Information Underload: Ecological Complexity, Incomplete Knowledge, and Data Deficits Create Challenges for the Assisted Migration of Forest Trees

ANDREW PARK AND CAROLYN TALBOT

Forest managers are considering assisted migration as a strategy to develop climate-resilient forests. Assisted migration (AM) is the translocation of species or genotypes from their current ranges to areas predicted to have a supportive future climate. Although correlations of species ranges with climate are traditionally used to explore AM potential, successful AM strategies will have to consider many other variables. In this article, we review recent research that informs the complexity of AM decisions. Local microenvironment, herbivory, and intraspecific interactions frequently outweigh climate in determining species establishment and survival. Species adopt several strategies to cope with drought, heat, and cold, but translocated genetic material can display cryptic maladaptation when challenged by extreme, out-of-range weather events. Phenology, photoperiod, and climate are related in complex, often provenance-specific ways. We discuss the implications of our findings for forestry AM and make recommendations for incorporating these insights into future research and AM practice.

Keywords: assisted migration, forest management, climate change, temperate and boreal forests

Anthropogenic climate change (ACC) is a fact of twenty-first-century life. Although the December 2015 Paris Agreement committed nations to holding average global warming to "well below" 2 degrees Celsius (°C), current international commitments are inadequate to meet this goal (Höhne et al. 2015). Without stronger measures, average global temperatures could rise by 1.4°C–4.6°C above 1990 levels by the year 2100 (Knutti and Sedlacek 2013). The hunt is on, therefore, to develop tools and strategies to help humanity adapt to unprecedented, rapid climate change during the twenty-first century.

One such tool, proposed by conservationists and resource managers, is assisted migration. *Assisted migration* (AM) refers to the translocation of species or genotypes from their current ranges to facilitate range expansion in response to climate change (Williams MI and Dumroese 2013). In recent years, AM has been discussed as a tool for conserving endangered species (Hoegh-Guldberg et al. 2009), increasing climate resilience of commercial forests (i.e., forestry AM; Pedlar et al. 2011, Williams MI and Dumroese 2013),

and enhancing resilience in restoration projects (Dumroese et al. 2015).

Whereas conservation AM emphasizes species rescue, forestry AM is proposed as a tool to ensure that adapted seed varieties continue to contribute to productive and healthy commercial forests (Pedlar et al. 2012, Williams MI and Dumrose 2013). Three scales of forestry AM are defined on the basis of short- to long-distance movements of genetic material: assisted population migration (APM) of seed sources within the current species range, assisted range expansion (ARE) to areas just beyond current range limits, and assisted species migration (ASM) far beyond current range boundaries (Williams and Dumroese 2013, Messinger et al. 2015, SilviFuture 2017).

APM is already incorporated into forest management policy in some jurisdictions. Several Canadian provinces have modified their seed-transfer guidelines (rules governing the geographical sources of locally planted seedlings) in anticipation of moderate climate warming (Pedlar et al. 2011). In the United Kingdom, "predictive provenancing"

(a synonym for AM) uses general-circulation-model (GCM) projections to targeted seed sources of native species from two to five degrees of latitude south of their local populations (Barsoum 2015, Whittet et al. 2016). Forestry AM is the subject of common garden field trials and experiments (O'Neill et al. 2011) and retrospective analyses of old plantations (Isaac-Renton et al. 2014), as well as species-specific APM (Benito-Garzon and Fernandez-Manjarres 2015) and ARE and ASM modeling (Barsoum et al. 2016, Iverson et al. 2016). Aitken and Bemmels (2016) argued that intraspecific genetic clines that cross North American climatic gradients provide sufficient data to guide APM, which the authors framed as "assisted gene flow."

Key premises underpinning AM are that (a) organisms are tightly adapted to the climate of their current ranges (i.e., realized niche approximates fundamental niche) and (b) climate will shift geographically, leaving organisms stranded in climates to which they are maladapted (Barsoum 2015). Species distribution models (SDMs) that project future "climate envelopes" for species or provenances (geographically specific varieties) of species are based on these premises. Older SDMs were criticized for ignoring biotic interactions, soils, and seed dispersal (Pearson and Dawson 2003) and failing to simulate "no-analog" future climates (Williams and Jackson 2007). Although recent models correct these deficits (Sormunen et al. 2011, Iverson et al. 2016, Prasad et al. 2016), concurrent advances in understanding species responses to climate extremes, species range limits, phenology, and local intraspecific and interspecific interactions pose new challenges to our ability to predict tree performance in future climates.

In this article, we summarize some recent insights about the probable responses of trees to climate change. Our goal is to expand the scope of discussions about forestry AM to embrace a holistic perspective that incorporates the multiple ecological facets of tree establishment and growth in novel environments. Our objectives are (a) to summarize and interpret recent advances, especially results that are not usually considered in climate-change and AM studies, and (b) to investigate the knowledge deficits, methodological problems, and uncertainties that affect our ability to use and interpret these fresh insights.

In the sections that follow, we explore the complexities of the tree species–climate relationship, giving special consideration to climatic extremes, phenology, the role of microsites and local interactions, and innovations in SDMs. Extreme weather, especially events beyond the historical range, may be more important than shifts in climate averages in determining future species ranges. Relationships among phenology, temperature, photoperiod, and precipitation are also more complex than traditional models imply and have large implications for AM practice. Microenvironment, herbivory, and interspecific interactions may be as important as climate in determining species establishment and survival, which underscores the importance of correctly selecting "the right tree for the right site." Finally, by incorporating

plant functional traits (FTs) and abiotic variables into SDMs, modelers are directly addressing species and provenance choices for AM and interrogating the robustness of model assumptions. We conclude by discussing the implications of our findings for AM practice. Our principal focus is AM in temperate and boreal forests, with an emphasis on North America and Europe, but we report findings from other geographical areas when they offer compelling insights.

Climate extremes and species range limits

A common assumption in adaptation research is that climate zones will shift too fast and too far for individual trees to acclimate in place (*sensu* Park et al. 2014), for tree populations to evolve in place, or for natural migration to keep up with climate (Pedlar et al. 2012, Williams MI and Dumroese 2013). Species distribution models project rapid geographic shifts in climate zones and the consequent extirpation of stranded populations. Early versions of these models generally based their projections on changing climatic averages (reviewed in Park et al 2014). However, evidence is growing that increased climatic variability and extreme events will be key determinants of long-run population persistence and range limits (Benito-Garzon et al. 2013, Reyer et al. 2013, Camarero et al. 2015).

