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REVIEW

Potential for evolutionary responses to climate change – evidence from tree populations

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Abstract

Evolutionary responses are required for tree populations to be able to track climate change. Results of 250 years of common garden experiments show that most forest trees have evolved local adaptation, as evidenced by the adaptive differentiation of populations in quantitative traits, reflecting environmental conditions of population origins. On the basis of the patterns of quantitative variation for 19 adaptation-related traits studied in 59 tree species (mostly temperate and boreal species from the Northern hemisphere), we found that genetic differentiation between populations and clinal variation along environmental gradients were very common (respectively, 90% and 78% of cases). Thus, responding to climate change will likely require that the quantitative traits of populations again match their environments. We examine what kind of information is needed for evaluating the potential to respond, and what information is already available. We review the genetic models related to selection responses, and what is known currently about the genetic basis of the traits. We address special problems to be found at the range margins, and highlight the need for more modeling to understand specific issues at southern and northern margins. We need new common garden experiments for less known species. For extensively studied species, new experiments are needed outside the current ranges. Improving genomic information will allow better prediction of responses. Competitive and other interactions within species and interactions between species deserve more consideration. Despite the long generation times, the strong background in quantitative genetics and growing genomic resources make forest trees useful species for climate change research. The greatest adaptive response is expected when populations are large, have high genetic variability, selection is strong, and there is ecological opportunity for establishment of better adapted genotypes.

Keywords: adaptive traits, conifers, local adaptation, natural selection, phenotypic plasticity, provenance trials, quantitative genetics

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Introduction

Populations can respond to environmental change through phenotypic plasticity, by moving to a new area corresponding to environmental conditions they are adapted to, by genetically adapting to the new conditions, or by combinations of these responses (Aitken *et al.*, 2008). Most attention has been paid to range expansion or contraction (Parmesan, 2006; Chen *et al.*, 2011), typically using models that assume the species are genetically homogenous. The potential for genetic responses has often been neglected, for instance in the IPCC reports (IPCC, 2001, 2007), even if it is well known that evolutionary changes, i.e., genetic responses, have historically accompanied changes in climate (Davis & Shaw, 2001). Furthermore, it is also now understood that the rate of adaptation required by

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climate change varies among geographic regions (Loarie *et al.*, 2009). Modeling work on the potential of populations and species to respond genetically to recent climate change is advancing (see Hoffmann & Sgrò, 2011; Franks & Hoffmann, 2012; Shaw & Etterson, 2012 for recent reviews). The immediate responses via phenotypic plasticity have also been considered in the context of climate change (Nicotra *et al.*, 2010).

Here, we examine the importance of and potential for genetic responses to climate change in forest tree populations. Trees are ecologically key species in many terrestrial ecosystems, including boreal and temperate forests in Europe and North America. Their response to climate change can substantively impact the global carbon cycle. Local adaptation (Kawecki & Ebert, 2004) is more common in trees than in some other plant species. Tree species are adapted to the current climate, and they are thus potentially greatly influenced by the rapid changes in climate (Savolainen *et al.*, 2007). The long generation times are a challenge for research, but trees also provide some advantages for these studies, as described below.

First, adaptation to climate change will depend on phenotypic traits relevant in the new environments, such as timing of growth and drought or cold tolerance. There is an extraordinary wealth of information on the quantitative genetics and population differentiation of trees for these traits, based on 250 years of forestry common garden experiments, known as provenance trials (Langlet, 1971; Morgenstern, 1996), and on extensive tree breeding experience.

Second, the demographic history since the last glacial maximum has been reconstructed for several tree species by combining phylogeographic and palynological approaches with coalescent-based studies of population demography (Petit *et al.*, 2002; McLachlan *et al.*, 2005; Cheddadi *et al.*, 2006; Heuertz *et al.*, 2006; Magri *et al.*, 2006; Soltis *et al.*, 2006; Eckert *et al.*, 2010; Parducci *et al.*, 2012). Rates of past adaptation of trees to climate changes can be inferred from these studies (Hendry & Kinnison, 1999). The increasing knowledge of the molecular basis of quantitative trait variation (see Neale & Kremer, 2011 for references) can improve predictive models (see e.g., Wilczek *et al.*, 2010). This body of background information allows us to examine the potential for adaptation in natural conditions better than in many other organisms. For instance, in butterflies, studies of responses to climate change have relied nearly exclusively on examining molecular marker variation (Hill *et al.*, 2011).

Trees have very long generation times, but they share population genetic characteristics with other outcrossing plants and animals with high levels of gene flow and large effective population sizes (Petit & Hampe, 2006). Trees are highly fecund, and may rapidly increase their population sizes. Because they are sessile, they generally have good tolerance of a range of environmental conditions and large plastic responses. There are ecologically and commercially important trees with large continuous distributions, such as *Picea abies*, *Pinus contorta*, and *P. sylvestris*, but also species with small, fragmented distributions more susceptible to genetic drift. The dispersal capacity of tree species will play a crucial role in their potential for adaptation. Hybridization between closely related tree species can also influence their adaptive capacity out of their current range, as it has been shown in other organisms (Hoffmann & Sgrò, 2011; Olson-Manning *et al.*, 2012 and references therein).

The focus of this review was on predicting evolutionary responses, with as much evolutionary, genetic, and ecological realism as possible. We examine the models needed for prediction, starting with the simplest models of evolution in individual populations, and continuing to more complex and more realistic models involving multiple populations in heterogeneous environments. We discuss what data are needed for realistic prediction of genetic responses, what information is already available, and what additional information we need in terms of new models, new data, or new analyses of existing data (Lindner *et al.*, 2010). Quantitative genetic models of evolutionary response deal with traits that will confer adaptation to future environments. While it is not easy to predict what traits will be most important in the future, it is reasonable to examine traits related to climate, such as the timing of growth and reproduction (Rohde & Bhalerao, 2007; Hänninen & Tanino, 2011) or cold and drought tolerance (Niinemets, 2010).

Evolution in one isolated population

A single population: the breeder's equation

According to the breeder's equation, the simplest model governing response to directional selection on a single trait, the response in a large population with no gene flow depends on the strength of selection, on the amount of genetic variation, and its ratio to total phenotypic variation (heritability; see Falconer & Mackay, 1996). If there is no genetic variation, any change in phenotype in a novel environment inducing directional selection would be due to phenotypic plasticity alone. Forest tree populations harbor considerable genetic variability in many quantitative traits (Cornelius, 1994; Morgenstern, 1996; Howe *et al.*, 2003) as well as at the DNA level (see Fig. 1 and Savolainen & Pyhäjärvi, 2007). While tree breeders can control the intensity of

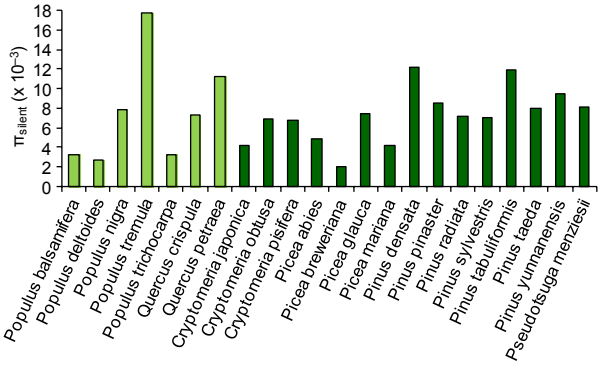

Fig. 1 Mean silent nucleotide diversity per site (π_{silent}) estimates for several tree species. Average nucleotide diversity at silent sites (for more details and references see Table S2). Angiosperms appear in light color and conifers in dark color.

selection and predict responses in breeding populations, it is much more difficult to make such predictions in the wild. Environmental variances will be higher, and heritabilities generally lower (Conner *et al*., 2003). Methods for estimating heritabilities in the wild are improving because of much better estimates of relatedness (Ritland, 1996; Sillanpää, 2011), and will be of critical importance to understanding responses to climate change.

