of continental origin have been introduced to Scotland since the 19th century (Forrest and Fletcher, 1995; Taylor, 1993) which potentially could cause genetic contamination of local populations via pollen flow. The coverage of Scots pine plantations, which are mainly used for timber production, totals 100,000 ha (Mason *et al.*, 2004). However, the extent to which they contribute to the pollen pool in Scotland is not known.

Management of pinewoods in Scotland

Since the late 1980s protection and expansion of pinewoods has been included in various policies and grant schemes (Mason *et al.*, 2004). For example, the ‘Native Pinewood Grant Scheme’ between 1989 and 2004 aided the regeneration of existing pinewoods and created 48,000 ha of new pinewoods (16% natural regeneration, 84% plantations) while the ‘Native Pinewood Habitat Action Plan’ aimed at increasing the remnant pinewood area by 5,600 ha by 2005 and assisting natural regeneration (McIntosh, 2006). However, there are no recent estimates available on the overall success of these projects or current coverage of (semi-)natural pinewoods. To guide seed transfers, the Scottish pinewoods have been divided into seven seed zones (figure 1) such that when (semi)-natural pinewoods are being expanded, in order to qualify for grant support, planting stock must come from within the same seed zone in an attempt to protect the local “genetic integrity” (Anonymous, 1998). For other planting objectives, such as timber production, the rules are somewhat less restrictive. The seed zones are based largely on monoterpene studies (Forrest, 1980) so that biochemically similar pinewoods are clustered within one zone.
[Figure 1]

The general purpose of seed transfer guidelines in forestry is to prevent planting of maladapted trees and to maximise survival and growth. Ideally, management of any economically important tree species would include transfer restrictions, zoning species on the basis of climate, soil and topography and the results of provenance trials replicated in multiple environments (White et al., 2007). In other words, guidelines would take into account broadly-assessed patterns of local adaptation, with quantified evaluation of the phenotypic effects of seed transfers along environmental gradients. As adaptation is driven by the environment, and the spatial scale of environmental heterogeneity can differ widely among regions, transfer rules are not easily transferable between different countries. Although apparently practical where field data are in short supply, applying single-source data (such as monoterpenes and allozymes which can be considered selectively neutral molecular markers) to devise seed zones is likely, at best, to poorly reflect adaptive patterns (McKay and Latta, 2002; Merilä and Crnokrak, 2001) or, at worst, result in detrimental effects on survival and growth if environmental conditions vary greatly among the origin of seed and the plantation site. Hence, whilst variation at molecular markers can accurately reflect other evolutionary features, such as population structure, demography and mating system (i.e. relative levels of inbreeding and outbreeding), they should be applied in combination with data on environments and adaptively significant traits if seed zoning is to be meaningful.

Local adaptation is common in trees

Adaptations to local climate conditions have been described in many tree species using provenance trials (see Howe et al., 2003; Savolainen et al., 2007 for reviews) and in Scots pine in other parts of its range. Despite significant phenotypic differentiation, molecular marker variation may show an opposite trend: due to efficient pollen-mediated mixing of pollen pools even distant populations can seem very similar at molecular markers that are not under selection (e.g. Karhu *et al.*, 1996). Phenotypic divergence is mostly driven by environmental variation among sites. In the Northern hemisphere, due to differences in length of the growing season and in the severity of seasonal periods of stress, trees alternate between periods of active growth and dormancy in order to avoid frost damage in the spring or the autumn (Howe et al., 2003), and traits chosen for studies are usually expected to be linked to these environmental factors. Growth patterns of Scots pine have been extensively studied and, for example, timing of growth cessation is thought to be influenced by both photoperiod and accumulated temperature (Koski and Sievänen, 1985). In common environment conditions, first-year pine seedlings from colder areas generally set their terminal buds and become frost hardy earlier than the ones from warmer conditions (e.g. Hurme et al., 1997). Also, when seedlings from different parts of Europe were grown under photoperiods typical of 50° latitude, seedlings from northern regions set buds earlier compared to seedlings from more southern locations (Oleksyn *et al.*, 1992). The same pattern has also been found in height growth cessation of older trees (Oleksyn *et al.*, 2001; Repo *et al.*, 2000). In Sweden, provenance transfers from north to south resulted in increased survival, but transferred provenances grew less than local ones due to phenological differences (Eriksson *et al.*, 1980; Persson and Ståhl, 1990). On the other hand, northward transfers increased mortality. Commonly, trees from sites experiencing harsher – e.g. drier or colder - conditions grow more slowly than those originating from milder environments, but they are also more tolerant of stress (Howe et al., 2003). Phenotypic divergence among populations is generally thought to be due to differentiation at multiple underlying genes driven by diversifying selection (for reviews on the genetic basis of complex trait variation in trees, see González-Martínez *et al.*, 2006; Howe *et al.*, 2003; Neale and Ingvarsson, 2008; Savolainen *et al.*, 2007), but so far candidate gene studies in trees have revealed more about past demographic processes than about effects of selection (see Lascoux *et al.*, 2008). However, additional factors can also contribute: in Norway spruce (*Picea abies* (L.) Karst.) it appears that maternal effects, e.g. differences due to environmental conditions during seed development, can greatly influence trait variation (Johnsen et al., 2005; Skrøppa, 1994; Skrøppa et al., 1994), but in Scots pine such effects seem much smaller (Ruotsalainen et al., 1995).