Reyer and colleagues (2013) suggested three scenarios for future extreme weather frequency. These were (1) changed mean with unchanged variance, (2) changes in variance but not the mean, and (3) unaltered mean and variance with rare, very extreme events. Other possibilities exist, of course; both means and variances could increase, and fat-tailed distributions (Pindyck 2011) could increase the frequency of the rarest, most extreme events. Raising mean event severity increases the incidence of weather extremes at the right-hand tail of the distribution, but altered variance and fat tails produce extreme events in both tails. For example, extremes of heat and cold could occur during the same year. Such extremes of heat, cold, and drought potentially determine range limits and the survival of tree populations, alter species phenology, and change community composition. Out-of-range events can expose previously unknown vulnerabilities (cryptic maladaptation, Benito-Garzon et al. 2013). Successful AM practice therefore requires the ability to accurately identify species range limits, and to predict provenance resistance and resilience in the face of weather extremes.

Cold, drought, and heat

Weather events that exceed the limits of historic records pose a particular challenge for AM practice. For example, hard frosts killed provenances of maritime pine (*Pinus pinaster* Ait.) translocated through a 3.5°C reduction in mean annual temperature between source sites in Iberia, Spain, and APM planting sites in Aquitaine, France. Tree mortality followed an estimated once-in-100-years frost with temperatures of –22°C, a full 15 degrees colder than the lowest temperature ever recorded in the area (Benito-Garzon et al. 2013). These authors described this mortality event as a case

of cryptic maladaptation because the Iberian provenance's frost sensitivity was only exposed by the out-of-range frost long after it was in Aquitaine. A once-in-100-years frost also caused widespread needle loss and mortality in Scots pine (*Pinus sylvestris* L.) at the southeastern edge of its range (Camarero et al. 2015). Cryptic maladaptation was also demonstrated when silver birch (*Betula pendula* Roth.) in an APM planting experienced elevated mortality (compared with local varieties) when late spring frosts followed a mild winter (Whittet et al 2016).

Timing and variability of cold may be as influential in determining species range limits as the magnitude of cold temperatures. Cold tolerance correlates with temperature heterogeneity across species ranges (Kreyling et al. 2015), with minimum winter temperatures in some North American and European softwoods and hardwoods, and with minimum April temperatures in European beech (*Fagus sylvatica* L.; Kreyling et al. 2014). Spring temperature minima appear to play a key role in controlling the range of some hardwoods (Kollas et al. 2014), because temperature fluctuations during dehardening put vulnerable flowers and expanding leaves at risk (Jönsson et al. 2004). Tree age differentially affects cold tolerance. Among temperate hardwoods and conifers, 4-week-old seedlings had similar cold tolerances regardless of species (–7.8 to –9.9°C), whereas tolerance varied interspecifically in 1-week-old seedlings (–6.0°C to –10.0°C) and adult trees (tolerances of –23°C to –45°C; Hofmann et al. 2014).

Increased drought frequency and intensity are expected consequences of ACC-induced intensification of hydrological cycles (Knapp et al. 2008) and need to be accounted for in AM selection strategies. In line with these predictions, drought frequency and severity are increasing (Knapp et al. 2008, Reyer et al. 2013), have reduced primary production, and have increased tree mortality globally (reviewed in Wang et al. 2012).

Provenances and species differ in their drought responses, and drought can alter successional trajectories and community dynamics in mixed-species stands. Species drought responses are distributed along a continuum between two contrasting coping strategies (Attia et al. 2015). At one extreme, anisohydric species allow leaf water potential (ψ_l) to fall but maintain photosynthesis. By contrast, isohydric trees maintain ψ_l within tight boundaries by closing their stomata (Wang et al. 2012). Anisohydric species risk mortality from cavitation and leaf desiccation under critically low soil-water potentials, whereas isohydric species risk death due to carbon starvation.

Both anisohydric and isohydric species have undergone mass mortality during severe droughts (McDowell et al. 2008, Anderegg et al. 2012), but whether one of these mechanisms produces greater resilience than the other is an area of active research. Recent findings suggest that isohydric species might enjoy an edge of survival at the expense of reduced growth rates compared with anisohydric species. Some anisohydric species appear able to maintain higher growth rates than isohydric species through moderate droughts in experimental (Attia et al. 2015) and natural (Elliott et al. 2015) conditions. Isohydric balsam poplar (*Populus balsamifera* L.) had lower growth but also lower stomatal conductance at 30% soil-water content than either anisohydric Chinese poplar (*Populus simonii* Carriére) or an anisohydric balsam–Chinese poplar hybrid (Attia et al. 2015). Similarly anisohydric, ring-porous *Quercus* species had greater growth on upland sites in the southern Appalachians during dry years than did several isohydric, ring-porous hardwoods (Elliott et al. 2015). Attia and colleagues (2015) advanced a conceptual model in which isohydric species experience a widening growth deficit concurrently with increasing survival advantage compared with anisohydric species as water stress increases. If this model receives widespread empirical support, it would suggest that anisohydric AM candidates would perform better in areas with abundant rain and short dry periods, whereas isohydric species would be a logical choice where droughts are long or severe.

Whether or not drought responses are observed in species or provenances depends on the duration, season, and relative severity of the event. Differences in hydraulic conductivity and needle damage among 3-year-old half-sib families of Norway spruce were observed in the early stages of experimental drought but disappeared as the treatment progressed (Chmura et al. 2016). Interspecific growth differences occurred among European *Abies* species during severe droughts in 2003 and 2007 but were not observed during earlier, less severe droughts (George et al. 2015). Furthermore, early summer drought, when conifer growth rates are usually maximal, reduced radial growth by up to 50%. By contrast, late summer drought, regardless of severity, did not affect growth. George and colleagues (2015) also noted that low-severity droughts induced growth differences among provenances of silver fir (*Abies alba* Mill.). Growth rankings among these provenances changed between droughts, however, and the authors concluded that they displayed little genetic differentiation in drought tolerance. Strong provenance–drought interactions were observed in Scots pine exposed to experimental drought and warming. In this study, growth allocation was rerouted from stems to tap roots in some provenances, with the strongest reallocation taking place in those from the dry southwest of Scots pine's range (Taeger et al. 2015).