Assessing the strength of directional selection is a demanding task, as we do not even know exactly which traits are most important for fitness, and the longevity of trees makes lifetime fitness estimates unattainable in a realistic timeframe. Estimates of directional selection are available for natural populations (Kingsolver *et al*., 2001; Kingsolver & Diamond, 2011), but studies on forest trees are lacking. Furthermore, selection is likely to be variable across environments, years, and life stages. In natural populations, the traits are also subject not just to directional selection but also to stabilizing and disruptive selection, not included in this simplest model. Thus, for most natural situations, the breeder's equation is far from the reality of populations responding to natural selection.

Temporal variation in selection

Two general classes of quantitative genetic models have been developed to study the risk of extinction in single populations: models with a sudden single step-change in the optimum phenotype (Pease *et al*., 1989; Gomulkiewicz & Holt, 1995; Gomulkiewicz & Houle, 2009; Gomulkiewicz *et al*., 2010), and models with a continuous change in the optimum phenotype (Lynch & Lande, 1993; Burger & Lynch, 1995; Björklund *et al*., 2009; Chevin *et al*., 2010). In single step-change models, extinction occurs as a consequence of decreasing population size due to selective deaths as the population adapts to the change in environment. In the continuous-change models, by contrast, extinction is assumed to occur when the pace of adaptation lags behind the rate of change in the optimum phenotype (see Aitken *et al*., 2008 for further discussion). There are several interesting ways in which these models could be extended to increase biological realism. Most of these models assume that the strength of selection does not vary with population density, which is unrealistic for most forest trees, as competition is likely greatly reduced at low densities (see Björklund *et al*., 2009 for a simulation model incorporating density dependent selection). Also, failing to account for changes in biotic interactions that may be associated with climatic change could cause models to under- or overestimate extinction risks (Gilman *et al*., 2010). Climate change may result in the introduction of new pests, as for instance the mountain pine beetle (Robertson *et al*., 2009) or new pathogens (Netherer & Schopf, 2010), but also losses of current competitors, insects, or diseases caused for example by phenological shifts between trees and associated pests (van Asch & Visser, 2007).

While it is possible to parameterize some of these models to make quantitative predictions about extinction risk, the assumptions involved greatly limit the faith that should be placed in any such predictions (see Aitken *et al*., 2008 for further discussion). Rather, they seem most useful as heuristic tools to identify the most likely factors causing population extinction and to compare relative risk among species. In general, these models find that the probability of extinction decreases for species with large population sizes, high fecundity, high heritabilities, and high amounts of standing genetic variation. While many forest trees present such characteristics, extra effort should be made to study species that are on the low end of the spectrum for any of these characteristics. Some examples of species that may be particularly vulnerable due to their small population sizes are *P. torreyana* in North America, or *A. pinsapo* in Europe. More study is necessary to see whether such vulnerable species also have lower levels of standing variation.

Genetic basis of adaptive trait variation

The expected genetic responses in many models depend on the genetic architecture of the trait (e.g., Gomulkiewicz *et al*., 2010). While the traditional polygenic model of Fisher (Fisher, 1918, 1930) is based on small effects at a very large number of loci, some models of selection predict larger effect sizes (Orr, 1998; Yeaman & Whitlock, 2011). Overall, quantitative trait locus (QTL) studies in forest trees have generally found

large numbers of loci with relatively small effect sizes, compared with some crop plants (Barton & Keightley, 2002; Howe *et al.*, 2003; Laurie *et al.*, 2004). Association studies have further confirmed this view of moderate effect sizes (summarized in Fig. 2), e.g., in *P. taeda* (Quesada *et al.*, 2010; Cumbie *et al.*, 2011), *Populus tremula* (Ingvarsson *et al.*, 2008), *P. sitchensis* (Holliday *et al.*, 2010a), and *Pseudotsuga menziesii* (Eckert *et al.*, 2009). These findings are consistent with the small effect sizes of flowering time and leaf trait variation loci in maize (Buckler *et al.*, 2009; Tian *et al.*, 2011), and human height (Hill *et al.*, 2008). In contrast, Atwell *et al.* (2010) found large effect SNPs for many phenotypic traits of *Arabidopsis*. There may also be major effect loci for disease resistance, such as for rust disease caused by fungal pathogens in North American conifers (Kayihan *et al.*, 2010). The associated loci may well differ between environments due to genotype by environment interactions (Jermstad *et al.*, 2003) or because of different genetic basis in different areas (Goldstein & Holsinger, 1992; Hancock *et al.*, 2011). In many conditions, the phenotypic differences between populations can be due to combined effects of several loci rather than differentiation at the level of individual loci (Latta, 1998; LeCorre & Kremer, 2003; Kremer & Le Corre, 2012).

Weak genetic correlations allow traits to respond to selection independently, whereas genetic correlations opposing the direction of selection will delay the response (Etterson & Shaw, 2001), and reinforcing correlations will accelerate it. Under stabilizing selection, responses are facilitated, if the selection is weak (Duputie *et al.*, 2012). The underlying causes of genetic correlations are so far not known in trees.

Overall, the limited findings so far suggest that the response to strong selection on phenotypes will often be based on many loci with small effects, and fairly weak selection on individual loci, as has been also found in humans (Turchin *et al.*, 2012). If larger effect loci are involved, response predictions could then use specific information on such loci. Alternatively, genomic selection methods could be used to build predictive models that do not need to identify the particular loci underlying adaptive genetic responses (Grattapaglia & Resende, 2011; Iwata *et al.*, 2011; Holliday *et al.*, 2012; Resende *et al.*, 2012).

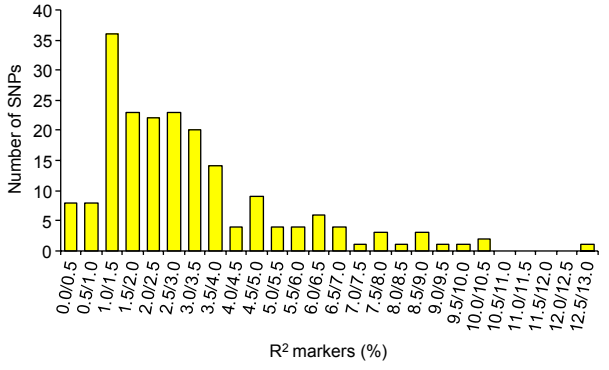

Fig. 2 Distribution of allelic effect sizes in tree species. Distribution of the percentages of phenotypic variance explained by genotypic classes at SNP loci (R^2 marker) detected in significant associations with quantitative traits (for more details and references see Table S3).