For maintenance of natural patterns of adaptive variation, the safest option is usually to use local seed material or seeds from an environment that matches conditions at the planting site (Aitken et al., 2008; McKay et al., 2005). Using genotypes from other locations might negatively affect the local population due to outbreeding depression (hybridization among excessively diverged populations) leading to decreased fitness (Frankham et al., 2002). The definition of "local" depends on the species: in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), genetic differentiation can occur at 100-200 metres (Campbell, 1979), while populations of western white pine (*Pinus monticola* Dougl.) seem genetically similar across a wide range covering 10° in both latitude and longitude (Rehfeldt et al., 1984). Relatively short transfers can actually be beneficial for growth and survival: some conifer populations on the northern edge of the species distributions have been found to perform better if transferred southward of their origin (e.g. Savolainen *et al.*, 2007), while in other species a similar response can be seen in transfers further north (Carter, 1996).

Is Scots pine locally adapted in Scotland?

The current abundance of pinewood in Scotland is only a small fraction of what it used to be, and potentially the exploitation of the resources could have interfered with local adaptation by randomly removing best-adapted trees. . However, the previous molecular marker studies based on monoterpenes (Forrest, 1980; Forrest, 1982) and allozymes (Kinloch et al., 1986) and recent work on nucleotide variation in candidate genes (Wachowiak *et al.*, 2010) show that even in relict populations, levels of molecular variation are similar to those observed in the continuous part of the species' range and, as is usual in the case of long-lived, randomly mating forest trees with effective gene flow by pollen (Hamrick et al., 1992), almost all of the variation was found within populations. In theory, colonization events (such as postglacial migration) are expected to decrease genetic variation through bottlenecks, but the life history characteristics of trees (longevity, multiple age and size classes, overlapping generations and late reproduction) seem to buffer against these effects (Austerlitz et al., 2000). For example, due to their postglacial colonisation history northern Fennoscandian Scots pine populations are much more recently established than those from Central Europe (Willis *et al.*, 1998), but despite their different histories the two parts of the range have very similar levels of nucleotide variation at candidate genes (Pyhäjärvi *et al.*, 2007). Some quantitative traits have been found to have less adaptive variation towards the northern range edges, but this pattern is not seen in all traits, and differences could be caused by varying selection pressure (Notivol *et al.*, 2007). In Scottish populations, low marker divergence among populations suggests that gene flow among sites has, at least historically, been sufficient to homogenise genetic variation across populations (Kinloch *et al.*, 1986). Also, when comparing differentiation at cpDNA markers between Scotland and eight European mainland populations, only around 1.5 % of the variation was found between populations, indicating high levels of gene flow (Provan et al., 1998). Within Scotland, 3.2% of the variation was among populations. Glen Falloch, a relict population consisting of less than 100 trees, had the lowest diversity. Despite drastic changes in the abundance of Scots pine in Scotland, it seems that the level of neutral molecular variation remains high, with the majority of this variation being found mainly within populations.