The consequences of drought may take years to decades to play out and are often contingent on interactions with other stressors. Carbon starvation and depletion of nonstructural carbohydrates (NSCs), which buffer disease and drought effects, may explain delayed mortality in holm oak (*Quercus ilex* L.; Galiano et al. 2012) and Scots pine (Galiano et al. 2011) several years after severe drought. Seedlings of trembling aspen and balsam poplar subjected to progressive, severe drought experienced root death during winter dormancy. Drought apparently reduced conversion of starch

to soluble sugars, which in turn may have compromised the cold tolerance of roots (Galvez et al. 2013).

There are many instances of interacting stressors amplifying the effects of drought and cold. In Camarero and colleagues' (2015) study of Scots pine killed by historically unprecedented frosts, growth and mortality were greater in trees stressed by drought during the previous year. Drought-induced defoliation, abetted by mistletoe infestation, decreased carbohydrate storage and leaf-nitrogen concentrations in Scots pine, reducing radial growth in affected trees for 4 years after a 2004 drought (Galiano et al. 2011). Extended mortality among European beech over five decades has been tentatively attributed to sequential droughts combined with infestations of *Phytophthora* fungi (Martin et al. 2015). Recent aspen dieback in Canada's Aspen Parkland occurred in two stages. Co-occurring drought and defoliation by forest tent caterpillar (*Malacosoma disstria* Hbn.) reduced tree growth, which predisposed stands to secondary damage by wood-boring insects, fungal pathogens, and freeze–thaw events during a winter with unusually low snowpack (Hogg et al. 2002).

At a regional scale, there are likely to be thresholds beyond which changing drought frequency and severity could produce state shifts from one biome to another. These thresholds may be decisive in determining whether AM is viable and, indeed, whether forest cover can be maintained. The 100-kilometer-wide ecotone from forest to prairie in Minnesota, United States, is characterized by a 100-millimeter reduction in precipitation minus potential evapotranspiration (Danz et al. 2013). The location and character of such transition zones may be rather fluid. The prairie–forest ecotone shifted northeast during Holocene warming episodes (Frelich and Reich 2010), and drought during the Medieval Climate Anomaly (1000–1400 years BP) caused a pronounced multidecadal contraction in the Great Lakes range of American beech (*Fagus grandifolia* (Ehrh.)). These results suggest that biome boundaries and species range limits may be sensitive to modest changes in precipitation, but as yet, these tipping points are poorly known.

Phenology and its determinants

Phenology is traditionally thought to respond predictably to light and temperature. Fall bud set and growth cessation correlate inversely with latitude (Barnes et al. 1998), mean annual temperatures, and risk of frost damage (Aitken et al. 2008). Budburst is generally linked to accumulated growing degree days (GDD), with obligate chilling requirements for many temperate and boreal species (e.g., Kriebel and Chi-Wu 1962).

While not falsifying this basic phenological understanding, recent research has revealed complexities in climate–phenology relationships that are not captured by simple phenological models. Studies have clarified relationships between spring temperatures and range limits (Korner et al. 2016, Zohner et al. 2017) and revealed dynamic interactions between climate, budburst, fall budset, and

therefore growing-season duration (reviewed in Way and Montgomery 2015). These findings have implications both for the persistence of trees in place during ACC, as well as our ability to predict the behavior of genetic material subjected to latitudinal AM.

Summarizing a series of field and laboratory studies, Körner and colleagues (2016) concluded that cold temperature range limits depend on interactions between spring freezing resistance, rates of growing-season tissue maturation, and provenance or species-specific phenology. When close to altitudinal and latitudinal range limits, earlier leafing species were more freezing resistant during budburst than those breaking bud later. Species and provenances most vulnerable to cold spring temperatures and temperature reversals (Jönsson et al. 2004) will therefore tend to leaf out later. Zohner and colleagues (2017) generalized this observation across continents, showing that many species break bud later in areas with high spring temperature variability. Fall bud formation and wood maturation are forestalled by cold or short growing seasons, suggesting that the ability to complete seasonal development also limits species ranges (Körner et al. 2016).

The characteristics of regional and continental climates interact with tree successional status and phenology. Temperate and boreal trees and shrubs from cold, dry winter climates tended to break bud earlier than species from other regional climates classified according to seasonal precipitation and temperature (Zohner and Renner 2014). Budburst was, however, also contingent on phenological cues. Species responding to forcing alone leafed out earliest, followed by those with low chilling or high chilling requirements, and finally, those responding to photoperiod and chilling (figure 1). The duration of winter chilling interacted with species successional status and photoperiod to change budburst rankings in a growth chamber study (Laube et al. 2014). Natural chilling was allowed in outdoor conditions for varying periods during the winter before cut twigs from adult trees were exposed to simulated forcing in growth chambers. Although longer chilling advanced budburst in 33 of 36 species, shorter chilling advanced budburst in pioneer species relative to mid- and late-successional species (figure 2). Budburst was also advanced in a few species by doubling the photoperiod from 8- to 16-hour days, but this effect was only observed under reduced chilling.

The timing of budburst and senescence may be interconnected via weather of the year. Using 24 years of data, Keenan and Richardson (2015) found that earlier and later budburst were associated with earlier and later fall senescence, respectively. This relationship occurred in a range of species and was observed via satellite across a large region of the northeast United States. This coupling of earlier budburst and senescence has been observed in other studies, and it can produce either a minor lengthening or even a shortening of the growing season (reviewed in Way and Montgomery 2014). Whether or not senescence is delayed by earlier budburst may depend on the primacy of
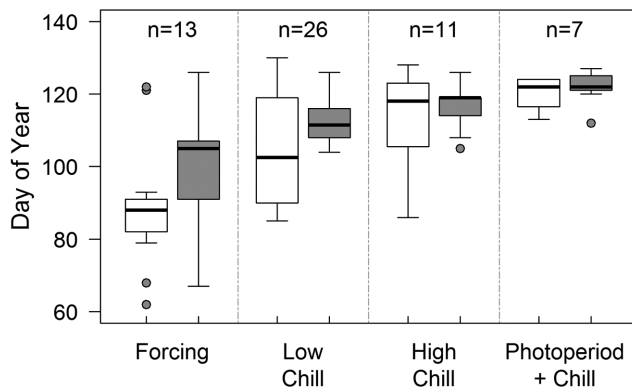
Figure 1. Leaf-out dates for 57 species grown in Munich Botanical Garden and sorted by chilling, forcing, and photoperiod requirements (adapted from Zohner and Renner 2014). Leaf-out day was defined as the day when 3–4 branches had leaves pushed out all the way to the petiole. Forcing = forcing degree days only, Low chill = photoperiod-independent species with low chilling requirements, High chill = photoperiod independent species with high chilling.

the photoperiod in the controlling budset. In a large meta-analysis, Gill and colleagues (2015) found that October temperatures and cooling degree days were stronger predictors of temperate hardwood leaf senescence than latitude or photoperiod. Increasing temperatures produced measurable delays in senescence at lower latitudes, but photoperiod (and therefore fixed senescence dates) continued to be the primary cue at high latitudes.