We do not know whether most adaptations in trees are due to existing variation or new mutations. During interglacial periods, tree populations have repeatedly colonized northern areas and have rapidly adapted to those conditions, likely because the north-adapted variants may have remained in southern populations at lower frequencies (De Carvalho *et al.*, 2010; Savolainen *et al.*, 2011). Typically, large effective population sizes in forest trees would have contributed to rapid fixation of adaptive variants. This supports an interpretation of evolution from standing rather than *de novo* variation.

Phenotypic plasticity and adaptation

Trees exhibit a high degree of phenotypic plasticity with respect to climatic variation. Phenological shifts of bud flush in response to recent increases in temperatures have been widely documented (Menzel & Fabian, 1999; Menzel *et al.*, 2006; Parmesan, 2006). Arid years or an arid microsite may favor the development of deeper and denser root systems (Kozlowski & Pallardy, 2002). In such a context, adaptive plasticity can buffer the impact of changing conditions on population size (Lynch & Lande, 1993). However, these plastic changes may take time to develop, as in the root example above. In addition, more plasticity also means less intense selection, causing populations to genetically track changing optima more slowly. Recent models have shown that the decreased selection is more than compensated for by the increased phenotypic match allowed by plasticity (Chevin & Lande, 2010). In fact, the evolution of plasticity can provide populations with a transient and efficient response to large environmental changes (Lande, 2009).

Multiple-site provenance trials can be used to examine the plastic responses of populations in new environments. This can be quantified with response functions for individual populations, which describe the change in a trait as a function of transfer distance or change in environmental factors (Rehfeldt *et al.*, 1999, 2002). Provenance trials have been planted in sites that vary with respect to many environmental variables, such as temperature or water availability (Morgenstern, 1978; Kramer, 1995; Shutyaev & Giertych, 1997; Rehfeldt *et al.*, 1999, 2002; Worrell *et al.*, 2000; Reich & Oleksyn,

2008; Vitasse *et al*., 2010). Transfers to the south have been used to predict responses to a warming climate (Beuker *et al*., 1998; Rehfeldt *et al*., 2002; Wang *et al*., 2006) even if the future conditions may be different (e.g., photoperiod). Furthermore, these experiments take place in spaced plantings of seedlings, and thus ignore germination, establishment, and early intra- and interspecific competitive effects. Response functions of individual populations have been developed for growth using very large datasets of multiple trials including more than a hundred populations available for *P. contorta* (Rehfeldt *et al*., 2001), *P. sylvestris* (Rehfeldt *et al*., 2002), and *Larix occidentalis* (Rehfeldt & Jaquish, 2010). Recently, Wang *et al*. (2010) developed a universal response function for *P. contorta*, which integrated populations and environment effects and can be used to predict the performance of any population in any climatic conditions. Incorporating provenance trial data on local adaptation and phenotypic plasticity in models predicting future distributions reduced dramatically the extinction risk in southern populations (Morin & Thuiller, 2009; Benito-Garzón *et al*., 2011). The plastic response of different traits (e.g., phenology in trees) to variation in climate is, however, often much more complex than in heuristic models of adaptation (see e.g., Valladares *et al*., 2007; Caffarra *et al*., 2011; Hänninen & Tanino, 2011).

Finally, epigenetic effects on phenotypic plasticity and inheritance of phenotypic variation need further investigation. Epigenetic variation can be partly inherited from one generation to the next while being still sensitive to environmental variation (Richards *et al*., 2010). Maternal epigenetic effects are known in *Arabidopsis* (Johannes *et al*., 2009), but so far their nature has not been studied much in trees (Bräutigam *et al*., 2013). Epigenetic effects can also occur during seed maturation. Temperature differences during embryogenesis caused differences in phenology in *P. abies* (Skrøppa & Kohmann, 1997) and the molecular mechanisms involved are being studied (Yakovlev *et al*., 2010). They could have significant implications for the interpretation of provenance trial data, explaining some of the phenotypic variation among populations that is commonly interpreted as genetic variation.

Evolution in multiple populations

Geographic distribution and genetic structure

Natural populations of a species in a heterogeneous landscape may have very different patterns of distribution, which can influence its population genetic characteristics (Fig. 3) as reviewed by Charlesworth & Charlesworth (2010). The classical island model assumes populations of equal finite constant size, with equal migration rates between them (Wright, 1931). These assumptions can be relaxed, with variable migration rates and changing population sizes. Species can also be distributed in large continuous populations where parts of the range are connected by symmetric gene flow, as described in the isolation by distance model by Wright (1943). Populations located at range margins represent a special case, as they are at the edge of environmental gradients where carrying capacity may be limited. In such cases, there is more migration from the core populations to the margin than *vice versa*, resulting in asymmetric gene flow (Kirkpatrick & Barton, 1997).

Many economically important temperate and boreal species have large populations covering vast areas, but other tree species do not fit this distribution model. We examined the population structure of European conifers in the *Pinaceae* (including pines, spruces and firs), a limited group of species with very good distributional and reasonable population genetics information. A compilation of the distributions of these 27 species (and sometimes subspecies; from Jalas & Suominen, 1973), allowed us to classify them as having northern or central large, southern large or southern small or fragmented distributions (Table 1). Note that the classification is based on the current distributions, although some currently fragmented species may have had much larger distributions in the past (Soto *et al*., 2010). Species with a predominantly northern distribution, but also occurring in the south (e.g., *P. sylvestris*) were classified as northern species. Figure 3 shows examples of distributions of three species (*P. omorika*, *P. pinaster*, and *P. sylvestris*). There are 11 species with predominantly northern or central, large, continuous distributions, and four southern species with large, but somewhat fragmented distributions. About half of the European conifers (12) have southern, small, or fragmented distributions. Furthermore, the southern margin of most species seems to consist of fragmented small populations, whereas in the north, the range margin is part of a continuous distribution for several species. This analysis shows that in many tree populations, the threats associated with climate change are accompanied by and likely exacerbated by the effects of fragmentation at southern range margins (see also Lynch, 1996). However, if there is still extensive gene flow among the fragments, the population structure should resemble that of a continuous population.