Despite the relatively small area covered by pinewoods in Scotland, the environmental conditions among them vary tremendously, providing potential for different selection pressures to lead to local adaptation. Furthermore, Scotland's populations form a unique part of the species' range due to its oceanic climate; only in western parts of Norway do Scots pine woodlands occur in similar environments (Øyen et al., 2006). To summarise climatic variation among Scottish native pinewood sites, we extracted data for all 84 pinewoods from the gridded (5 × 5 km) long-term average (1961-1990) UK Met Office data. Details on the climate data generation can be found elsewhere (Perry and Hollis, 2005). The climate data indicate that some western populations in Scotland experience an annual rainfall of close to 3,000 mm compared to only about 700 mm in the eastern parts. The length of the growing season (the number of days with average temperature above +5°C) varies from about 100 in some eastern pinewoods to 300 days near the west coast. To study whether climatically similar pinewoods were found within each seed zone, we performed a principal component analysis (PCA) to transform the seven variables into two components (figure 2, table 1). The data suggest that different pinewood sites within seed zones do not form climatically uniform clusters, which indicates that climatic variation within one zone can be large. For example, the North West seed zone covers areas with growing season lengths varying from about 130 to almost 300 days (table 2). Because of this extensive within-zone variation and considering for instance the effects of provenance transfers along latitudinal gradients in Sweden (Persson and Ståhl, 1990), it is possible that current guidance results in seedlings being planted at non-optimal sites. However, it should be kept in mind that this data was generated by interpolation from data from weather stations which are not equally distributed across the country, and the precision of models for different variables varies (Perry and Hollis, 2005). In addition to climate, there is also variation in soil types; generally pine prefers freely-draining podzol and ironpan soils with relatively low nutrient levels, but it is also found in brown earths, gleys and peats (Mason et al., 2004). In wet conditions, poor drainage can lead to poor growth and water-logging.

[Table 1, Table 2, Figure 2]

Some evidence of local adaptation in the native pinewoods exists, but the data currently available is not extensive. Old provenance experiments set up by the Forestry Commission in Scotland starting in the 1920s show that populations from the mainland of Europe generally perform worse than Scottish material (Lines and Mitchell, 1965). Within Scotland, trees transferred from continental to strongly oceanic areas usually perform worse than local populations, possibly due to pathogen stress (Mason et al., 2004). Perks and McKay (1997) found significant differences in root frost hardiness and growth in seedlings from four provenances; for instance, seedlings from Loch Maree, located in the west close to the Atlantic, had poorer height growth and slower development of frost hardiness than other provenances. The only study where genetic parameters of adaptive variation were estimated was by Perks and Ennos (1999) who also sampled four provenances, each represented by 100 open-pollinated progeny (ten from each of ten mother trees). Seedlings were grown at one site and measured at seven years of age. Significant differentiation among populations was found in diameter, height and bud burst. Adaptive variation was found in all of the measured characters, demonstrating the presence of genetic variation for adaptively important traits, but due to the sample size, estimates on the amount of adaptive variation are not precise. Also, while it was possible to show clear differentiation among populations in the traits considered, geographic coverage was too limited to offer a full picture of patterns of adaptive variation and the study did not attempt to link observed trends to variation in climatic variables.

Ideally, in Scotland, the seed transfer guidelines for Scots pine should be based on climatic and environmental characterisation of the remnant pinewoods and provenance trials, ideally replicated in different environments. Considering the environmental variation that exists within Scotland, differentiation in traits of adaptive importance such as phenology, stress tolerance, and growth seems likely. For the maintenance of healthy pinewoods in Scotland and to update existing seed transfer guidelines, it is essential to study adaptive variation in a number of traits across the whole Scottish range.