Variability is a key feature of most large phenological studies. Few universal patterns are observed, and both magnitude and direction of phenological responses vary among species within genera and provenances within species. Furthermore, data-selection bias leads to the overestimation of spring phenology advancement in response to climate warming. Parmesan (2007) showed that excluding species with 1 day or less per decade of phenological advance led to a large overestimate of mean advancement rates. Furthermore, across taxonomic groups, 20%–70% of species show no response to warming, and latitude of origin explained only 4% of phenological variance. These observations are borne out in a multitaxon analysis of phenological time series from China (Ge et al. 2015). As in Parmesan (2007), geography (latitude, longitude, altitude) explained little of the variance in either spring advance or autumn phenological delay with warming. Among trees, no significant trends were observed for many species, and in at least one case, both magnitude and sign of the phenological trend varied within and between species (S1 in Ge et al. 2015).

Compelling evidence for variation in phenological responses to climate among provenances comes from an extensive study of budburst, cold hardiness, and seedling growth in hybrid spruce (*Picea glauca* x *engelmannii*) and lodgepole pine (*Pinus contorta* Douglas ex Loudon; Liepe

et al. 2016). Growth chambers were used to test 254 populations of spruce and 281 populations of lodgepole pine against a temperature gradient spanning nine degrees of latitude in western North America. The authors found contrasts in phenology and susceptibility to cold among pine and spruce provenances that were geographically close and from somewhat similar climates. Boreal Plains populations combined cold hardiness with early bud break and relatively late bud set, whereas high-elevation populations had late bud break, early bud set, and limited cold tolerance. The authors concluded that northern provenances traded off early bud-break with the risk of late-spring frosts to maximize growth, whereas montane populations adopted a more conservative phenology and were protected from frost damage by deep snowpacks.

Three general lessons for AM practice emerge from recent phenological studies. First, phenological responses to climate vary widely, even within provenances, and the details of such responses may determine success or failure in AM. Second, spring temperatures and spring temperature variability are strong determinants of range limits and budburst timing. In fact, Körner and colleagues (2016) reported that neither average annual temperatures nor minimum winter temperatures exert any influence over range limits. Finally, as has been discussed by Way and Montgomery (2014), ACC will fundamentally change the relationships between chilling, forcing, and photoperiod. Reduced chilling may reveal hitherto-unknown spring photoperiodic dependencies, as was reported by Laube and colleagues (2014). The influence of earlier spring forcing could potentially be counteracted by the influence of photoperiod when provenances or species are moved north (Way and Montgomery 2014). On the other hand, trees adapted to short fall photoperiods that are moved north may be exposed to enhanced frost risks. The modulation of photoperiodic-dependent phenology (earlier or later) by northward movement of trees may depend on whether critical photoperiods occur before or after the spring or fall equinoxes. Actual timing of equinoxes gets earlier and later with increasing latitude for spring and fall equinoxes, respectively (Time and Date AS 2017). The effects of latitudinal shifts in photoperiod-sensitive trees are therefore likely to depend on latitudes of origin and destination.

Individual tree and community responses

Variation among individuals and microsites modulates growth and survival in heterogeneous landscapes. Such microsite-mediated variation may influence tree communities more than climate, at least in the short term (Whittet et al. 2016). Clark and colleagues teased apart the relative influences of climate and local environment among 26,000 individuals from 38 species in the southern Appalachians and Carolina Piedmont (Clark et al. 2010, 2014, Early and Sax 2014). Hierarchical analyses within and between species at multiple spatial scales showed that intraspecific variation in growth, survival, and fecundity exceeded interspecific

Left margin (successional status) and species — Low Chill (Late → Early):

C Acer.saccharum
C Fagus.sylvatica
I Quercus.rubra
C Acer.pseudoplatanus
I Acer.negundo
I Juglans.ailantifolia
P Pinus.sylvestris
I Juglans.regia
I Aesculus.hippocastanum
P Juglans.cinerea
I Quercus.bicolor
C Pseudotsuga.menziesii
I Fraxinus.excelsior
C Abies.alba
I Quercus.robur
C Carpinus.betulus
I Fraxinus.chinensis
P Pinus.nigra
P Populus.tremula
I Prunus.serotina
I Prunus.avium
P Amorpha.fruticosa
I Fraxinus.pennsylvanica
P Symphoricarpos.albus
I Pinus.strobus
P Acer.tataricum
P Pinus.wallichiana
P Robinia.pseudoacacia
P Cornus.alba
P Betula.pendula
P Cornus.mas
P Larix.decidua
P Corylus.avellana
P Syringa.vulgaris

Right margin — High Chill (Late → Early):

P Amorpha.fruticosa
I Juglans.regia
I Fraxinus.pennsylvanica
P Pinus.nigra
I Fraxinus.excelsior
I Fraxinus.chinensis
C Acer.pseudoplatanus
P Juglans.cinerea
C Acer.saccharum
C Pseudotsuga.menziesii
C Abies.alba
I Quercus.robur
I Juglans.ailantifolia
I Quercus.rubra
C Fagus.sylvatica
I Quercus.bicolor
I Pinus.strobus
P Pinus.sylvestris
I Aesculus.hippocastanum
P Populus.tremula
P Robinia.pseudoacacia
P Pinus.wallichiana
P Acer.tataricum
P Cornus.alba
P Cornus.mas
P Betula.pendula
I Acer.negundo
P Syringa.vulgaris
I Prunus.serotina
P Larix.decidua
P Symphoricarpos.albus
C Carpinus.betulus
I Prunus.avium
P Corylus.avellana

