SYNTHESIS

Adaptation, migration or extirpation: climate change outcomes for tree populations

Sally N. Aitken,[1] Sam Yeaman,[2] Jason A. Holliday,[1] Tongli Wang,[1] and Sierra Curtis-McLane[1]

1 Centre for Forest Conservation Genetics and Department of Forest Sciences, University of British Columbia, Vancouver, British Columbia, Canada

2 Department of Zoology, University of British Columbia, Vancouver, British Columbia, Canada

Abstract

Species distribution models predict a wholesale redistribution of trees in the next century, yet migratory responses necessary to spatially track climates far exceed maximum post-glacial rates. The extent to which populations will adapt will depend upon phenotypic variation, strength of selection, fecundity, interspecific competition, and biotic interactions. Populations of temperate and boreal trees show moderate to strong clines in phenology and growth along temperature gradients, indicating substantial local adaptation. Traits involved in local adaptation appear to be the product of small effects of many genes, and the resulting genotypic redundancy combined with high fecundity may facilitate rapid local adaptation despite high gene flow. Gene flow with pre-adapted alleles from warmer climates may promote adaptation and migration at the leading edge, while populations at the rear will likely face extirpation. Widespread species with large populations and high fecundity are likely to persist and adapt, but will likely suffer adaptational lag for a few generations. As all tree species will be suffering lags, interspecific competition may weaken, facilitating persistence under suboptimal conditions. Species with small populations, fragmented ranges, low fecundity, or suffering declines due to introduced insects or diseases should be candidates for facilitated migration.

Introduction

With evidence of global warming and biological responses to that warming accumulating rapidly (Parmesan 2006; IPCC 2007a,b), considerable attention has turned to predicting the fate of trees and forests. Nearly half of the earth's terrestrial surface is covered by forests (Melillo et al. 1993), and many tree species play foundation or keystone roles, providing habitat, food or mutualisms with many animals, fungi, micro-organisms, and other plants in addition to other ecosystem services and resources for human use. Forests also contain around three quarters of the earth's terrestrial biomass and thus are tightly linked with atmospheric carbon budgets.

There are three possible fates for forest tree populations in a rapidly changing environment: persistence through migration to track ecological niches spatially; persistence through adaptation to new conditions in current loca-

tions; and extirpation. Climate-based species distribution models predict the necessity of wholesale redistributions of tree species over the next century (Malcolm et al. 2002), usually without any intrinsic consideration of the biological capacity of populations to do so, or recognition of the extent and role of local adaptation. The past glacial and postglacial migrations of these taxa, inferred from fossil pollen records and genetic data, suggest a robust capacity for range shifts (Davis and Shaw 2001, Hamrick, 2004). Anecdotal evidence of the capacity of forest trees to adapt rapidly to new environments includes the development of steep genetic clines during post-glacial migration (Davis and Shaw 2001), and the existence of locally adapted land races of introduced tree species within one or two generations of introduction (Saxe et al. 2001). A rich history of common garden experiments has revealed high among-population levels of genetic variation for quantitative traits related to adaptation, geographic

structuring of that variation along climatic gradients, and genotype-by-environment interaction, providing strong evidence of local adaptation of populations to climate (Howe et al. 2003; Savolainen et al. 2007). Will natural populations of temperate and boreal forest trees be able to adapt or migrate sufficiently rapidly to keep pace with rapid climate change? Will their moderate to high average levels of genetic diversity be sufficient to allow for rapid adaptation despite long generations? What light can the wealth of existing field common garden experiments or rapidly growing knowledge on the genomic architecture of adaptation to climate shed on this capacity? Answering these questions will require the application of knowledge from disparate fields within genetics and ecology.

Predicting the fate of forest tree populations in a rapidly changing climate requires the integration of knowledge across biological scales from individual genes to ecosystems (Namkoong 2001), across spatial scales from seed and pollen dispersal distances to the breadth of species ranges, and across temporal scales from the phenology of annual developmental cycle traits to glacial and interglacial cycles. Here we review the wealth of theoretical and empirical literature pertaining to this question to evaluate how climate-change outcomes will be affected by a range of factors. First we review the available predictive tools to address this question, focusing on species distribution models, potential for and limitations to migration, and quantitative genetic models addressing constraints to adaptation. Then we summarize available data on local adaptation of forest trees from seedling common-garden experiments, provenance trials, hybridization, and genomics that inform these predictions. Finally, by integrating knowledge across these topics, we identify areas for research, forest management, and operational conservation that might improve predictions of responses to climate change, increase the probability of maintaining sufficient populations of forest trees in protected areas, improve seed-source selection for reforestation, facilitate adaptive responses of natural populations, or accelerate range shifts through facilitated migration.

Constraints on migration

Estimates of past rates of species migration from paleobotanical and genetic evidence are frequently used in order to inform predictions of contemporary migration potential. Studies of range shifts over the last 25 000 years show that species ranges have migrated in close correlation with global climatic cycles. Pollen records, and more recently chloroplast DNA (cpDNA) analyses, have been used to recreate the latitudinal and altitudinal migrations of trees outward from glacial ranges and refuges (Davis and Shaw 2001; Petit et al. 2004). Initial analyses using

pollen records showed post-glacial migration rates of up to 200 m per year, but cpDNA evidence of low-density refugial populations of angiosperm trees much farther north than previously thought has caused these estimates to be revised (McLachlan and Clark 2004; McLachlan et al. 2007). With seeds spreading both from the northern edge of the continuous species range and from previously unidentified, disjunct refugial populations, actual migration rate estimates have been revised to less than 100 m per year.

Rare long-distance seed dispersal events have likely played a crucial role in increasing effective migration rates relative to the effects of average seed dispersal distances, but such events are hard to quantify or model (Clark et al. 2003; Petit et al. 2004). Once small founder populations are established, the longevity and phenotypic plasticity of most tree species may allow for the persistence of these nucleated populations until sufficient genetic variation is input via long-distance pollen flow for the establishment of populations sufficiently large and genetically variable to be viable and become locally adapted (Petit et al. 2003; Mimura and Aitken 2007a, 2007b). This suggests it may be worthwhile to initiate new populations through facilitated migration as new habitat becomes available (McLachlan et al. 2007), and that these populations do not necessarily need to be large. In some cases at high-latitude or high-elevation tree limits, advanced colonization may have already created islands of stunted "krumholtz" individuals that can develop into erect tree form and become reproductively capable with climate warming, e.g., black spruce (*Picea mariana*) (Laberge et al. 2000; Gamache 2005). Such colonies that have historically tolerated harsh conditions may be difficult to separate from those established through recent long-distance colonization events, but either may provide a nucleus for range expansion via seed dispersal as climates become more hospitable.