Consistent with the theoretical predictions, the European conifers with continuous distributions have higher genetic diversity (H_e) than the fragmented ones (Table 1). The widespread northern species such as *P. abies* and *P. sylvestris* have low levels of genetic

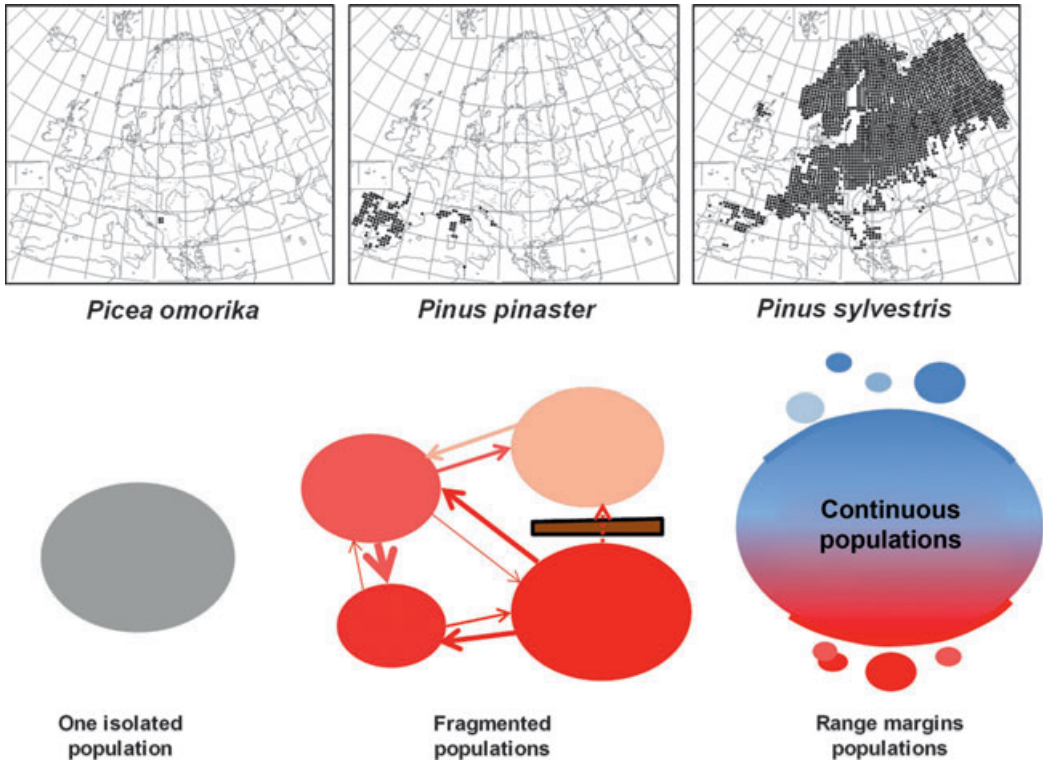

Fig. 3 Schemes of the population models used to discuss evolutionary responses. The three different schematic models of population structure encountered in tree species illustrated by the different cases of *Picea omorika* (one limited population), *Pinus pinaster* (several fragmented populations) and *Pinus sylvestris* (large and continuous population). The color of the circle indicates the environmental condition of the population which is either undefined (in gray) or following a temperature gradient from warm (in red) to cold (in blue). The arrows represent gene flow connecting populations, with thickness indicating gene flow intensity. For the fragmented populations, the brown line symbolizes a physical barrier to gene flow, such as a mountain.

differentiation (F_{ST}) in their main range (Heuertz *et al.*, 2006; Pyhäjärvi *et al.*, 2007). Similar findings have been made in North America for species such as *P. menziesii* (Eckert *et al.*, 2010), *P. sitchensis*, *P. glauca*, and *P. mariana* (Namroud *et al.*, 2008; Chen *et al.*, 2009; Holliday *et al.*, 2010a,b). In contrast, the level of population differentiation is almost twice for the southern fragmented species compared with the northern widely distributed ones (Table 1). Thus, the genetic data available are broadly consistent with the population structure classification based on species distribution and census size. However, current census size may ignore effects of past demographic history such as population size changes or hybridization, and we do not expect the current distributions to account for all variation in patterns of diversity.

Next, we examine the patterns of quantitative genetic variation in tree species in general and in these European conifers in particular to evaluate the effects of selection for local adaptation. We reviewed the literature of provenance trials and found a total of 112 studies on 19 relevant traits related mostly to phenology, growth, cold or drought tolerance or other ecophysiological traits, among which were 36 studies on European conifers (Table S1). Among 59 tree species studied, most were native to Europe and North America (23 and 29 species, respectively) while conifers were more studied than angiosperms (36 and 23 species, respectively). Only three traits had been measured in a sufficiently large number of experiments (Table 2) to make general comparisons and draw general patterns. We focused on the patterns of genetic variation for height increment and for the timing of bud flush, at the beginning of the growing season in spring, and the timing of bud set, an indication of cessation of growth in fall. Among all studies, these three traits had comparable levels of genetic differentiation between populations (mean value equal to 0.249, 0.324, and 0.392 for bud flush, height increment, and bud set, respectively; Table 2).

Quantitative variation in fragmented populations

In Europe, small and fragmented conifer populations occur mainly in the southern Mediterranean area. Provided population sizes are sufficiently large, species with greater differences among populations in local phenotypic optimum and higher levels of genetic vari-

Table 1 Distribution range and genetic estimates for the 27 European conifers

Species	Range	Distribution	Mean Q_{ST}*	Q_{ST} range*	F_{ST}	H_e	Reference †
Abies nebrodensis	Sicilia	South small				0.201	Ducci *et al.* (1999)
Abies pinsapo	Andalusia	South small				0.056	Scaltsoyiannes *et al.* (1999)
Pinus nigra ssp dalmatica	South Croatia	South small			0.091	0.292	Nikolic & Tucic (1983)
Picea omorika	Croatia Serbia	South small			0.261	0.067	Ballian *et al.* (2006)
Pinus nigra ssp laricio	Corsica Calabria Sicilia	South small			0.005	0.182	Scaltsoyiannes *et al.* (1994)
Abies cephalonica	Balkans	South small	0.140	0.100–0.170	0.048	0.221	Fady & Conkle (1993)
Pinus peuce	Balkans	South small			0.083	0.124	Zhelev & Tsarska (2009)
Pinus brutia	Aegean Sea	South fragmented	0.040		0.053	0.196	Kara *et al.* (1997)
Pinus heldreichii	Balkans	South fragmented			0.054	0.177	Boscherini *et al.* (1994)
Abies borisii-regis	Balkans	South fragmented				0.273	Scaltsoyiannes *et al.* (1999)
Pinus nigra ssp pallasiana	Greece Serbia Bulgaria	South fragmented	0.028	0.020 - 0.040	0.070	0.114	Tolun *et al.* (1999)
Pinus nigra ssp salzmannii	East Spain South France	South fragmented				0.216	Scaltsoyiannes *et al.* (2009)
Pinus nigra ssp nigra	North Italy Croatia Greece	South large fragmented				0.264	Scaltsoyiannes *et al.* (2009)
Pinus pinaster	South West Europe	South large fragmented	0.616	0.441–0.791	0.076	0.142	Salvador *et al.* (2000)
Pinus pinea	South Europe	South large fragmented			0.279	0.011	Fallour *et al.* (1997)
Pinus halepensis	South Europe	South large fragmented	0.130			0.040	Schiller *et al.* (1986)
16 species with small or fragmented range			0.192		0.082‡	0.171‡	
Pinus cembra	Alps Romania	North large continuous	0.830		0.040	0.081	Belokon *et al.* (2005)
Pinus uncinata	Central West Europe	North large continuous			0.006	0.260	Lewandoski *et al.* (2000)
Larix decidua	Central Europe	North large continuous			0.051	0.223	Maier (1992)
Pinus sibirica	East Siberia	North large continuous			0.027	0.278	Goncharenko *et al.* (1992)
Pinus mugo	Central East Europe	North large continuous			0.041	0.214	Slavov and Zhelev (2004)
Abies alba	Central Europe	North large continuous	0.075	0.000–0.150		0.252	Ducci *et al.* (1999)
Abies sibirica	Siberia	North very large continuous			0.102	0.083	Semerikova & Semerikov (2006)
Larix sibirica	Siberia	North very large continuous			0.082	0.159	Semerikov *et al.* (1999)
Picea abies ssp obovata	Lapland Siberia	North very large continuous			0.011	0.213	Krutovskii & Bergmann (1995)
Picea abies ssp abies	North Central Europe	North very large continuous	0.417	0.106 - 0.727	0.044	0.252	Krutovskii & Bergmann (1995)