Axis labels: Late / Early (left vertical axis); Low Chill, Intermediate Chill, High Chill (horizontal axis).
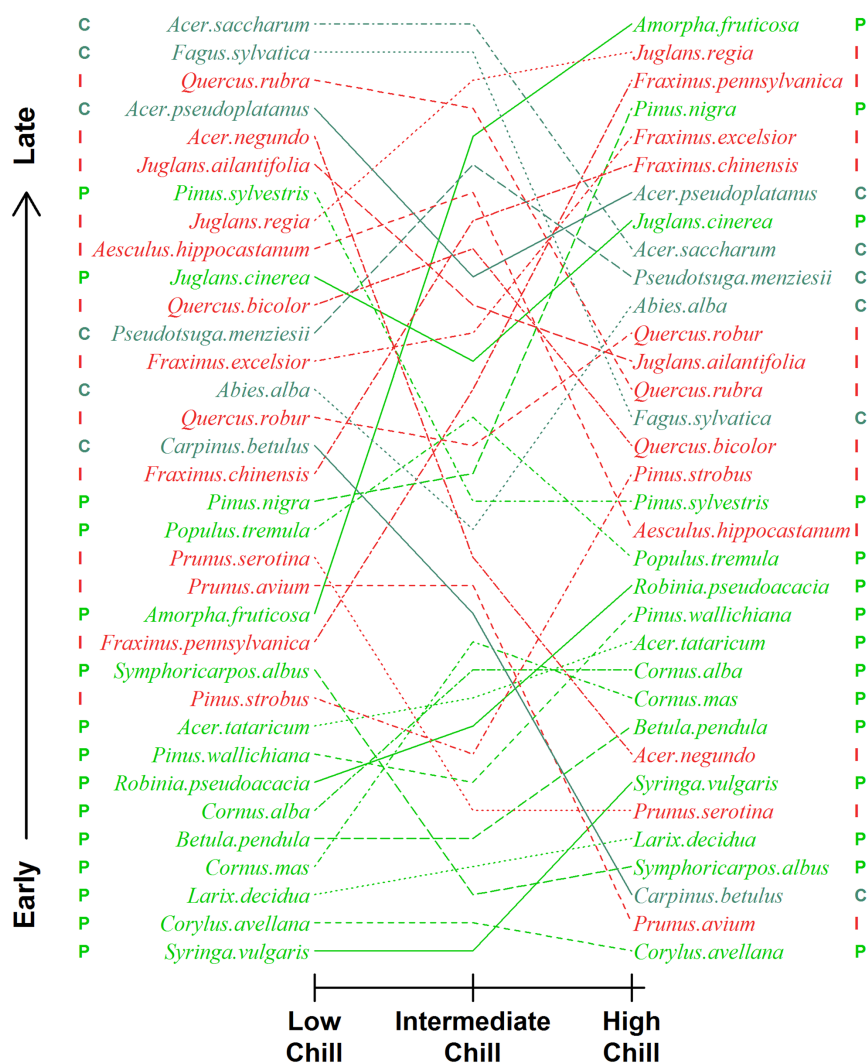
Figure 2. Ranking of leaf-out phenology for twigs of 34 hardwood and conifer species under low, intermediate, and high chilling treatments (adapted from Laube et al. 2014). Chilling treatments were divided into roughly 6-week periods from November to mid-March. Color-coded successional status is shown in the left- and right-hand margins: P = pioneer, I = mid-successional, and C = climax species.

genera *Tsuga*, *Fagus*, and *Cercis* were vulnerable to summer drought and/or winter warming, whereas others, especially *Quercus*, were insensitive to broad climatic signals. Local patterns could also differ from broader-scale projections derived from forest resource inventory (FRI) data. Loblolly pine (*Pinus taeda* L.), for example, experienced its greatest reductions in growth and fecundity in moist bottomlands during summer drought, even though its highest mortality occurred on xeric sites. The authors attributed this result to trees fully exploiting available growing space on wet sites, which enhanced intraspecific competition relative to dry areas.

Competitive effects dominate or covary with climate in a variety of other species. Competition dominated climate as a driving variable of radial growth in mature Scots pine (Sanchez-Salguero et al. 2015). Here, growth sensitivity to climate was principally observed under low competition. Climatic effects limited growth at low winter temperatures at high elevations and enhanced growth at middle elevations, but excessive heat reduced growth at low elevations. Elevation also interacted with competition in a study of elevational range shifts in three conifer species on Mount Rainier in Washington, United States (Ettinger and HilleRisLambers 2013). Growth was sensitive to snow depth and cold near tree line, but competition and life stage (saplings versus adults) determined performance in closed-canopy forests at lower elevations. By contrast, in a rare study of climate–herbivory interactions, a 16-year decline in regional precipitation consistently reduced height growth

differences in these demographic variables. Although interspecific differences in low-light mortality and size at sexual maturity were observed, the authors concluded that high diversity in southern temperate forests is maintained by partitioning multiple axes of local environmental variation among individuals (Clark et al. 2010).

The importance of local environment and competition was also evident in investigations of optimal temporal and spatial scales at which to measure species responses to aridity. In their work, Clark and colleagues (2014) found that the responses of trees to winter temperature and summer drought were heavily conditioned by local microenvironments, particularly light. Climate only achieved parity with local environment in determining fecundity and growth in a few life stages of a subset of species. For example, the

in Scots pine and Austrian pine (*Pinus nigra* Arnold), whereas the impacts of browsing by red deer varied widely among sites and individual trees (Herrero et al. 2016). Individual responses also varied more than mean differences between species under elevated carbon dioxide, where local shade was the principal influence on individual growth patterns (Mohan et al. 2007).

The importance of microsites and competition are well known to forest managers but have not generally been emphasized in broader-scale provenance tests or SDMs. Some researchers are re-emphasizing the importance of local adaptations, including the conservative survival strategies that adapt local provenances to weather extremes (Benito-Garzon et al. 2013, Whittet et al. 2016). In the context of AM, Whittet and colleagues (2016) suggested that managers should match AM candidates to local site conditions, as well

as projected future climates, and in the United Kingdom's Climate Match project, mixed provenance and species plots were established to reflect a risk-spreading "portfolio" planting strategy (Barsoum 2015).

Models that think outside the envelope

Recent climate-envelope SDMs incorporate various combinations of local environmental variables, species traits, and niche boundaries. The influence of GCM choice on mapped species distributions has also been considered, which underscores the complexity and variety of GCMs that exist. Each GCM incorporates different spatial scales and parameterizations, and different Earth System processes are included or excluded, depending on the model. They therefore produce a wide range of projections future species ranges. Near-term range projections from seven GCMs applied to the dwarf birch (*Betula nana* L.) and sweet chestnut (*Castanea sativa* Mill.) varied more than those of different representative (greenhouse gas) concentration pathways (RCPs) within a given model (Goberville et al. 2015). In other words, individual GCM characteristics mattered more to range projections than assumptions about radiative forcing. The common practice of reporting average projections based on GCMs ensembles may therefore disguise potential future climate variability and mask climatic extremes to which species might be subjected.