Maintenance of variation in pinewoods

The current seed zones of Scots pine are meant to protect the "genetic integrity" of local populations. However, the definition of genetic integrity remains unclear. While maternally-inherited mtDNA variation might show differentiation among some of the pinewoods (Sinclair et al., 1998), this does not mean that populations containing the diverged mtDNA lineages are unconnected. In forest trees, the fact that most of the variation measured with neutral molecular markers occurs within populations can be attributed to efficient pollen-mediated gene flow (Hamrick et al., 1992). Pollen flow can effectively mix the gene pools of populations even if they are under diversifying selection.

However, although a significant proportion of pollen can originate from sites located even a few dozen kilometres away, the great majority of fertilizing pollen usually comes from trees located within the same stand as the mother tree (e.g. Smouse and Sork, 2004). Nonetheless, such mixing can contribute to the maintenance of variation in adaptive traits (Barton, 1999; Slatkin, 1978) which in turn can facilitate adaptation to changing conditions, as potentially beneficial alleles are introduced to the gene pool of the population. Yeaman and Jarvis (2006) studied effects of environmental heterogeneity on variation in height growth in 142 populations of lodgepole pine (*Pinus contorta* Douglas ex. Loudon) and found that variability among the populations in drought occurrence, annual precipitation and temperature explained 7-20% of the variation in height growth. Due to influx of genetic variation from other populations gene flow can also counteract adaptation, especially in peripheral populations (Garcia-Ramos and Kirkpatrick, 1997). It is unlikely that the native pinewoods represent independently evolving units. Previous studies on Scottish pinewoods show low levels of population differentiation (Kinloch *et al.*, 1986; Provan *et al.*, 1998), although the gene flow estimates are indirect and may not reflect current landscape-level processes (Smouse and Sork, 2004; Sork et al., 1999).

Ongoing climate change is affecting forests all over the world, and changes in temperature, rainfall and frequency of extreme weather events are expected (e.g. IPCC, 2007). In Scotland, models predict warmer summers and milder winters, with changes in the distribution of rainfall (Ray, 2008). In the east, summers are predicted to become drier, possibly leading to drought, while winters may become wetter, also a problem if it leads to water-logging and anaerobic conditions in soils. Warmer conditions may help pests and pathogens spread to new areas. For example, the northward spread of the pine processionary moth (*Thaumetopoea pityocampa* Dennis and Schiff) in Italy has been attributed to increasing winter temperatures (Battisti et al., 2005), and since the late 1990s, the occurrence of red needle blight, a fungal disease infecting a wide range of *Pinus* species, has increased in the UK with first outbreaks occurring in Scotland in 2002 (Brown *et al.*, 2003). Changes in climate can lead to situations where environments are no longer optimal for the populations growing in them. Trees have experienced warming conditions before, following the retreat of continental ice at the end of the ice age (e.g. Davis and Shaw, 2001). In current conditions the problem for trees is likely to be the rate of change which is projected to be faster than that following the latest ice age. After the last glaciation, European trees migrated at average speeds of around 100-700 metres per year, depending on the species (Brewer et al., 2002; Magri et al., 2006). According to Malcolm and Markham (2002), trees will have to be able to migrate at a rate of over 1,000 m per year to be able to keep pace with human-induced change. This time, however, trees face environments already occupied by other species.

For a change in fitness of the population, selection must work on the variation present in the population (Falconer and Mackay, 1996). Genetic variation in phenotypic traits can be assessed by growing seedlings in a common environment in which environmental variation is kept to a minimum (e.g. White *et al.*, 2007). Only variation that can be passed on to the next generation has evolutionary significance; therefore, estimating levels of such variation requires observations based on samples of a known family structure (e.g. open-pollinated half-sib families). In the majority of the forest trees studied, populations generally maintain high levels of adaptive variation (Aitken et al., 2008; Howe et al., 2003; Savolainen et al., 2007), even in range-edge populations under extreme conditions (Notivol *et al.*, 2007; Savolainen *et al.*, 2004). In traits with high levels of such variation, the change in the phenotypic mean in response to new selection pressures can be rapid

(Falconer and Mackay, 1996). However, the life history characteristics of trees can slow down rates of adaptation: they are long-lived, have long generation times and, due to phenotypic plasticity, can continue to grow and reproduce even in changed environments (Hamrick, 2004; Mátyás, 1996; Savolainen *et al.*, 2004; Savolainen *et al.*, 2007). For example, Swedish provenance trials suggest that climate-related mortality in Scots pine occurs mainly in the early stages (first 20 years) of a tree's life cycle (Persson and Ståhl, 1990). In addition, if grazing pressure prevents natural regeneration, the adaptive variation present in seedlings is lost.