Table 1 (continued)

Species	Range	Distribution	Mean Q_{ST}*	Q_{ST} range*	F_{ST}	H_e	Reference †
Pinus sylvestris	Whole Europe	North very large continuous	0.519	0.080 - 0.860	0.033	0.286	Goncharenko *et al.* (1994)
11 species with continuous range			0.463		0.044	0.209	

*Mean Q_{ST} and Q_{ST} range were calculated from estimates only for height increment, bud flush, and bud set (for more details and references see Table S1). Q_{ST} estimates corresponds to the levels of population differentiation measured either as the proportion of phenotypic variation between populations (V_{pop}) or as the proportion of additive genetic variance between populations (Q_{ST}) in the provenance trials (for more details see Table S1).

†References of the studies using allozyme markers to assess F_{ST} and H_e. See supporting information references for full reference information.

‡*Pinus pinea*, which has hardly any within-population variation (Vendramin *et al.*, 2008), was not included in the calculation of mean F_{ST} and mean H_e.

ance would be expected to have higher equilibrium differentiation. Gene flow in contrast, would reduce differentiation (Hendry *et al.*, 2001). In general, if there is strong differential selection between populations, we would expect that the proportion of total genetic variance found between populations, Q_{ST}, should be higher than F_{ST} calculated from neutral markers with appropriate mutation rates (Leinonen *et al.*, 2008; Edelaar *et al.*, 2011).

In the limited set of provenance trials on European conifers, estimates of quantitative genetic differentiation among populations for species with small or fragmented range were low over all traits (mean Q_{ST} = 0.192, five species; Table 1). This average is about twice as high as the neutral F_{ST} (0.082; nine species; Table 1). Even though sampling across an environmental gradient is clearly not concordant with the assumptions of the island model, data of this kind are frequently analyzed by comparing Q_{ST} and F_{ST} estimates for distinct samples from large and continuous populations. The average Q_{ST} estimate for large populations in northern areas is 0.463 while average F_{ST} is 0.044. Thus, in this small set of studies, the ratio of Q_{ST} to F_{ST} is much lower for species with small or fragmented range than that found in more widespread species. In small populations or fragments, selection for local adaptation is less efficient because of the effects of genetic drift on individual loci, and further, on the associations of alleles at different loci (Le Corre & Kremer, 2012). A review by Leimu & Fischer (2008) found that in plants only about 50% of all population pairs in reciprocal transplantations studies showed evidence of local adaptation, i.e., each population at its native site had higher fitness than other populations introduced to that site. Local adaptation was much less likely in small than large populations. However, Q_{ST} values could also differ because the studies on species with limited distributions have sampled a smaller range of environmental variation than studies in species with large ranges, or because the scale of fragmentation does not match the scale of environmental variation. Reciprocal transplant experiments are needed to assess the level of local adaptation directly. In the large provenance trial data set over all 19 traits and 59 tree species, 264 of 294 analyses (around 90%) showed significant differentiation across populations (Table S1), in most cases likely due to climatic selection.

There is also some evidence in the literature for local climatic adaptation in southern European fragmented populations, such as for water use efficiency in *P. halepensis* (Voltas *et al.*, 2008). Furthermore, some allelic variants at candidate loci for drought tolerance have also been found to be associated with environmental variables (Grivet *et al.*, 2011). In some of these species, selection may have been strong enough for local adaptation to evolve. Clearly, more studies on the patterns of local adaptation are needed in the species with fragmented southern distributions. Forests at Mediterranean southern limits are threatened by faster changes in precipitation than in the northern range limit. If indeed their adaptive capacity is lower, this could make southern fragmented populations even more vulnerable.

It is also possible that these populations have evolved high adaptive phenotypic plasticity in response to environmental variability instead of genetic differentiation, either for some specific traits or across the genome (Nicotra *et al.*, 2010). This could be likely if there is also a strong temporal component of environmental variation (Hedrick, 2006). In a changing climate, the responses due to phenotypic plasticity may maintain fitness despite climatic changes. More growth chamber or reciprocal transplant experiments will be needed to assess the response functions for these species.

Table 2 Genetic differentiation (Q_{ST}) estimates for the 19 quantitative traits studied in provenance trials

		Q_{ST} estimates*			Qualitative estimation †	
Trait	Category	Mean Q_{ST}	Q_{ST} range	Nb‡	Trend	Nb‡
Dark respiration	Ecophysiology			0	Moderate	2
Leaf mass per area	Ecophysiology	0.022	0.000 – 0.044	2	Variable	6
Net assimilation	Ecophysiology	0.045	0.015 – 0.075	2	Variable	8
Nitrogen leaf content	Ecophysiology	0.042	0.000 – 0.083	2	Variable	6
Photosynthetic capacity	Ecophysiology	0.101	0.000 – 0.201	2	Variable	1
Stomatal conductance	Ecophysiology	0.061	0.000 – 0.150	4	Variable	4
Stomatal density	Ecophysiology	0.028	0.000 – 0.056	2	Low	5
Water use efficiency (A/gs)	Ecophysiology	0.075		1	Variable	7
Water use efficiency ($\delta^{13}C$)	Ecophysiology			0	Variable	6
Fall frost hardiness	Frost hardiness	0.581	0.030 – 0.890	9	High	10
Spring frost hardiness	Frost hardiness	0.126	0.000 – 0.352	4	Variable	3
Winter frost hardiness	Frost hardiness	0.170	0.000 – 0.291	3		0
Growth rate per day	Growth	0.284	0.050 – 0.710	8	Moderate	3
Height increment	Growth	0.324	0.040 – 0.880	36	High	33
Root allocation	Growth	0.340	0.251 – 0.430	2	Moderate	4
Bud flush	Phenology	0.249	0.000 – 0.700	24	Moderate	37
Bud set	Phenology	0.392	0.040 – 0.904	16	High	16
Germination	Phenology	0.521	0.200 – 0.940	6	High	3
Senescence	Phenology	0.108	0.080 – 0.180	5	Low	3

*Q_{ST} estimates corresponds to the levels of population differentiation measured either as the proportion of phenotypic variation between populations (V_{pop}) or as the proportion of additive genetic variance between populations (Q_{ST}) in the provenance trials (for more details see Table S1).