Whether range expansions associated with climate change are yet occurring is a research topic receiving considerable empirical attention, with mixed results. One of the best places to seek potential changes in species ranges is at altitudinal and latitudinal treelines, where climate is expected to be the primary limiting factor (Parmesan 2006). On a relatively local scale, some researchers have seen advancements in elevation, as well as increasing height and diameter growth and density of tree species (Danby and Hik 2007a, 2007b; Millar et al. 2004). However, other studies have found no evidence of significant expansions. For example, an analysis of vegetation in northern Canada using infrared satellite imaging showed little to no forest expansion over the last 25 years, despite regional warming of 0.6°C (Masek 2001). Hypothesized reasons for the slow movement include lack of seed

sources, barriers to seed dispersal, and poor soil conditions.

A growing array of correlative species distribution models (SDMs) is being used in combination with global circulation models (GCMs) to predict climate change-driven habitat shifts for a wide variety of taxa. The premise behind these models is that environmental conditions are the primary determinant of realized species niches, and that the future preferred range distribution of species can be predicted by transferring the environmental parameters associated with the present distribution onto maps representing future climate scenarios (Pearson and Dawson 2003). Most of these models rely primarily on presence/absence or presence only data for species distributions, and temperature and precipitation interpolations from existing weather station data adjusted using digital elevation models for environmental conditions, but levels of sophistication are increasing rapidly as the field matures (Guisan et al. 2006). Mechanistic models that rely on physiological data such as flowering phenology to predict the range of environmental conditions in which a species can exist are also being developed (Chuine et al. 2000); however, these models require a sophisticated understanding of the physiological characteristics of the species in question, and as such very few have been published to date. Findings of relatively slow tree migration rates in response to historical changes in climate (potentially < 100 m per year) are unfortunate in light of model predictions of how fast tree species will need to migrate to track current climates under climate change scenarios. Tests of 14 combinations of GCMs and global SDMs show up to 100% of the models predicting migration rates of 1000 m per year or higher to be necessary to track habitat under $2\times$ CO_2 climate forcing (Malcolm et al. 2002). High-latitude biomes in particular are projected to necessitate unprecedented rapidity of migration for trees due to the more extreme warming that is occurring towards the poles (IPCC 2001). However, model predictions for the migration potential of five tree species in the eastern United States under climate change scenarios show very low probabilities of dispersal beyond 10–20 km from current species boundaries by 2100 (an average of 100–200 m per year) (Iverson et al. 2004). Species with low abundances at the range margin have low, if not null, migration potential projections, irrespective of forest density in the area into which the species is projected to migrate.

Early generations of SDMs have been outperformed by novel methods in recent years, including machine-learning methods and community models (Elith et al. 2006). Few methods to date have the capacity to account for non-climatic factors that determine the difference between the fundamental and realized niche of a species, including biotic interactions; life history characteristics such as age to

sexual maturity, fecundity, and seed dispersal; and degree of range fragmentation (Pearson and Dawson 2003; Guisan and Thuiller 2005). However, these non-climatic factors can have a major impact on the migratory capacity of a species, thus future distributions of appropriate habitat and realized species distributions may differ considerably. In addition, novel multivariate climates may occur in the future, for which species presence or absence cannot be predicted from current distributions.

From a population genetics and life history (e.g., reproductive) trait perspective, there are many shortcomings to most of the SDMs currently available for predicting species migration rates and future distributions. They do not account for population differences within the species range including differential adaptation of populations to recent local climates, central-peripheral structure in population density, genetic diversity levels and degree of local adaptation (Mimura and Aitken 2007a), differences between leading and trailing edge populations (Hampe and Petit 2005), or varying levels of gene flow received by populations in different positions relative to the species range (Mimura and Aitken 2007b). Given often strong population differentiation for traits relating to adaptation to local climate (Howe et al. 2003; Savolainen et al. 2007), the size of climatic envelopes of individual populations is likely much smaller in most species than the climate envelope of the species as a whole, as inferred from species distributions and climate modeling. Chuine et al. (2000) found genetic variation among populations did not have to be invoked to produce accurate SDMs for five of six European tree species using a mechanistic approach driven by phenology; however, the model utilized timing of flowering which is likely correlated with timing of vegetative bud break and growth initiation, and may vary less genetically among populations than bud set and growth cessation (Howe et al. 2003).

Populations at the species margin are often under greater abiotic stress or more intense interspecific competition at the limits of their realized niches than in the centre, with lower relative fecundity and lower local population densities (Case and Taper 2000). These sink populations tend to have higher mortality than local recruitment rates, and are primarily sustained by the influx of seeds and pollen from source populations (Watkinson and Sutherland 1995). Although stunted krummholtz trees at treeline have been found to display fast phenotypic responses to positive environmental changes (Gamache and Payette 2004), in general, sink populations should be excluded from estimates in order to more accurately model potential dispersal and migration. Competition from neighboring species can further restrict the ability of species to track a moving climate (Case and Taper 2000; discussed below), while any

decrease in fecundity under novel non-optimum conditions can further limit the pool of propagules and the effective distance of dispersal. For example, lodgepole pine (*Pinus contorta*) populations transferred south 5–10° latitude into a common garden experiment produced less than half as many male and female strobili, on average, as populations originating from more southerly environments (Hannerz et al. 2001). This level of ecological detail is unavailable for many species, possibly leading to overestimations of the speed at which species may migrate.

Despite their potential shortcomings, SDMs are one of the best tools available for predicting potential global impacts of climate change, extinction rates, and important geographic areas for conservation of tree species. It has been argued that the relatively slow generation lengths, and potentially infrequent opportunities for mutations, may make future species range models more accurate for long-lived species such as trees than for annuals (Pearson and Dawson 2003). A global study that analyzed potential changes in the extents of climate envelopes for plant species on a regional scale found 3% to 38% committed to extinction by 2050 under mid-range climate change scenarios (Thomas et al. 2004). Similarly, 6 to 11% of European plant species are projected to disappear from existing conservation areas by the mid-21st century due to climate change (Araujo et al. 2004). A. Hamann and S.N. Aitken (unpublished manuscript) used SDMs (Hamann and Wang 2006) to predict persistence of 49 indigenous tree species in 906 conservation areas in British Columbia under scenarios that allowed adaptation to conditions found elsewhere in the species range, migration to other locations within conservation areas, both adaptation and migration, or neither (Fig. 1). They found under the scenario allowing neither adaptation nor migration, over 60% of tree species currently well represented in existing protected areas are predicted to become inadequately conserved in these areas on average (below the conservation targets set in Hamann et al. 2005). Migration would reduce this loss to approximately 50%, adaptation to just over 20%, and adaptation and migration together would maintain all but 15% of species with adequate populations for conservation based on predicted climates for 2085. Large, topographically variable protected areas are predicted to maintain more species adequately than small or flat reserves under scenarios allowing migration within reserves. Populations may be able to respond to modest rates of climate change, particularly in mountainous areas, by migrating short distances among microsites, slope aspects, or elevations, but predicted rates of climate change will likely exceed the scale of local environmental heterogeneity in the longer term in many cases.
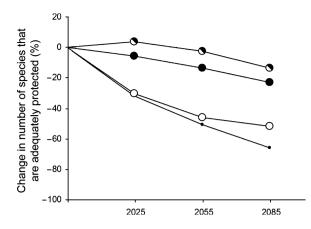

Figure 1 Change in the number of tree species predicted to be adequately conserved (cumulative cover of 10 ha, Hamann and Wang 2006) into the future, under the assumption that species are capable to adapt to changed climate, (●), migrate to suitable habitat within a reserve, (○), both, migrate and adapt, or neither (•). The analysis is based on bioclimatic envelope models for 49 tree species and 906 protected areas in British Columbia (Hamann and Wang 2006; A. Hamann and S.N. Aitken, unpublished manuscript.).