Due to within-species genetic differentiation adaptive responses may vary among populations from different parts of the range. According to Rehfeldt et al. (2002), the immediate response to a warming climate will be positive in Scots pine populations growing in harsh (suboptimal) conditions, e.g. northern parts of Europe, while populations in mild (optimal) environments, e.g. southern Europe, will suffer. Using simulations, Savolainen et al. (2004) concluded that while Finnish Scots pine populations have potential to adapt in timing of bud set and frost hardiness, their response will be delayed and will lag behind the moving optimum, partly because of the already established trees growing at the site.Increased mortality could facilitate adaptation by creating open spaces for regeneration (Kuparinen *et al.*, 2010). Specific forest management practices have also been suggested as methods for enhancing adaptation; for instance, seedlings could be transferred according to the predicted climate (St. Clair and Howe, 2007), or the interval between recruitment events could be shortened (Kramer et al., 2008).

Before specific provenances can be chosen for future climate, data on the effects of tree transfers between variable sites and on variation of adaptively important traits is needed.

With such data in hand, models may be developed to test responses to specified variables, although making predictions will remain challenging. Not only is adaptation a complex process involving a number of traits simultaneously, but environmental change may also involve changes in the structure of stands, stress frequency, growth rates and competition (Richardson et al., 2007), and it is impossible to include all possible variables at the same time. Current models have yet to combine genetics and ecology effectively, for example models based on niche concepts often fail to take into account the possibility of adaptation, while genetic models deal inadequately with ecology. There is a pressing need, for climate change mitigation, for the development of new, landscape-scale models that integrate these fields.

Studies on adaptive variation would also benefit from an understanding of current patterns of genetic connectivity among forest fragments. For example, if only local material is used for planting and gene flow is limited, local genetic "integrity" of small populations will be maintained, but the population might become vulnerable to changing conditions due to insufficient adaptive variation for natural selection to operate on. In the case of isolated populations, variation could be introduced by bringing seedlings from other locations; however, if gene flow occurs naturally and if natural regeneration occurs, such practices might be unnecessary. Due to differences in the sizes of the native pinewoods (from less than one to over 2,000 ha), there might also be variation in the patterns of mating system. In small populations, random drift becomes a powerful force shaping allele frequencies, and along with inbreeding, this can lead to lower fitness as detrimental alleles increase in frequency (Frankham *et al.*, 2002). Like other pines, Scots pine is mainly outcrossing (Muona and Harju, 1989), i.e. matings usually occur between unrelated trees, but self-pollination, the most severe form of inbreeding, is also possible due to the lack of a genetic system preventing self-fertilization (Sarvas, 1962). Normally, selfed embryos are aborted early in their development due to early inbreeding depression. However, in stands with limited numbers of trees, bi-parental inbreeding (mating between relatives) is a potential risk. Despite efficient gene flow, inbreeding might become a significant factor when isolation is extreme. In Scots pine, gene flow and mating system have been studied in e.g. Spanish populations occurring in isolated stands in mountainous regions. Although the proportions of self-pollinationwere eight times larger (25% vs. 3%) in a population of 36 trees spread across a 15-ha area compared to that of larger populations covering thousands of hectares (Robledo-Arnuncio et al., 2004), the rates were nevertheless low when the degree of isolation of the trees is taken into account. In the small population, 4.3 % of the pollen originated from other populations, the closest one being located 30 km away (Robledo-Arnuncio and Gil, 2005). Kärkkäinen et al. (1996) documented variation in levels of inbreeding depression within larger populations in Finland: outcrossing rates in northern populations were somewhat lower than in the south, but inbreeding depression was weaker in the north, possibly due to selection having already removed detrimental recessive alleles exposed by inbreeding. Understanding the mating system is also beneficial for studies on adaptive variation in phenotype, as departures from the assumed family structure can lead to biased estimates of adaptively significant genetic variation (Namkoong, 1966; Squillace, 1974).