†Qualitative estimation of genetic differentiation between populations corresponds to studies where no Q_{ST} estimate was available, but significance of genetic differentiation was mentioned in the text.

‡Nb, number of studies used to calculate mean Q_{ST} and Q_{ST} range, and the trend of population differentiation.

Quantitative variation in continuous populations along environmental gradients

Species present in Central and Northern Europe generally have continuous distributions covering large areas encompassing much heterogeneity in abiotic and biotic environmental factors with large effective population sizes connected by extensive gene flow. If there is differential selection along environmental gradients, we expect to see patterns of clinal variation in traits (Barton, 1999). These patterns can be described by the slope of a regression along an environmental gradient. The proxies for environmental gradients most frequently used are latitude and altitude. For height increment, populations from warmer environments generally grew faster in the provenance trials (see Table S1), but quantitative estimates of the slopes were rarely available. Populations from cold environments cease growth earlier, as an adaptation to the approaching winter (see e.g., Savolainen *et al*., 2004). To compare slopes of clinal variation, we focused on the two phenological traits, the timing of bud flush and the timing of bud set, and compared altitudinal and latitudinal clines. To summarize data across species and environments, we considered that one degree of latitude corresponds approximately to a temperature change of 0.6 °C, and correspondingly, 100 m of altitude (Jump *et al*., 2009). We show examples of an altitudinal cline in bud flush in *Q. petraea* (Fig. 4a) and a latitudinal cline in bud set in *P. sylvestris* (Fig. 4b).

The results of the summary in Table 3 show that the two phenological traits differ in their patterns. For bud flush, both altitudinal and latitudinal clines showed similar shallow slopes, but the direction of adaptation varied greatly among species (Table 3a). For example, high altitude populations from the same transect flushed late in *Q. petraea* (Fig. 4a), whereas in *F. sylvatica* they flushed early (Vitasse *et al*., 2009). This could reflect different compromises in the adaptive tradeoff between maximizing the growing season length and exposing new leaves to late frosts. Bud flush is triggered by the accumulation of cold (or chilling) sums followed by heat (or forcing) sums above a threshold temperature sum. These genetically determined critical temperature sums and thresholds may vary among species, and to a lesser extent among populations of the same species (Hänninen & Tanino, 2011). Bud flush in late successional species is also more influenced by

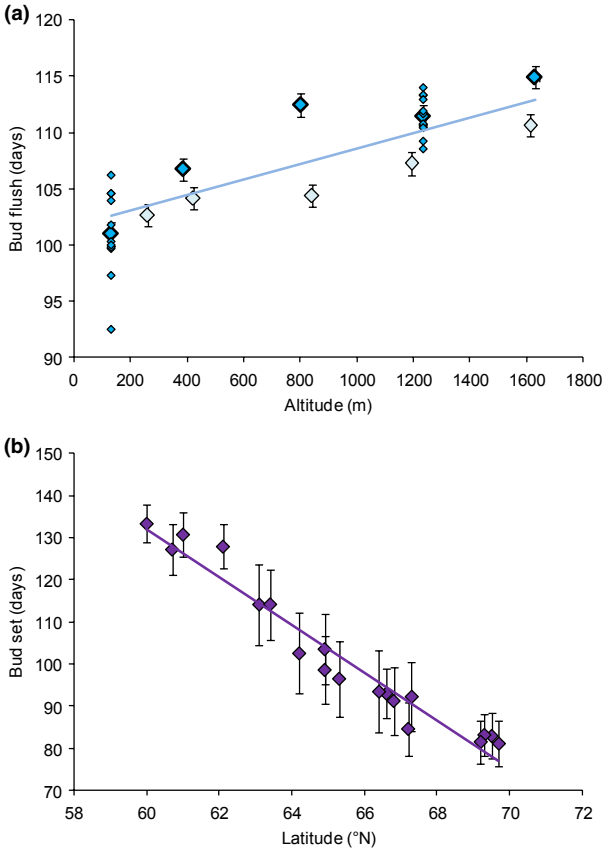

Fig. 4 Clines of phenological traits along environmental gradients. (a) Timing of bud flush along an altitudinal gradient in *Quercus petraea*, based on data from Alberto *et al.* (2011). The timing of bud flush is expressed as the number of days from 1st January to reach the fourth developmental stage of leaf unfolding. Means of populations (large diamonds) are plotted against the altitude of origin. Bars represent standard deviations of the populations. Means of maternal tree progenies (small diamonds) in populations located at 131 m and 1235 m of elevation illustrate high additive genetic variance within populations, slightly decreasing with increasing altitude. Dark colored points represent populations and maternal trees from Luz valley while light colored points represent populations from Ossau valley. (b) Timing of bud set along a latitudinal gradient in *P. sylvestris*, based on data from Mikola (1982). The timing of bud set is measured as the number of days from the day of sowing. Means of populations (large diamonds) are plotted against latitude of origin. Bars represent standard deviations of the populations.

photoperiod than in early successional species (Körner & Basler, 2010; Basler & Körner, 2012). Bud set showed steeper slopes for both gradients and in all species more northern or higher altitude populations had earlier bud set (Table 3b). These data suggest that differential selection on bud set is systematically stronger than on bud flush. Bud flush may display higher phenotypic plasticity as temperatures increase. In contrast, bud set is largely governed by photoperiods, and modulated by temperatures and drought, which results in a more predictable environmental signal from year to year and location to location (Böhlenius *et al.*, 2006). In a warming climate, spring phenology can likely respond and advance without much genetic change, as has already been seen in many species (Gienapp *et al.*, 2008), provided that the chilling requirement has been met. However, if chilling temperature requirements have not been met, in some cases bud flush may even be delayed (Hänninen & Tanino, 2011), as already seen recently in Tibet (Yu *et al.*, 2010). In the fall, a change in bud set date is more likely to require a genetic change in photoperiodic responses. Some studies suggest that the heritability of bud flush is higher than for bud set (Howe *et al.*, 2003), but estimates of the additive genetic component are rarely available in the literature. The latitudinal slopes were also much steeper than the altitudinal ones (Table 3b). Sundblad & Andersson (1995) have suggested that along the altitudinal gradients there may be more gene flow so populations do not become as differentiated. The simple calibration factors we used also may not capture all aspects of the environment.

In the large set of provenance trial studies, clinal variation along environmental gradients was very common. In the 112 studies, 309 analyses of clinal variation in different quantitative traits, 243 (78%) showed evidence of clinal variation with latitude, altitude, and sometimes longitude (Table S1).