Constraints on adaptation: keeping pace with change

In an early attempt to formulate quantitative genetic predictions about extinction risk due to adaptive constraints, Lynch and Lande (1993) examined a model where fitness is determined by a single quantitative trait and the population must adapt to a continuously changing optimum to persist. They found that populations can survive by maintaining a steady rate of adaptation as long as the rate of change in optimum is below a critical threshold, which is determined by the standing genetic variation, individual fecundity, effective population size, environmental stochasticity, and strength of selection. Above this threshold, the rate of adaptation fails to keep pace with the rate of change in the optimum, and absolute fitness decreases with increasing adaptational lag, eventually causing extinction. By assuming large effective population size and no stochasticity, Lynch and Lande presented a simplified equation for the threshold rate of change k_c (in units of phenotypic standard deviations, σ_p) that depends only on the strength of stabilizing selection (σ_w^2) and maximum rate of population increase (r_{max}):

$$\frac{k_c}{\sigma_p} = \sigma_p \sqrt{\frac{2r_{max}}{\sigma_w^2}} \qquad (1)$$

This equation is often taken to suggest that most populations can only tolerate very gradual changes in optimum (~10% σ_p) (Lynch and Lande 1993; Bürger and Lynch 1995), but this assumes a very low fecundity ($r_{max} = 0.5$).

For many forest trees, fecundity is several orders of magnitude higher; if an average tree produces 10 000 seeds, its r_{max} = 9.2, and populations could potentially sustain steady rates of adaptation when the optimum changes as much as ∼0.42 σ_p per generation, following these assumptions. It is important to note that equation (1) predicts the maximum possible rate of adaptation, but that low heritability, pleiotropy, environmental stochasticity around the changing optimum, or drift could reduce this prediction considerably (limitations of these types of models are reviewed more thoroughly in Bürger and Krall (2004)). This model exhibits unrealistic behavior under very strong and very weak selection and does not account for density-dependent changes in the strength of selection that would facilitate survival at low densities (in the absence of other competitors).

Where the Lynch and Lande model assumes a population will survive as long as it can keep pace with the changing optimum, Bürger and Lynch (1995) examined how the fitness loss due to the lag in adaptation affects population demography, further increasing the potential for extinction. Their simulations include demographic fluctuations due to viability selection and the effects of this stochasticity on genetic variation and adaptive potential. They found that extinction risk is greatly increased when effective population sizes are small (N_e < 100; their Fig. 2A) due to the combined effects of genetic drift and demographic stochasticity. They conclude the critical threshold for many species may be as small as 0.01 σ_p per generation, but this prediction seems to be directed more towards species with small population size and low fecundity. Because drift does not seem to significantly affect genetic variance when N_e > ∼1000 (Johnson and Barton 2005), these synergistic stresses are likely less relevant for most temperate forest tree species, which typically have larger population sizes than for many other life forms. Gomulkiewicz and Holt (1995) have developed similar models that apply to population persistence in the face of a single dramatic shift in the optimum phenotype, and have made qualitatively similar conclusions.

The models discussed above generally focus on directional changes towards a new phenotypic optimum for a single trait under selection; however, overall fitness and local adaptation are functions of multiple traits. These traits may be correlated, either due to pleiotropy or to linkage disequilibrium, and if genetic correlations are unfavourable, meaning increased fitness in one trait leads to a correlated response decreasing fitness in another, then rates of evolution can be slowed (Etterson and Shaw 2001). If genetic correlations are due to linkage disequilibrium, these will break down over time through recombination and phenotypes will occur that combine favourable traits. However, if they are due to pleiotropy, they may narrow the range of possible phenotypic combinations markedly. Genetic correlations limit the ability of populations to respond to selection in any direction that is antagonistic to the genetic line of least resistance (G_{max}) (Lande 1979). Hellmann and Pineda-Krch (2007) simulated the adaptational lag in a changing climate when fitness is determined by two pleiotropically linked traits and confirmed that genetic correlations increase the lag and decrease the amount of environmental change a population could tolerate, especially when the change in environment runs against the genetic line-of-least-resistance (Bürger and Krall 2004).

As climates change, interspecific competition dynamics among tree species will also change as all species may be suffering substantial adaptational lag, and if growth rates slow, so will competition for light. Thus the strength of
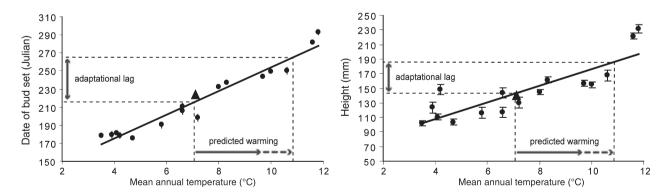

Figure 2 Genetic clines along gradient in mean annual temperature for mean Julian date of bud set (r^2 = 0.94) and for total height (r^2 = 0.72) for 17 populations of *Picea sitchensis* from across the species range (data from Mimura and Aitken 2007a). The horizontal arrow illustrates the range of magnitude of warming predicted from global circulation models from 1961 to 1990 climate normals to the 2080s for the central population at Prince Rupert, BC population (indicated with triangle; current mean annual temperature 7.1°C, predicted for 2080s CGCM A2X 10.8°C; CGCM B2X 9.8°C; Hadley GCM A2X 10.5°C, estimated using Climate BC (Wang et al. 2006a)).

selection (σ_w^2) may weaken, allowing populations to tolerate a more rapid change than predicted by the above models, potentially allowing population persistence in suboptimal conditions. The ability of trees to persist well outside their realized niche under reduced competition is evidenced by many trees in arboreta and botanical gardens. Species likely to both adapt and migrate more quickly will be those that have high fecundity, small seeds capable of long dispersal, and short generation lengths. These characteristics describe many pioneer tree species, and their prevalence will depend on the generation of appropriate habitat for colonization through disturbance agents such as fire, wind, and insect or disease outbreaks, and the spatial distribution of such disturbances.