Comparisons of actual versus modeled species distributions further demonstrate that climate–range correlations describe realized rather than fundamental niches. In a comparison of European and naturalized North American distributions for 51 plant species, all species occupied a wider climate space in North America than in their native ranges. This was especially true for species with geographically restricted or climatically narrow European ranges (Early and Sax 2014). Reversing this approach, Boiffin and colleagues (2017) found that an SDM with high predictive power for the North American range of Douglas fir failed to predict most of the species' range in Europe, where it grows in climates with no analogue to its native range. Using a broader set of climatic variables and a different modeling approach, Isaac-Renton and colleagues (2014) found high climatic congruence of North American and European ranges of Douglas fir. They go on to use their model to recommend changes to source provenances targeted at future European climates.

Direct climatic influences over species' realized niches may have been overestimated, and many range limits are likely dictated by factors other than climate. However, the addition of plant functional traits (*sensu* Violle et al. 2007) and local environmental variables has added complexity and realism to SDMs. Sormunen and colleagues (2011) found that topographical and edaphic variables (measured on an 1100-square-kilometer grid at 1-hectare resolution) greatly improved GCM projections of current species ranges. Like Goberville and colleagues (2015), these authors found that different models produced widely differing projections of

future species distributions. Species traits, especially susceptibility to natural disturbances, significantly modified projected future ranges of over 100 North American tree species (Matthews et al. 2011). Iverson and colleagues (2016) extended this approach to investigate AM candidate species to replace black ash (*Fraxinus nigra* Marsh.) in Minnesota. This species is critically vulnerable to the exotic emerald ash borer (*Agrilus plannipenis*). The authors ranked AM candidates, in part, by exploring their co-occurrence with black ash in more southerly tree communities.

Climate–trait interactions may indicate important tradeoffs among traits in AM candidates. Significant site by provenance interactions among Spanish provenances of maritime and Scots pine showed that interprovenance differentiation of acclimation and phenotypic plasticity was driven by local conditions (Garzón et al. 2011). Species distribution models that incorporated phenotypic plasticity showed a greater percentage of the native range being occupied in the future compared with SDMs that treated species traits as homogeneous. Species distribution models based on common garden data projected improved performance of warm climate provenances of trembling aspen transferred to cooler seed zones (Gray et al. 2011). However, late frosts and spring drought are associated with later budburst in aspen from dry regions in western North America relative to environments with more rainfall (Li et al. 2010). Echoing concerns over cryptic maladaptation, Li and colleagues (2010) suggested that long-distance transfers of aspen provenances from warm and wet to cold and dry environments could buy high growth rates at the expense of increased vulnerability to spring droughts and frosts.

Discussion

Forest managers are caught in a vice between the need to make current decisions and the fact that the consequences of those decisions will be realized in a distant and uncertain future. Although this has always been the case, climate change exacerbates uncertainties and imposes decisions that may carry greater risks than in the past. To these risks are added the challenge of translating a flood of research across multiple disciplines into management actions. From this review, we believe a number of important lessons emerge for those considering AM as a preemptive strategy for coping with climate change: (a) Provenances within species often display coordinated suites of adaptive traits whose character varies across regional climates (e.g., Liepe et al. 2016). Such regional adaptation is not always evident, however, and many species show no apparent phenological response to multidecadal climate change (Parmesan 2007). As a corollary to these findings, the results of manipulative and survey-type experiments are frequently contingent on tree size and age, as well as on the local communities of species in which they are embedded. (b) Phenology responds to climate in more complex ways than many models of budburst or bud set predict. Budburst dates affect the timing of budset (Keenan and Richardson 2015). Spring temperatures (Körner et al. 2016),

temperature reversals (Jönsson et al. 2004), and spring temperature variability (Zohner et al. 2017) provide important parameters for understanding phenological strategies. (c) Study duration and the length of time series influence our perspectives on the ability of species to adapt. Short time series disguise cryptic maladaptation (Benito-Garzon et al. 2013, Whittet et al. 2016), and conclusions based on a single extreme weather event are likely to be misleading because the characteristics of such events vary widely (George et al. 2015). (d) Individuals and microclimates matter. Local reactions of individuals, embedded in specific competitive spaces and microenvironments, often supersede regional climatic influences on species growth and survival (e.g., Clark et al. 2014). (e) Projections of current and future species ranges are greatly influenced by the details of the GCMs and climatic variables chosen to drive SDMs. Median projections from model ensembles are unlikely to capture the full range of climates that species can inhabit (Early and Sax 2014, Goberville et al. 2015). However, the incorporation of species traits, local variables, and even species communities into modern SDMs is providing new insights into and possibilities for AM practice (e.g., Iverson et al. 2016).

These observations suggest some conclusions about and recommendation for AM experiments and practice. First, uncertainties about the magnitude and precise details of future climate change imply that it may be unwise to search for "optimal" AM genotypes to fit climate targets when these are based on single models or a lone RCP. Average global temperatures could increase by as little as 1.4°C or as much as 4.6°C above 1990 levels by 2100 (Knutti et al. 2013). In boreal and polar ecosystems, greater temperature increases are expected (Price et al. 2013). Model-based uncertainties about future temperature are therefore likely to be amplified. AM strategies therefore need to be diversified to include provenances from a greater variety of regional climates, as well as local varieties growing at a given site (Whittet et al. 2016, Andrew Leslie, National School of Forestry, Cumbria, United Kingdom, personal communication, day Month year). Provenances should also be drawn from a wider range of precipitation regimes, because regional precipitation projections are variable and often inaccurate (Wang et al. 2016). By extension, this suggests that AM candidates should be selected using a range of GCMs rather than relying on single projections gleaned from ensemble averages. Some of these candidates are likely to be nonnative species. Cedar of Lebanon (*Cedrus libani* A. Rich) is one species whose varieties are resistant to climates harsher than those targeted for ASM (Messinger et al. 2015). In the United Kingdom, over 70 novel trees are being considered for planting into a tree flora where forest plantations are already dominated by North American exotics (SilviFuture 2017).