Adaptation at range margins

An important hypothesis for species range limits is that gene flow constraints adaptation (Haldane, 1932; Mayr, 1963). Many models suggest that gene flow could limit adaptation, and even more so with asymmetrical gene flow toward small peripheral populations (see Lenormand, 2002 for review). In a model of species range involving local adaptation, a strong coupling between fitness and population size favors a feedback effect (a 'migration meltdown') that acts to stabilize a range margin, as exemplified in the now well-known Kirkpatrick & Barton (1997) model. However, there is limited evidence to evaluate this model, and some issues that complicate the predictions. Some models assume that genetic variance is fixed (Pease *et al.*, 1989; Kirkpatrick & Barton, 1997), while gene flow may also increase genetic variance and the response to selection (Barton, 2001; Polechova *et al.*, 2009). Evidence in *P. contorta* suggests that gene flow between populations inhabiting heterogeneous environments can increase levels of standing genetic variation (Yeaman & Jarvis, 2006), but it remains unclear whether this effect would be important in other species. Genetic drift can also

Table 3 Slopes of the linear regressions of (a) bud flush and (b) bud set along altitudinal, and latitudinal gradients

Gradient	Species	Pop *	Cline	Slope	Reference
(a)					
Altitudinal	*Abies amabilis*	5	High early	−1.18	Worrall (1983)
	Abies lasiocarpa	2	High early	−0.83	Worrall (1983)
	Fagus sylvatica	9	High early	−0.43	Vitasse *et al.* (2009)
	Fagus sylvatica	158	High early	−0.17	Von Wuehlisch *et al.* (1995)
	Pseudotsuga menziesii	7	High early	−4.38	Acevedo-Rodriguez *et al.* (2006)
	Pseudotsuga menziesii	18	No cline	0.00	Rehfeldt (1978)
	Picea abies	23	No cline	−0.22	Chmura (2006)
	Picea abies	8	No cline	−0.03	Skroppa & Magnussen (1993)
	Abies alba	6	No cline	−0.20	Vitasse *et al.* (2009)
	Acer pseudoplatanus	7	No cline	−0.20	Vitasse *et al.* (2009)
	Fraxinus excelsior	9	Low early	1.90	Vitasse *et al.* (2009)
	Larix occidentalis	82	Low early	0.23	Rehfeldt (1982)
	Quercus petraea	10	Low early	1.15	Alberto *et al.* (2011)
	Quercus rubra	4	Low early	1.93	Mc Gee (1973)
	Total			−0.17	
Latitudinal	*Picea abies*	9	North early	−2.08	Sogaard *et al.* (2008)
	Picea glauca	63	No cline	0.43	Li *et al.* (1997a)
	Picea sitchensis	17	No cline	−0.08	Mimura & Aitken (2007)
	Pinus strobus	66	No cline	−0.83	Li *et al.* (1997b)
	Populus balsamifera	4	No cline	0.10	Farmer (1993)
	Fagus sylvatica	158	South early	0.20	Von Wuehlisch *et al.* (1995)
	Quercus petraea	16	South early	4.17	Deans & Harvey (1996)
	Tsuga heterophylla	8	South early	2.17	Hannerz *et al.* (1999)
	Total			0.51	
(b)					
Altitudinal	*Abies lasiocarpa*	5	High early	−3.33	Green (2005)
	Larix occidentalis	82	High early	−1.28	Rehfeldt (1982)
	Picea abies	23	High early	−9.07	Chmura (2006)
	Picea abies	8	High early	−2.63	Skroppa & Magnussen (1993)
	Picea glauca	5	High early	−1.00	Green (2005)
	Picea contorta	5	High early	−1.67	Green (2005)
	Picea contorta	173	High early	−0.22	Rehfeldt (1988)
	Pseudotsuga menziesii	7	No cline	0.37	Acevedo-Rodriguez *et al.* (2006)
	Total			−2.35	
Latitudinal	*Betula pendula*	7	North early	−4.63	Viherä-Aarnio *et al.* (2005)
	Picea glauca	63	North early	−3.83	Li *et al.* (1997a)
	Picea sitchensis	17	North early	−4.90	Mimura & Aitken (2007)
	Picea strobus	66	North early	−3.33	Li *et al.* (1997b)
	Pinus sylvestris	4	North early	−5.00	Hurme *et al.* (1997)
	Pinus sylvestris	4	North early	−2.35	Notivol *et al.* (2007)
	Pinus sylvestris	2	North early	−6.83	Savolainen *et al.* (2004)
	Populus balsamifera	4	North early	−5.00	Farmer (1993)
	Populus tremula	12	North early	−8.33	Luquez *et al.* (2008)
	Total			−4.91	

Slopes of linear regressions are given for each study and expressed as days/°C (for details about the calculation see in the text and for references see Table S1). No cline indicates a nonsignificant regression.
*Number of populations in the provenance trial.

reduce genetic variance and thus adaptation in peripheral populations (Alleaume-Benharira *et al.*, 2006; Polechova *et al.*, 2009; Bridle *et al.*, 2010), but gene flow may replenish genetic variation. Gene flow may even introduce better adapted genes than local ones, especially in a changing climate (Alleaume-Benharira *et al.*, 2006).

Some environments, in particular some polar or arid range margins, are intrinsically less favorable than

others, and would sustain only very low population sizes even after a very long history of adaptation. Mainland-island models of local adaptation implicitly address this issue with population sizes, but spatially continuous models are still more informative. In particular, Nagylaki (1975) showed that extrinsic asymmetries in habitat quality strongly modified or could even compensate for asymmetries in selection across habitats. In other words, alleles showing a local advantage can be maintained despite having considerable antagonistic effects in other habitats, provided that the local habitat is of better quality (Nagylaki, 1978). Incorporating differences in carrying capacity in quantitative models could critically affect the potential for population adaptation (Bridle *et al*., 2010).

The leading and the trailing edge of migrating tree distributions face quite different challenges due to the warming climate (Hampe & Petit, 2005). At the southern range edge (in northern hemisphere), the distributions are likely already limited by high temperatures or drought conditions, and associated biotic and abiotic stresses, whereas at the northern margin, many populations have been limited by the cold temperatures (Rehfeldt *et al*., 2002). For the southern margin, at least at low altitudes, the environment is clearly deteriorating. The risk of extinctions will come from the interplay of multiple factors. In particular, the reduction of water availability and a longer growing season with excessively warm temperatures (IPCC, 2007) could lead to massive diebacks of trees due to drought stress or carbon starvation (Sabate *et al*., 2002; Bréda *et al*., 2006) higher mortality due to reduced defense of trees against insects (Rouault *et al*., 2006), and more frequent forest fires (Mouillot & Field, 2005). Increased mortality due to heat and drought stress has already been observed in many locations globally (Allen *et al*., 2010). The impact of environmental change will be higher in small populations due to high demographic or environmental stochasticity (Hampe & Jump, 2011).

At the southern margin, there are no populations further south contributing genes conferring necessary adaptation, but gene flow from similar environments could still increase the variance within populations (Barton, 2001). Experimental evidence of gene flow from like populations increasing fitness at warm range-edges exists for some plant species (e.g., *Mimulus* species, Sexton *et al*., 2011), and long distance dispersal can be important in fragmented landscapes (Klein *et al*., 2006; Fayard *et al*., 2009; Kremer *et al*., 2012).