Interspecific interactions with insects and diseases are also likely to change. For example, the mountain pine beetle (*Dendroctonus ponderosae*) has caused extensive mortality in many western North American forests of lodgepole pine, ponderosa pine (*Pinus ponderosa*), and whitebark pine (*Pinus albicaulis*) in the past decade. One of several drivers of this unprecedented epidemic is thought to be the lack of extreme low winter temperatures capable of reducing populations of this insect (Hicke et al. 2006). In British Columbia, an endemic but previously low-impact disease caused by the fungus *Dothistroma* is now causing substantial damage to lodgepole pine in a region experiencing warmer and wetter summer conditions over the past decade compared to the previous century (Woods et al. 2005). Such biotic stresses are likely to be much more severe than maladaptation caused by a warming climate (except where drought is a problem); unfortunately, our means to predict their impacts are much more limited. With much shorter generation lengths, insects and diseases may be able to adapt to new climatic conditions more rapidly than trees. Tree populations may be able to rebound following insect or disease epidemics from seed banks or pockets of trees escaping infection, and suffer little loss of genetic variation if effective population sizes remain large. For example, seeds in the closed serotinous cones of lodgepole pine can remain viable for decades until high temperatures allows cones scales to flex, releasing seeds.

Another general prediction of climate models is an increase in the occurrence of extreme weather events and increased fluctuations in climate (IPCC 2007b). Even if climate means remain constant, increasing amplitude of fluctuations is expected to decrease the mean fitness of populations due an increase in the average deviation from the optimum; this effect is compounded by the fitness costs imposed by adaptation lags when mean climatic conditions are also changing (Lynch and Lande 1993; Bürger and Lynch 1995). An increase in mean alone will increase the frequency of extreme events in that direction

over injurious yet relatively unknown thresholds. Such extreme events may have played a major role in selection in the past but are relatively unstudied (Gutschick and BassiriRad 2003).

Although the above models have sometimes been used to formulate quantitative estimates of extinction risk, these predictions have a very high degree of uncertainty due to the somewhat unrealistic assumptions of the models and the limited data available for parameters of importance. On the one hand, these models (especially equation 1) can overestimate the critical rate of environmental change if pleiotropy, population size, demography, or environmental stochasticity, or interspecific competition somehow compromise adaptation. On the other hand, they can underestimate the ability of a population to survive if density-dependent factors described above weaken the effective strength of selection, or if non-additive genetic effects make substantial contributions to the standing genetic variation. As such, these models are more useful as heuristic devices to compare relative risk among species and assign priority for future study based on more direct approaches (e.g., common garden studies). Generally speaking, they show that species with small population sizes, low fecundity, low genetic variance, and long generation times will be least able to adapt to changes and are therefore most at risk of extinction.

Constraints on adaptation: gene flow

A common observation in nature is a gradual decrease in population density from the center towards the periphery of a species range. Changes in density can affect evolution at the meta-population level, which can have significant consequences for how populations adapt to environmental change. A robust finding from models examining the effect of this pattern is that the differences in density cause asymmetries in migration, with a net flow of alleles from the center to the periphery of the range. Garcia-Ramos and Kirkpatrick (1997) found that such gene flow inhibits local adaptation in the periphery, reducing mean fitness. This finding was echoed by Kirkpatrick and Barton (1997), who further posited that this effect could be a major factor determining geographical range limits. Similar results have been found by Butlin et al. (2003) and Alleaume-Benharira et al. (2006a, 2006b), who used stochastic simulations to examine the added effect of drift in central-peripheral models. A key difference between earlier deterministic models and more recent stochastic simulations is in the effect of gene flow. When drift is included in stochastic simulations, gene flow can facilitate local adaptation in peripheral populations by replenishing genetic variation lost to drift,

although drift effects are weak in most tree populations due to large effective population size. Two other studies have examined how change in the local optimum would affect the position of species range limits along an environmental gradient. An early model by Garcia-Ramos and Kirkpatrick (1997) found that a species will tend to track its optimum via migration as long as the temporal rate of change in optimum does not exceed the spatial change in environment over the dispersal distance of the species, which is unlikely to be true for most tree species. Case and Taper (2000) used a similar model that also included the effect of competition with another species at the range limit, and found dramatically different results. While they predicted some migration to track the spatial movement in optimum, they found that competition would limit the potential for this response, forcing species to adapt to some extent. These studies indicate that peripheral populations may be more susceptible to the stresses imposed by climatic change due to their already compromised fitness and reduced genetic variation, especially if competition with other species limits their ability to migrate. However, a warming climate would be expected to cause relatively less stress to peripheral populations that inhabit the high-latitude or high-elevation leading edge of a range, because gene flow from central populations would introduce alleles pre-adapted to a warmer climate (Davis and Shaw 2001). Conversely, populations at the low-latitude periphery would be doubly stressed by the reduction in fitness due to gene swamping from colder climates, and the further maladaptation of the immigrant alleles under warming conditions. However, asynchrony in reproductive phenology may limit gene flow among distant populations inhabiting different climates despite long-distance dispersal of pollen.

Using these theories to make predictions about extinction risk in peripheral populations requires the critical assumption that the meta-population has achieved equilibrium. Hampe and Petit (2005) make the important point that in many tree species, this is far from true, due to contraction and expansion of ranges during the Quaternary glaciations. Many European tree species have high levels of neutral marker divergence between populations inhabiting the low-latitude Iberian, Italian, and Balkan peninsulas, suggesting much diversity is maintained in these peripheral populations (Petit et al. 2003). However, levels of within-population diversity in the same species tend to be highest in central Europe and lower in both northern and southern peripheral populations due to admixture of different lineages during recolonization, rather than differences in density. It is thus unclear whether the genetic swamping envisioned by the central-peripheral models would apply. Mimura and Aitken

(2007a) found central-peripheral structure in microsatellite marker diversity in Sitka spruce (*Picea sitchensis*) without evidence of multiple refugia contributing to diversity of central populations. Results from a study in lodgepole pine (Yeaman and Jarvis 2006) seem to follow the central-peripheral pattern for variation in quantitative traits, but this study also found a twofold stronger correlation between quantitative trait variation within populations and regional environmental heterogeneity, suggesting a further effect of gene flow and landscape on genetic variance and adaptive potential. Predictions of the risk to individual populations should be further informed by focused studies of the quantitative genetic variance and fitness under reciprocal transplant and controlled environment experiments.

Hybridization and adaptation

Many ecologically and economically important genera in temperate and boreal regions contain species pairs capable of interspecific hybridization, including spruce (*Picea*), pine (*Pinus*), poplar (*Populus*), and oak (*Quercus*). Periodic or ongoing introgression may provide novel alleles for adaptation to new conditions, and may have been a significant factor for adaptation to new environments in the past (Morjan and Rieseberg 2004). This possibility is of particular interest in western North America, where several pairs of maritime and more continental taxa have distributions largely separated by major north–south mountain ranges, but have some opportunity for genetic contact through a few major east–west river valleys or over the crest of lower parts of these ranges (e.g., *Picea sitchensis* and *P. glauca* (Bennuah et al. 2004), *Pinus contorta* and *P. banksiana* (Rweyongeza et al. 2007), and *Pseudotsuga menziesii* var. *menziesii* and *P. m.* var. *glauca* (St Clair et al. 2005). Hybridization followed by backcrossing or further introgression and selection can lead to transgressive segregation, whereby some individuals can have phenotypes outside of the range of parental species due to complementary allelic effects (Lexer et al. 2004). This may offer a rapid evolutionary path to adaptation to novel environments, as demonstrated for *Helianthus* species (Rieseberg et al. 2003). Natural hybrid zones also offer great opportunity for identifying genes and quantitative trait loci (QTL) involved in adaptation to local environments, and may circumvent the slow process of controlled crossing and field testing long-lived tree species (Lexer et al. 2004).