Conclusions

Due to its economic and biological significance across two continents, Scots pine is one of the most thoroughly studied forest tree species in the world, and its biology has been studied from DNA to the whole ecosystem level. Native remnant pinewoods of Scotland represent a distinct part of the distribution because of their proximity to the Atlantic Ocean, highly variable climate conditions and the 500 km distance to the closest continental populations. Scots pine's current coverage in Scotland is only a fraction of what it used to be, but there are plans to expand old and plant new native woodlands. . If local adaptation has occurred and provided that other management practices (e.g. cultivation and deer management) support successful regeneration, modifications to existing seed transfer guidelines could improve the effectiveness of re-plantation efforts by minimising seedling mortality due to maladapted stock and the consequent ecological, economic and strategic effects. Current transfer rules are based primarily on molecular variation that does not reflect the likely pattern of environmental adaptation across Scotland. To update the existing management guidelines, further research is recommended, with a particular focus on the following:

1. Rangewide progeny trials are needed to characterise general trends of adaptive variation in traits such as phenology, growth, and stress tolerance in relation to the environment. Such data can also reveal whether plantations have diluted local adaptation in native pinewoods.
2. Effects of provenance transfers along climatic gradients can be obtained by replicating trials at multiple environmentally diverse sites across Scotland. In such a design, the performance of local trees can also be compared to that of trees from more distant sources.
3. Neutral genetic markers should be used to assess other types of natural processes occurring in populations, such as effects of population fragmentation, mating system variation and current gene flow dynamics.

4. Potential role of pollen contamination can be assessed by e.g. observing synchronisation of reproductive events between plantations and nearby native woodlands.

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Table 1 List of climatic variables used in the principal component (PC) analysis. Values in the table are correlation coefficients that vary between -1 (strong negative correlation) and 1 (strong positive correlation); the further the coefficient is from zero, the stronger the association between the variable and the PC. PC1 is the main component, explaining 69% of the variation.

Variable	PC1	PC2
Length of the growing season	-0.45	-0.12
February mean temperature	-0.45	-0.12
July mean temperature	-0.35	-0.47
Annual extreme temperature range	0.10	-0.72
Air frost days per year	0.44	-0.03
Ground frost days per year	0.43	-0.13
Annual precipitation	-0.30	0.46
Percentage of variation	69.20	23.99

Table 2 Range of climatic variation in four variables within each seed zone according to the UK Met Office long-term average data (Perry and Hollis, 2005). Seed zones: EC=East Central, N=North, NC=North Central, NE=North East, NW=North West, SC=South Central, SW=South West. Climatic variables: LGS=length of the growing season, FMT=February mean temperature, JMT=July mean temperature, AP=annual precipitation.

	LGS (days)		FMT (°C)		JMT (°C)		AP (mm)	
Seed zone	min	max	min	max	min	max	min	max
EC	154	216	-0.8	1.0	10.6	13	743	1223
N	162	251	-0.5	2.4	10	13.9	1215	1778
NC	208	299	0.6	4.0	11.1	14.4	1346	2900
NE	108	234	-2.0	1.9	9.4	13.7	785	1343
NW	134	295	-0.9	4.0	8.5	14	1912	2790
SC	219	238	0.8	1.8	11.9	13.4	1159	2904
SW	179	297	0.0	3.9	9.7	14.1	1563	2934

Figure 1 Map of the current Scots pine seed zones in Scotland.

Figure 2 Plot of the first two principal components, which account for 69 and 24% of total variation, respectively, of climatic variation among 84 native pinewood sites. The seven variables used are shown in table 1. Current seed zones are represented by different symbols, and the closer the populations are in the graph, the more similar they are climatically. PC1 represents a gradient in annual rainfall and temperature: populations with more negative values are generally located in the west (high rainfall, mild climate); positive values represent more eastern pinewoods with less rainfall and colder winters.

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