Until now, the severe climatic conditions at boreal northern range margins have constrained growth, pollen production, seed maturation and dispersal (Sarvas, 1962; Savolainen, 1996), as well as survival (Persson, 1998), and have limited expansion to the north (Chuine & Beaubien, 2001; Morin *et al*., 2007). In the northernmost areas, temperatures are expected to increase by about 4 °C (Kattsov & Källen, 2005). Ecophysiologists have used the immediate plastic responses of trees to increased temperature to predict changes in species composition (Kellomäki & Kolström, 1992; Kellomäki *et al*., 2001). However, these predictions have not explicitly taken into account the possibilities of genetic response (Davis & Shaw, 2001; O'Neill *et al*., 2008). The warming in the north will improve survival, increase growth (Rehfeldt *et al*., 2002; Reich & Oleksyn, 2008), increase sexual reproduction (Andalo *et al*., 2005), and increase pollen production (Savolainen *et al*., 2011). Based on modeling studies, pollen and seed are predicted to be dispersed further than before (Kuparinen *et al*., 2009, 2010). Production of mature filled seed will likely increase many fold (Kellomäki *et al*., 1997) and the warmer air and soil may result in improved germination and establishment. Northern range margin populations are already colonizing more northern and higher altitude areas (Kullman, 2002; Juntunen *et al*., 2006; Chen *et al*., 2011). The increased survival rates of existing, established trees may, however, reduce establishment opportunities for better adapted genotypes generated by gene flow and local selection (Kuparinen *et al*., 2010).

At altitudinal range limits, adaptation could be facilitated by the short geographical distance between populations, associated with low climate change velocity (Loarie *et al*., 2009). Gene flow from populations at low altitudes could help the populations at higher altitudes to adapt, as has already been observed, e.g., in oak phenological shifts *in situ* (Alberto *et al*., 2010). Both colonization of new areas at higher altitudes, if available, and local selection aided by gene flow may contribute to adaptation, as many altitudinal gradients show clinal genetic differentiation (see above).

Conclusions and suggestions for future research

Forest trees are exceptionally well characterized with respect to adaptive quantitative variation, and with respect to responses to different climatic variables. The existing set of provenance trials can be used to extract even more information, for instance on the level of local adaptation, or even on the strength of selection, when the datasets are further analyzed. Long-term estimates of the strength of selection, in particular in natural conditions, would be very valuable for providing parameter range estimates for the prediction models. New reciprocal transplant experiments are needed for commercially less-important species, which may be most threatened, but which are under-represented in existing provenance trials. Furthermore, the present provenance

trials ignore the likely important early fitness components of germination and establishment – these components also need to be studied (as is being done in herbaceous plants, Huang *et al.*, 2010; Stanton-Geddes *et al.*, 2012). The new experiments should include field sites at and beyond existing range margins. Experiments in controlled growth chambers can also help identify those abiotic aspects of temperature and moisture regimes to which populations are locally adapted, and to generate climatic regimes analogous to those predicted for the coming century.

The role of plasticity and its interaction with natural selection is just starting to be explored in the climate change context (Chevin *et al.*, 2010) – provenance trials can also provide more information on these aspects. The extent and significance of adaptive phenotypic plasticity is still debated (Valladares *et al.*, 2007), and experimental studies on range margins are still few (Angert, 2009; Stanton-Geddes *et al.*, 2012). Wang *et al.* (2010) universal response function approach could be used as a mechanistic model to predict population responses.

Commercially less-important species are poorly represented in previously established common gardens, whether they have narrow or wide distributions. The species with smaller ranges are especially vulnerable. Are these species locally adapted to climate? Do these species have limited adaptive potential due to their historically small effective population sizes? While many important boreal and temperate species in the northern hemisphere (and some eucalypts or tropical acacias) have been extensively studied, there is much less information on subtropical or tropical species, which are outside the scope of this review. These species will also be affected by the changing climate, through both abiotic and many complex biotic factors.

Most of the studies on quantitative traits have been conducted in spaced, reasonably well-tended provenance trial experiments. Within or between-species interactions, such as competition or diseases have largely been ignored. Many between-species interactions depend on the synchronous timing of events in the different species. Even before any evolutionary responses, phenotypic responses will affect such biotic interactions (Gilman *et al.*, 2010; Yang & Rudolf, 2010). During the past decade, phenological shifts have been already observed between trees and pest populations (Visser & Holleman, 2001; van Asch *et al.*, 2007; Desprez-Loustau *et al.*, 2010; Gordo & Sanz, 2010).

Much of the information on northern trees has been accumulated through decades of field experiments. Combining genomic tools with results from the quantitative and ecological approaches can significantly aid in predicting selection responses to climate change (for crop plants, see Morrell *et al.*, 2012). Genomic studies will allow researchers to examine the geographical pattern of alleles conferring adaptation – are they globally occurring alleles with varying frequencies or very localized ones? Coupled with studies at the quantitative trait level, genomic surveys will aid in assessing the prospects for adaptation at the level of the population. Furthermore, the contribution of epigenetic and maternal effects to phenotypic variation needs to be assessed.

This review has pointed to several areas where management and breeding can possibly contribute to maintenance of populations. An evaluation of such options is beyond the scope of this review (see e.g., McLachlan *et al.*, 2007; Aitken & Whitlock, 2013).

In conclusion, the concordant patterns of current local adaptation among tree populations in numerous northern species in Europe and North America show that selection has repeatedly established such patterns. Populations facing the largest evolutionary challenges are at the range margins, but the northern and southern margins face quite different limitations. Better data and models are thus necessary to evaluate accurately whether natural selection, and migration, may again allow evolutionary responses for populations to sufficiently match their new climates.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Description of the provenance trial studies. [a]Number of populations sampled. [b]Mean number of individuals sampled within populations. Bulk indicates that mixes of seeds without knowledge of genetic identity were collected in the populations. [c]Number of provenance trials in the study. [d]Amplitude of the environmental gradient is given in meters of elevation above sea level for altitudinal gradients and in decimal degrees for latitudinal and longitudinal gradients. When values appear in italic the approximate amplitude is given. [e]The levels of population differentiation in the provenance trials were measured either as the proportion of the total phenotypic variation which is between populations (V_{pop}) or as the proportion of the additive genetic variance which is between populations (Q_{ST}), which appear in bold. For simplicity, we used Q_{ST} for both parameters in the text. No differentiation indicates that population differentiation was not significant. [f]Slopes were calculated for bud flush and bud set only because they were the only traits with enough data to make comparisons between traits and between environmental gradients. No cline indicates that clinal variation was not significant along the environmental gradient considered. *n.i.* means that the information was not indicated.
Table S2. Nucleotide diversity estimates per gene. [a]π_{total}: Nucleotide diversity per gene calculated for silent and replacement sites. [b]π_{silent}: Nucleotide diversity per gene calculated for silent sites only, which correspond to synonymous sites and sites located in noncoding regions (introns or 3′- and 5′-UTR) *n.i.* means that the value was not indicated. Cells highlighted in gray indicate studies for which average nucleotide diversity were calculated for a set of genes or fragments of genes.
Table S3. SNP effect sizes in association studies. [a]R^2 marker: Percentage of phenotypic variance explained by the marker.