Local adaptation to climate

There is a long tradition of provenance testing in forest trees, primarily as a tool to determine optimal seed

sources for reforestation based on tradeoffs between productivity of wood and adaptation to climate (Langlet 1971). This tradition has resulted in extensive seedling-nursery or growth-chamber and field common-garden experiments containing population samples planted on multiple sites spanning a range of climatic conditions. These studies can be used retrospectively to study traits involved in local adaptation to climate and characterize genetic clines (reviewed by Morgenstern 1996). For climate change studies, spatial climatic variation sampled among test sites is substituted for temporal variation in climate and used to make predictions about the responses of populations to future climates predicted by GCMs. Here we use the term provenance to reference a particular location sampled, and population to describe individuals from that location (Rehfeldt et al. 2002).

The strongest patterns of local adaptation in temperate and boreal forest trees reflect the critical synchronization of the annual growth and dormancy cycle of populations with their local seasonal temperature regimes. If trees have a shorter than optimal period of active growth relative to their local climate and available growing season, they will not have competitive growth rates, but if growth is initiated too early in spring or continues too late in summer or early fall, cold injury may result (reviewed by Howe et al. 2003; Savolainen et al. 2007). In most temperate and boreal species, the initiation of growth in spring occurs from buds when first a genetically determined chilling sum is met in winter, followed by a genetically determined heat sum in spring. Both chilling and heat sums have been shown to vary among populations in some species (Howe et al. 2003). In seedlings, bud set occurs and height growth ceases when a genetically determined critical night length is experienced; however, some experiments suggest that night temperatures or day/night temperature differential may also be important (Howe et al. 2000). Older trees of species where height growth is predetermined in buds formed the previous summer usually set bud as a function of primary shoot elongation and maturation, and bud set often occurs before nights start to lengthen in summer. Climate change will not alter photoperiodic cues for growth cessation and bud set, but may delay the satisfaction of chilling requirements in winter, or accelerate the satisfaction of heat sum requirements, and may also change the degree of synchrony of reproductive bud development among populations, affecting the potential for long distance gene flow via pollen.

Seedling common garden experiments, usually conducted in uniform nursery bed, greenhouse or growth chamber environments, have found significant geographic variation in phenotypic traits corresponding to climatic gradients on scales ranging from a single watershed (e.g., Douglas-fir (*Pseudotsuga menziesii*) (Campbell 1979)) to

regions (e.g., Douglas-fir (St Clair et al. 2005); western larch (*Larix occidentalis*) (Rehfeldt 1995)) to across the entire species range (e.g., Sitka spruce, Mimura and Aitken 2007a; Fig. 2). These studies have revealed latitudinal and elevational clines for height growth, or bud phenology (particularly timing of primary growth cessation or bud set, but also timing of bud flush in some species), and cold hardiness that correlate most strongly with temperature gradients of population origin (e.g., mean annual temperature, mean coldest month temperature, number of frost free days). Moderate to strong tradeoffs typically exist between population mean growth and timing of growth cessation; that is, seedlings of populations from colder climates cease growth and set bud earlier in summer, develop cold hardiness sooner in fall, and achieve less total growth (Saxe et al. 2001; Howe et al. 2003; Savolainen et al. 2007). In any given climate, there is likely stabilizing hard selection for timing of growth and dormancy due to the risk of cold injury during active growth, and directional soft selection for height growth capacity due to inter- and intraspecific competition.

Typical clines in timing of bud set and total height growth, and the tradeoff between them, are illustrated for 18 populations of Sitka spruce sampled across the species range spanning 30° of latitude (Fig. 2, based on data from Mimura and Aitken (2007a)). The corresponding estimate of population differentiation Q_{st} (proportion of total genetic variation due to differentiation among populations; Spitze (1993)) for bud set in these data was 0.89, similar to those observed for Scots pine (*Pinus sylvestris*, $Q_{st} = 0.82$ (Karhu et al. 1996), and black spruce (*Picea mariana*, $Q_{st} = 0.91$ (Morgenstern 1996), among others (reviewed by Howe et al. 2003; Savolainen et al. 2007). Genetic clines for timing of growth initiation in spring are, on average, weaker than those for growth cessation, and less consistent across species, although are strong in some cases (e.g., needle flush timing in whitebark pine, $Q_{st} = 0.47$; Bower and Aitken (2008). The timing of bud break and bud set are correlated with levels of spring and fall cold hardiness, respectively, and artificial freeze tests also show relatively high population differentiation for cold hardiness in many species (Howe et al. 2003).

Combing equation (1) and related theory with data presented in Fig. 2, we can predict the capacity of Sitka spruce to adapt to rising temperatures. The relationship between temperature and Julian date of bud set in Sitka spruce is approximately linear, with the mean date of bud set changing about 13 days per °C of change in mean annual temperature. If climate change causes shifts in mean annual temperature of 3–5°C over the generation time of Sitka spruce, then we would expect the optimum date of bud set to change by approximately 39–65 days, assuming populations are currently locally adapted. Within

populations of Sitka spruce, measures of σ_p (phenotypic standard deviations) are on the order of 10–25 days (smaller σ_p for more northern populations due to a positive correlation between mean and variance in Julian date). If we consider a mild scenario with a 3°C change affecting the most variable populations, the change in temperature would require a change in mean phenotype of 1.56 σ_p. This is well above the critical threshold of ∼0.4 σ_p derived above, suggesting that Sitka spruce could not tolerate prolonged change at this rate of climate change (∼1°C per generation would be the fastest rate of change tolerable over a long period of time). Of course, this crude approximation of risk ignores many biological details, especially density dependent effects (described above), the fact that local adaptation and fitness are a function of many traits, and that analyses of multivariate traits may provide more realistic predictions.

Populations are unlikely to decline quickly as a result of not fully utilizing the lengthening growing season; rather, this sort of maladaptation would more likely unbalance dynamics of interspecific competition (favouring weedy invaders), which could eventually lead to extirpation if populations failed to adapt and compete. While tradeoffs between growth and traits related to adaptation to low temperatures (cold hardiness and growth phenology) are the norm among populations, this will not likely constrain adaptation to warming climates, and may even promote it, as selection for faster growth rates for competitiveness in warmer climates will extend the growing period and decrease cold hardiness, or vice versa, through correlated responses to selection, assuming adequate soil moisture. Correlations between growth and adaptation to low temperatures within populations are often weaker than those among populations, suggesting they result from linkage disequilibrium and not pleiotropy (Hannerz et al. 1999; Howe et al. 2003). The magnitude of correlated response to selection is a function of trait heritabilities, phenotypic variation, and strength of correlation, and in some situations, indirect selection responses can exceed direct responses (Falconer and Mackay 1996). Heritabilities for phenological traits and cold hardiness are typically higher than those for growth rate, but there is usually more within-population phenotypic variation for growth than for phenological traits (Howe et al. 2003).