Data deficits and the choice of metrics used to measure key variables (e.g., leaf senescence; Gill et al. 2015) further complicate interpretation and prediction. Efforts to quantify long-term interactions between climatic and biotic variables are hampered by short time series and long census intervals,

which average out the effects of weather variability and extreme events (reviewed in Clark et al. 2014). As has been pointed out by Parmesan and Hanley (2015), it is difficult to identify functional traits that will explain plant performance under different conditions. Strong interactions between climatic and biotic variables further complicate the interpretation of trends and patterns. Parmesan and Hanley (2015) concluded that deficits in data and theory and the failure to integrate ecophysiological traits into holistic models of plant behavior confound our ability to predict plant responses to ACC.

How does uncertainty affect assisted-migration policy and practice?

Because projections are probabilistic, they always arrive with associated degrees of uncertainty. Forestry management, however, has traditionally been based on the premise that tree establishment and growth take place in a relatively constant climate. This tension between the desire for certainty and coping with the unknowns that attend AM science helps to explain why AM is a contested policy arena (Neff and Larson 2014) and why some forest scientists are skeptical whether it can succeed (Whittet et al. 2016).

A recent survey demonstrated that forest managers and scientists hold a number of divergent views (within and among their own professional groups) about AM (Neff and Larson 2014). Although the survey participants agreed that AM (which the authors call "assisted colonization") has a potential role in adapting forests to climate change, some believed that it would cause more problems than it solves. The respondents also disagreed about whether or not allowing forests to adapt naturally to climate change would be better than adopting AM, on whether species should be moved outside of their native ranges, and on the need for wider public debate about AM.

Whittet and colleagues (2016) explored some management concerns with, and implications for, AM practice of findings such as those reviewed in this article. Among other things, they point out that the challenges posed by cryptic maladaptation go beyond the mortality imposed by rare, extreme weather events. When mixtures of local and nonlocal provenances are planted as a hedge against climatic uncertainty, vigorously growing nonlocal provenances could outcompete and eliminate slower growing local material, only to succumb to environmental stress themselves at a later date. AM species that get infected with high levels of pathogens in the recipient location could raise endemic inoculum levels to the point at which normally nonthreatened local species are threatened. Whittet and colleagues (2016) also underscored the importance of local edaphic and topographic adaptation, speculating that local provenances will often be better adapted to these conditions than AM genetic material. They concluded by arguing for a precautionary approach to AM in the United Kingdom, suggesting that nonlocal seed sources should be planted only under well-defined conditions. Assisted migration thus emerges as

Table 1. A summary of some recommended future directions in assisted migration (AM) research and practice.

Recommendation	Rationale
Long-term studies of growth and phenology	• Need to study acclimation to climate over lifetime of the tree. • Capture a wider range of climatic variation, including extreme events. • Study critical latitudinal shifts as they relate to phenological signals (e.g., chilling, forcing, and photoperiod).
Experiments designed to probe cryptic maladaptation to target climates	• Cryptic maladaptation has been shown to cause mortality in trees otherwise adapted to average climate but will likely only show itself under once-in-100-years (or even l) events. • The incidence of extreme events is widely expected to increase as climate change proceeds.
Experiments that combine multiple variables and stressors—including climate extremes, competition, and pathogens—but also facilitation	• Focus on single variables or a limited selection of variables will lead to misleading conclusions about tree–climate interactions. • A planned program of experiments incorporating different combinations of variables is likely to be necessary to tease out individual variable contributions.
Studies that incorporate individual variability among plants in local environments	• We need to know the circumstances under which local conditions are more important than climate in determining growth and survival—and vice versa. • Microclimate (e.g., soils, topography, and water-table depth) filters the global influence of climate.
Studies of provenance responses to multiple axes of climate averages and seasonality	• Provenances may experience similar average climates but be adapted to distinct patterns of seasonality, as well as physical conditions (e.g., snowpack depth and seasonal patterns of soil water).
Design and study growth and survival of novel tree communities designed for AM	• Tree communities and stands combining provenances may be more resilient to climate change than single tree stands. • Species planted in intimate mixtures affect each other's morphology and growth in ways that may not be easily predicted from their growth in isolation. • In mixtures of provenances, need to know whether local provenances outcompeted by AM provenances.
Models that capture climate variability, as well as shifts in climatic averages	• Weather extremes are likely to be more influential than shifts in average climate on tree growth and survival. • Need to capture the probable effects of weather extremes on cryptic maladaptation. • Such models might be parameterized using daily rather than annual weather data.
Two (or more) stage models incorporating local abiotic variables, community dynamics, etc.	• Recent species distribution models incorporate abiotic constraints (e.g., soils, topography, and vulnerability to disturbance) and sometimes knowledge-based evaluation. However, these models have, so far, been applied across a fairly limited geographic range.

a classic "wicked problem," in both its ecological and technical aspects, and in its policy and subjective dimensions (Neff and Larson 2014).

Conclusions and recommendations

The research reviewed here could indicate a number of fruitful directions for AM practice and research. In table 1, we report and expand on recommendations for future AM research (see also Benito-Garzón et al. 2013, Parmesan and Hanley 2015, Whittet et al. 2016). In figure 3, we offer a preliminary framework that links the different research themes discussed in this article. In this framework, detailed knowledge of local conditions, community composition, and phenology are likely to be key predictors of tree responses to translocation. A knowledge of species and provenance tolerances for out-of-range extremes is also important. The suite of AM candidates will also be informed by SDMs that incorporate a range of GCMs and RCPs, as well as using soils and topography as filters on potential distributions.

To provide calibration data for such models, researchers need to investigate interactions between climate, local environment, and individual plant variation. More work is also needed to understand climatic responses among trees as they interact with other species in forest communities rather than as isolated taxonomic units. Phenological rankings of species in mixed forests will change as climate change alters the balance between chilling and forcing (Laube et al. 2014). AM candidates can be studied for their potential to be translocated among similar southern and northern communities (Iverson et al. 2016), but the potential effects of latitudinal shifts on responses to phenological signals also need to be understood.