While most broad genetic clines are best explained by geographic variation in temperature, in some cases, population mean phenotypes are correlated with precipitation-related variables. Precipitation and soil moisture are more difficult to model than temperature due to the complex effects of topography, and vary more widely in precipitation predictions than for temperatures (IPCC 2007b). As such, there is more uncertainty around the extent to which moisture stress will change with climate warming, and the extent to which natural selection pressures will change as a result. The degree to which variation among populations in precipitation explains phenotypic variation is greater in general for populations from continental than from maritime climates, and stronger at lower latitudes than at higher ones. It appears that the importance of precipitation is often strongest in its interaction with temperature (Andalo et al. 2005). Therefore, heat to moisture index or aridity is probably more important than precipitation by itself (Wang et al. 2006b). Weak to moderate genetic clines have been characterized that significantly correspond to moisture gradients, particularly for summer precipitation (e.g., Douglas-fir (St Clair et al. 2005); lodgepole pine (Rehfeldt et al. 1999)). Multivariate analyses of numerous phenotypic traits and provenance climatic variables simultaneously typically find that the first canonical vector or principal component for phenotypic traits is most strongly correlated with temperature variables reflecting winter or annual temperatures, and the second is most strongly correlated with moisture variables (e.g., whitebark pine (Bower and Aitken 2007); western larch (Rehfeldt 1995), lodgepole pine (Wang et al. 2006b), Scots pine (Rehfeldt et al. 2002), and Douglas-fir (St Clair et al. 2005)).

Carbon dioxide concentrations have risen from a pre-industrial value of 270 μmol mol^{-1} to 382 μmol mol^{-1}, and are predicted to at least double in the next century (Millard et al. 2007). Rising CO_2 concentrations will likely increase tree growth rates and carbon sequestration through a fertilization effects in the short term, but increases may decline subsequently due to soil nutrient limitations (Millard et al. 2007). As field experiments do not sample substantial or testable variation in CO_2 levels, and growth chamber experiments or open-top chamber installations testing population responses to temperature and CO_2 treatments are in their infancy, our knowledge of genotypic variation in response to increased levels is low. Enhanced CO_2 should also increase water-use efficiency (net carbon fixed per unit water) in both the short and long term. This may affect local adaptation in drier locations. While variation among populations in water-use efficiency as measured by stable carbon isotope ratios has been documented for various forest trees (e.g., lodgepole pine, Guy and Holowachuk 2001), little is known about whether genotypes will differ in effects of increased CO_2 on water-use efficiency and adaptation to drought.

To derive climate-related responses from provenance trials consisting of numerous field sites spanning a range of climatic conditions, two primary approaches have been developed: population transfer functions, and population response functions (e.g., Fig. 3A, B, respectively). Both have been used to predict the response of natural popula-
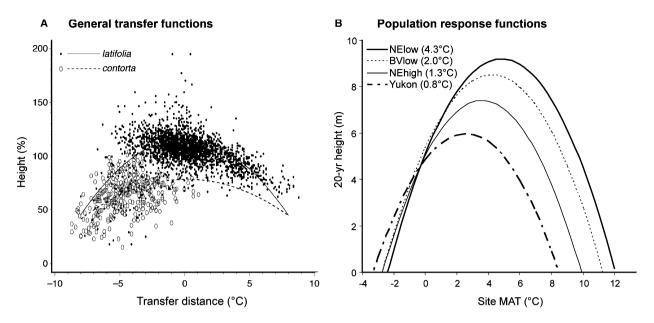
Figure 3 (A) Example of general transfer functions for *Pinus contorta* spp. *latifolia* and spp. *contorta* (figure from Rehfeldt et al. 1999). (B) Growth response functions for four populations of *Pinus contorta* (from Wang et al. 2006b). Populations comprise seed collections from the Bulkley Valley (BV), Nelson high elevation (NE high: 1400–2000 m), Nelson low elevation (NE low: 700–1400 m) seed planning zones in British Columbia, and from the Yukon Territory (Yukon). Mean annual temperatures (MAT) (°C) for each population are shown in brackets in the legend following the population codes.

tions or plantations of forest trees to climate change, and to make recommendations about provenance selection for seed collection, breeding population establishment, and reforestation for uncertain future climates. Population transfer functions relate population survival and growth of planted seedlings to geographic or climatic distances between provenances and common garden locations (Fig. 3A). They estimate how well populations are adapted to planting environments based on their provenance characteristics. The fitness of a given population in its provenance is assessed by comparing its actual performance with the phenotypic optimum for its provenance climate as predicted by the transfer model, as illustrated in Fig. 3A. In most cases, data from different test sites, sometimes from different experiments, are pooled together to develop a general transfer function assuming that the shape and peak locations of transfer curves do not vary significantly among environments (Carter 1996; Rehfeldt et al. 1999; Andalo et al. 2005).

A null transfer (e.g., the traditional use of local populations for reforestation) has been found to be optimal, on average, for current climates in terms of temperature for most of the forest tree species studied in North America, indicating local populations have higher fitness on average than non-local populations in local climates (Carter 1996; Rehfeldt et al. 1999). Populations from more central locations in the species range may be more closely adapted to their current climates than those from closer

to range margins due to the effects of asymmetric gene flow from central to peripheral populations (Garcia-Ramos and Kirkpatrick 1997; Kirkpatrick and Barton 1997). For example, Rehfeldt et al. (1999, 2001) found that northern populations of lodgepole pine inhabit colder than optimal climates than their mean phenotypes would suggest, while more southern populations occupy warmer than optimal climates for mean phenotypes, although this result depends to some extent on the method used to anchor response functions when climatically extreme test sites are lacking (Wang et al. 2006b). M. Mimura and S.N. Aitken (unpublished manuscript) found that geographically isolated populations of Sitka spruce are better adapted to their environments in terms of growth rate and phenology combined than peripheral populations from the continuous species range, suggesting that gene flow restricts local adaptation in the latter. Better performance can be achieved for some species by transferring some or all populations to warmer, cooler or drier conditions from their provenances (Carter 1996; Andalo et al. 2005), suggesting the existence of adaptational lags due to gene flow, recent migration from different environments, or recent changes in local climate on an evolutionary timescale. General transfer functions can also be used to estimate the breadth of a population's realized niche (Rehfeldt et al. 1999). There is a possibility that apparent adaptational lags are the result of relatively short-duration experiments compared to the frequency of

extreme climatic events such as extreme cold or extended droughts (Gutschick and BassiriRad 2003).

Several factors may affect the reliability of general transfer functions. The shape and peak location of transfer curves often differs among environments (Raymond and Lindgren 1990; Rehfeldt et al. 2003; Wang et al. 2006b). Thus, independent transfers between different locations might cancel each other when data are pooled. Using ecological or climatic distance as an independent variable may somewhat compromise the prediction power of the transfer functions because the effect of a fixed climatic distance on genetic variation among populations varies across the species realized niche. For example, the effect of 2°C difference in mean annual temperature derived from 8 versus 10°C is likely quite different from that derived from −2 versus 0°C.

A response function of a population, in contrast to a general transfer function, describes the norm of reaction of an individual population to a range of test site environments (e.g., Fig. 2B). It also visually depicts the phenotypic plasticity of a population or a genotype. These norms of reaction can be used to predict the effects of climate warming on the relative growth of individual populations, and to select populations that will grow well under both current and predicted climates (see discussion in Bower and Aitken 2008). Response functions characterized for lodgepole pine populations (Wang et al. 2006b) have several evolutionary implications. Temperature is the major driver affecting phenotypic variation in growth among test sites, and also appears to be the primary driver of differential selection in growth rates for lodgepole pine (Rehfeldt et al. 1999; Wang et al. 2006b) and others species in general (Carter 1996; Saxe et al. 2001). A combined measure of temperature and moisture is usually the second climatic factor that needs to be considered. Lodgepole pine temperature response functions based on field results do not differ much among populations at low temperatures, only at higher temperatures, and this trend has been confirmed in seedling growth chamber experiments designed to generate response functions (P. Smets and S.N. Aitken, unpublished data). This may reflect a species physiological limit to adaptation to colder, but not warmer, temperatures. Populations with realized niches and suitable for future climates are not necessarily from the warmest provenances (Wang et al. 2006b), suggesting factors other than climate play critical roles in the evolutionary process, such as spatial autocorrelation, migration history, gene flow, adaptational lag and interspecific competition (T. Wang, unpublished data). Finally, the level of phenotypic plasticity varies among populations and species. The evolutionary significance of phenotypic plasticity has long been recognized (Bradshaw 1965; Stearns 1989). Populations with higher levels of phenotypic plasticity are likely to have greater tolerance to changing climates. On the other hand, they may also be slower to adapt to new environments.

While long-term field provenance trials provide a tremendous resource for evolutionary ecology and climate change studies, there are limitations to inferences about natural populations from these trials. These experiments are typically established through growth of seedlings under optimal nursery conditions with abundant water and nutrients, then field planted after 1 or 2 years. Extrapolations to natural populations should be made cautiously as considerable opportunities for natural selection occur during seed germination, establishment, and early growth are largely circumvented. Competing vegetation is often controlled, trees are planted at a wide spacing, and trials are often fenced against large herbivores, potentially widening the apparent realized niche of a population and flattening response and transfer functions. Older provenance trials were typically only planted on productive sites and usually did not include sites at the edges of the species realized niche, and these data require extrapolation to predict responses to much warmer climates (Wang et al. 2006b). Spatial climatic variation is being substituted for temporal changes in climate, and we do not have a good idea of how the effects of climate differ with tree age and stand development. Finally, for both seedling and field common gardens, seeds are usually collected from natural populations experiencing different climatic conditions, and conditions during seed development can have epigenetic effects on seedling growth, phenology and cold hardiness that will inflate estimates of population differentiation (described below).

Genomic architecture of local adaptation to climate

In spite of great interest in recent years, a clear picture of the genomic basis of locally adaptive traits in forest trees remains elusive. Nearly all important questions related to the genomics of adaptation in general, and local adaptation in particular, are unanswered (Orr 2005). With respect to the potential for adaptation in forest trees in response to climate change, three questions take precedence. How many genes govern traits related to local adaptation? What is the distribution of their effect sizes? And, what is the distribution of the relevant genes within the genome? Approximate answers to these questions lie in quantitative trait loci (QTL) mapping and gene expression studies. Neale and colleagues have improved our understanding of the genetic architecture of local adaptation in conifers through a series of QTL studies of bud phenology and cold hardiness in coastal Douglas-fir. For fall cold hardiness, 11 QTL were detected, with percent

variance explained (PVE) per QTL ranging from 2.0 to 6.8, whereas nine were detected for spring cold hardiness, with PVE of 2.0 to 7.5 (Jermstad et al. 2001b). For timing of budflush, no fewer than 33 unique QTL were identified (Jermstad et al. 2001a).

Drought tolerance may become an increasingly important trait, particularly in some geographic areas, with increasing global temperatures and changes in the distribution of rainfall (IPCC 2007b). Recent studies in *Populus trichocarpa* × *P. deltoides* hybrids suggest comparable numbers of QTL for osmotic potential to those observed for bud phenology and cold hardiness, but somewhat higher PVE for drought (5.8 to 12.8%) (Tschaplinski et al. 2006). There has been relatively little research on the molecular genomics of response to increased CO_2 concentrations, but work to date suggests that QTL × CO_2 level interactions are relatively small. Rae et al. (2007) found three separate QTL for each of enhanced shoot growth and enhanced root growth in hybrid poplars growing in open-topped outdoor chambers with ambient and enriched CO_2 treatments, but these QTL explained relatively little variation in overall growth rates (PVE from 1.1% to 3.0%).

Taken together, these results indicate that many genes underlie locally adaptive traits in forest trees, and that modest effect sizes are presumably the norm. In addition, it is important to remember that these data paint a simplified picture of the genomic architecture of the traits in question. Specifically, the number of QTL is usually underestimated, and the effect sizes of the individual QTL are often overestimated (Howe et al. 2003). Linkage disequilibrium is high in QTL mapping pedigrees (e.g., Neale and Savolainen 2004), and individual QTL typically encompass many megabases. Although it is often assumed that a single gene underlies each QTL, in some cases QTL may reflect the cumulative effects of several or many genes. Depending on the physical proximity of genes underlying QTL, they may or may not co-segregate. Coinheritance of adaptive alleles could facilitate or hinder adaptation to a changing climate. However, QTL also tend to be scattered throughout the genome, and unique QTL, whether the result of one or more genes, will segregate independently.

Within natural populations, linkage disequilibrium is very low, typically decaying to non-significant levels in a much shorter distance than the length of the average gene (Brown et al. 2004; Neale and Savolainen 2004; Heuertz et al. 2006) due to large populations and high outcrossing rates. As a result, many genes affecting traits key to local adaptation to climate are inherited largely independently, and selective sweeps are likely to affect relatively few genes determining a phenotype simultaneously. The high fecundity levels of most species mean that many seeds are produced per seedling that is established, and recombination across the large genome will produce a wide array of genotypes combining different alleles from different loci. This may create a tremendous opportunity for selection from this broad array of genotypes for those with the right genetic background to be well adapted to local environments due to small effects of many alleles simultaneously, and provides genetic redundancy in that different allelic combinations can produce similar phenotypes. Unravelling these complexities in conifers can be achieved in part through candidate gene-based association mapping. This involves selecting a number of candidate genes for the trait of interest, surveying those genes for segregating variation in the form of single nucleotide polymorphisms (SNPs), and testing for statistical associations between SNP variants and phenotypes. The approach differs from QTL mapping in that it uses large outbred populations with low linkage disequilibrium instead of family pedigrees (Neale and Savolainen 2004; Gonzalez-Martinez et al. 2006). When associations are found, they will usually be the result of either having genotyped the causative variant, or, perhaps more often, having genotyped a variant that is tightly linked to the causative locus. In either case, the benefit of association mapping over QTL mapping is that it provides very fine resolution of the genomic regions contributing to trait variation, and markers can be transferred between populations within a species, and perhaps even between closely related species. Several large candidate gene-based association studies are underway in conifers and poplars, and this work holds great promise to unravel the genetic complexities of local adaptation.