Long-term studies are needed to capture the full spectrum of climatic variability and early warning signs of cryptic maladaptation to local climates. The effects of extreme events and nonclimatic abiotic variables should be further integrated into SDMs, and empirical studies to investigate interactions among multiple stressors and climate extremes should be established. Anticipating the use of ARE and ASM, we also need to investigate the performance and resilience of novel tree communities (Park et al. 2014, Parmesan and Hanley 2015) and phenological plasticity in the face of novel environments. Novel communities may arise naturally as trees disperse into newly suitable environments or intentionally as part of multispecies ARE and ASM plantings. Given the rapidly closing window for constraining global warming to 2°C, ARE and ASM could be used to modify species composition in existing forests, to import climate-resilient ecological analogs to local species, or to design novel tree communities chosen for their complementary traits (Tobner et al. 2014, Whittet et al. 2016) or resilience to disturbance.
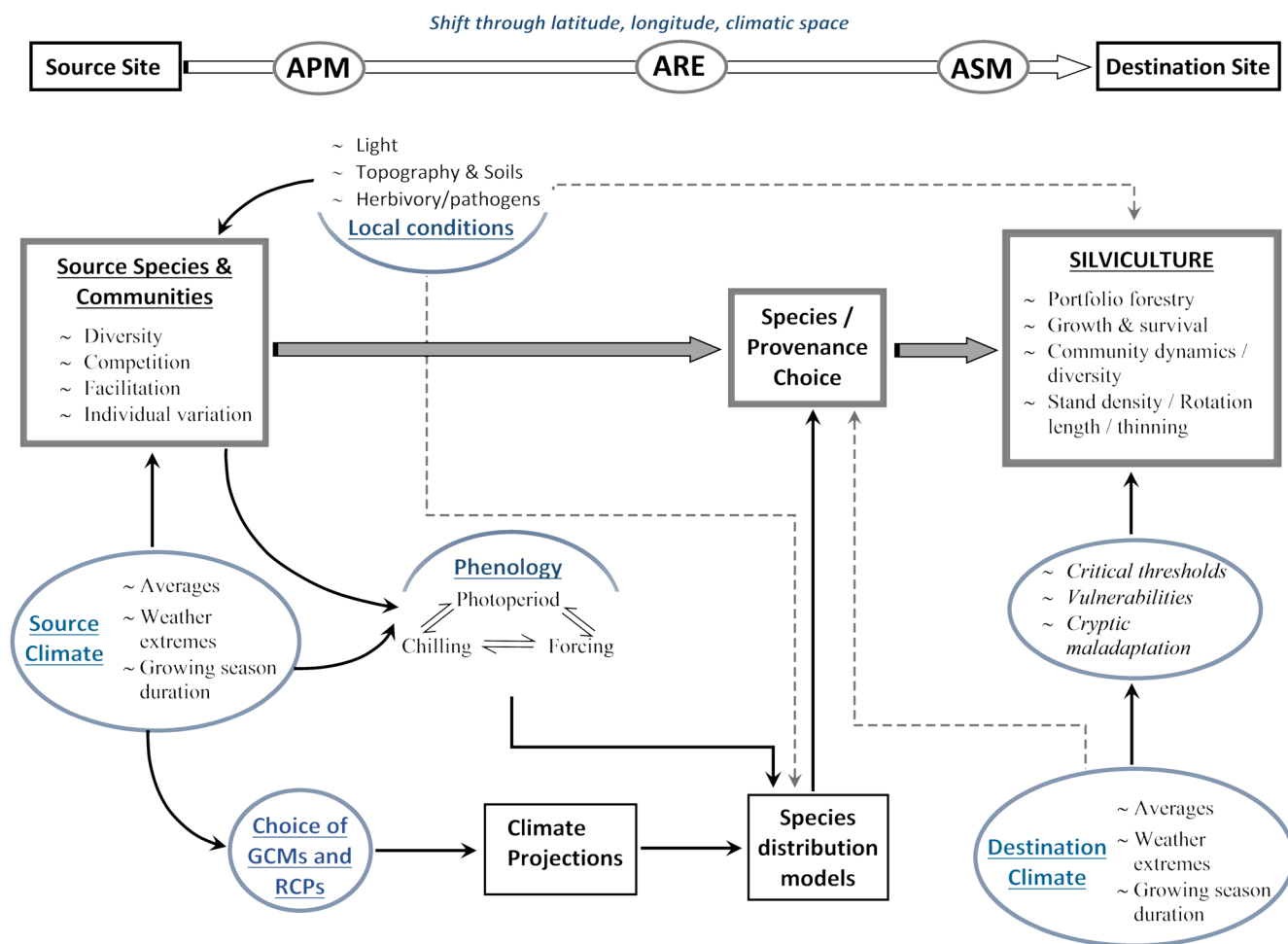
Figure 3. Conceptual diagram of relationships among the research themes discussed in the text. Boxes indicate inputs or outputs to decisions, with key considerations outlined in thick grey lines. Ellipses indicate key variables and processes that have to be considered in moving genetic material. Local conditions determine community dynamics at the level of stands and small groups of trees, while source area climate influences the limits of adaptation. Source climate also determines the timing and stimuli of phenological events. The distance through which genetic material is translocated (at top, with three AM categories) is likely to determine the vulnerability of trees to key vulnerabilities at the planting site, particularly the exposure of cryptic maladaptation by extreme events. Ideally, climate, phenology and local conditions to which species are adapted should all inform the SDMs that influence species choice. Species or provenance choice, planting site climate, and local conditions at the planting site will determine silvicultural strategies adopted for AM candidates. Planting a portfolio of different genotypes, monitoring growth and survival, and judicious use of thinning and other stand management techniques may improve stand resilience.

In conclusion, AM research requires a renewed focus on the influence of local environments, intraspecific and interspecific interactions, and subsequent variability in individual tree performance. It is at this local level that the generalized effects of regional and global climatic change will be played out. The design parameters adopted at this level (e.g., species and provenance combinations, planting density, microsite quality, and stand-level silvicultural treatments) may determine the success or failure of AM projects more than the climatic shifts to which species are subjected, although this may change as species are moved through increasing latitudinal distances. With that in mind,

managers considering AM should move beyond single-species models and common garden trials to study the ways in which community composition affects tree growth, morphology, survival, and mortality (e.g., Menalled et al. 1998, Paquette and Messier 2011).

The multifaceted nature of climate adaptation requires a flexible, community-oriented approach to AM projects. If adopted, AM will become part of a portfolio of management approaches focused on building climate-resilient forests. These approaches will likely involve maintaining (and improving) stand, species, and structural diversity, as well as learning to cope with the unpredictable effects of

interacting, nonadditive stressors that attend rapid environmental change (Lindenmayer et al. 2016). Such a program of research and practice will require changes to forest management policies and practices, but given the inadequate international response to the climate crisis, these changes may be needed as a matter of urgency.

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Andrew Park (a.park@uwinnipeg.ca) is affiliated with the Department of Biology at the University of Winnipeg, in Manitoba, Canada. Carolyn Talbot (talbot.cg@gmail.com) completed her master's degree in Bioscience, Technology and Public Policy at the University of Winnipeg.