Although they do not provide information on segregating variation, gene expression studies are a useful complement to the genetic work outlined above. Global gene expression has been monitored in forest trees during developmental transitions (e.g., bud set, dormancy induction) and stress responses (e.g., cold, drought), and points to wholesale transcriptional remodelling in each case (Schrader et al. 2004; Street et al. 2006; Druart et al. 2007; Ruttink et al. 2007; Holliday et al. in press). These studies inform our understanding of the genomics of locally adaptive traits in two ways. First, many of the genes that are upregulated will be involved in the trait of interest, and nucleotide variation in some of these genes likely contributes to variation in the phenotype within- and among-populations. Second, variation in expression of the genes themselves could contribute to phenotypic variation. This could be the result of nucleotide variation in cis- or trans-acting elements, or it could be caused by differences in epigenetic silencing among individuals. Indeed, although mutation and selection undoubtedly shape the genetics of local adaptation, it is becoming

increasingly apparent that epigenetics may play an important, and possibly pivotal, role in the adaptive response to climate change. Recent studies in Norway spruce (*Picea abies*) show that the temperature during both zygotic and somatic embryo development can dramatically affect cold hardiness and bud phenology in the offspring (Johnsen et al. 2005a,b; Kvaalsen and Johnsen 2007). In some cases, the offspring's phenotype varied the equivalent of 6 degrees of latitude from what was expected given the geographic origin of the parents. A crucial question that remains outstanding in this area is the extent to which these traits are persistent, both within an individual's lifetime and in its offspring and subsequent generations.

Data from QTL and gene expression studies suggest many genes underlie adaptive variation in forest trees. Ongoing association studies will fine-tune our understanding of just how many genes are involved, but that number is likely to be large, at least on the order of tens of genes. In spite of this complexity, forest trees have been able to adapt to local environments relatively rapidly in the past. This paradox may be resolved when we have a better understanding of interaction between epigenetics and mutation/selection. Does the epigenome provide a buffer against climatic variability that provides time for the genome to 'catch up'? Rapid advances in high-throughput sequencing technologies have put the sequencing of a conifer genome and epigenome within reach, and answers to these outstanding questions will lie in the application of such technologies.

Research needs

To better understand the capacity of forest trees to adapt to rapid climate change, a comprehensive research agenda should include attention to the following. Continued investigations of the genomics of local adaptation should be pursued using association approaches (Neale and Savolainen 2004). Quantifying the role and mechanisms of epigenetics in apparently rapid local adaptation in conifers should be pursued using the extensive '-omics' toolbox being generated for model organisms and humans. Short-term seedling common-garden experiments should be conducted in highly controlled environments using genetic materials also represented in field studies to determine the physiological basis of local adaptation, and to better determine population tolerances of extreme climatic events (e.g., high temperatures, droughts) and genetic responses to CO_2 and drought. New field common-garden experiments should sample as wide a range of populations as possible, attempt to include disjunct and peripheral populations from both leading and rear edges of migration, and select field sites based on predictions from SDMs. The development of more complex

and more realistic SDMs that better incorporate factors such as age to sexual maturity, fecundity, dispersal ability, and competition effects is needed to move from predicting where habitat will be to where species will likely be without intervention. Estimation of parameters for such models will require field-based studies of reproduction and dispersal. Older field common-garden sites should be used to study variation in fecundity with transfer distances. They should also be used to conduct controlled crosses and provide seed from different populations that develops in the same environments, reducing epigenetic effects of maternal environments, and allowing the study of these effects in a greater number of taxa. Studies of phenotypic, neutral marker, and nucleotide variation in genes involved in adaptation to climate in natural hybrid zones spanning steep climatic gradients may yield considerable knowledge about genes and traits involved in rapid adaptation to climate, and will allow the assessment of the potential for transgressive segregation to produce phenotypes for new climates.

Looking forward

Can integrating information on genetic diversity and complexity at different phenotypic and genetic scales shed light on the ability of populations of forest trees to develop relatively steep phenotypic clines for traits controlled by many genes, despite high levels of gene flow? For most conifers, the many genes and genomic regions determining phenotypes are distributed across a large genome. Genetic redundancy may result from the genomic architecture of adaptive traits, with many genes of small effect determining adaptive phenotypes, and this may facilitate local adaptation despite high levels of gene flow to a greater extent than for phenotypes determined by one or few genes. Genetic clines for alleles at any of these causative loci independently may be weak and appear selectively neutral, but resulting phenotypic clines may be strong (Barton 1999). These clines may be further enhanced through epigenetic effects of local climate on maternal parents. As long as populations can maintain sufficiently high fecundity and levels of genetic variation, the capacity to adapt to a rapidly changing climate may be sufficient to maintain trees across the landscape, although these populations may suffer some adaptational lag for several generations.

With a myriad of factors to consider, it is clearly impossible to predict the fate of all populations of forest trees under climate change. However, the extensive knowledge we have for these long-lived organisms can be used to rank species in terms of risk based on a variety of characteristics. Widespread species with high fecundity occurring in large populations will likely be able to adapt

to climate change in relatively few generations, and will likely survive in the interim as major competitors will be facing the same fate of short-term maladaptation. High rates and distances of seed and pollen dispersal will also contribute positively to their capacity to both adapt and migrate. Species that occur in small, fragmented populations, or those with low fecundity or late age of sexual maturity, reproductive characteristics more typical of later successional species and high-elevation habitats, will likely suffer greater adaptational lag. Reproduction and regeneration should be monitored in protected areas to determine if facilitated migration of populations is necessary among protected areas or to extend species ranges. Translocations of populations for reforestation from milder to colder environments may eventually provide a source of pre-adapted alleles into conservation populations through gene flow, once planted areas reach reproductive maturity. Population response curves should be used to predict the maximum extent to which seed can be moved from milder to colder climates for reforestation in the short term and tree growth in the longer term, and seed transfer guidelines should be changed accordingly. To end on a cautionary note: the above predictions all suggest that lodgepole pine should be one of the species least affected by climate change. However, the recent climate-associated population explosion of the mountain pine beetle and the resulting decimation of vast tracts of lodgepole pine forest in western North America underscore the difficulty of predicting complex ecological interactions and the limitations of the models described herein.

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