Forest Ecology and Management 551 (2024) 121552

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Framing recent advances in assisted migration of Trees: A Special Issue

1. Introduction

Climate is changing faster than long-lived species, such as forest trees, can migrate or adapt, risking adverse impacts on tree growth and forest composition (Aitken et al., 2008; Alberto et al., 2013; Sittaro et al., 2017). Nevertheless, current forest management and restoration tools, from tree breeding and seed zones to growth and yield models, assume a stable climate and that local sources are the best adapted (McKay et al., 2005; Bucharova et al., 2017; Alía et al., 2022; Park and Rodgers, 2023). Increasing frequency and severity of extreme events, including heat waves, drought, pest and disease outbreaks, windstorms, and altered wildfire regimes have caused lowered productivity and increased mortality in many biomes (Sullivan et al., 2020; de Dios et al., 2021; Hartmann et al., 2022; Martinez del Castillo et al., 2022; Robbins et al., 2022). One response to the threats to forests posed by rapidly altered climate is the intentional movement of tree species and populations to more hospitable habitat and to replace species unable to thrive. This assisted migration (AM) is an adaptation strategy for overcoming the gap between a changing climate and an evolutionary response by forest trees that facilitates natural range expansion in response to climate change (Aitken and Whitlock, 2013; Aitken and Bemmels, 2016; Sang et al., 2021).

Assisted migration (often described many ways including species translocation; (Griffith et al., 1989; Dumroese et al., 2015) applied to plants is essentially moving seeds or other genetic material from one bioclimatic zone to another. Approaches to AM are differentiated by the three target migration distances: assisted population migration (moving species or provenances within their current range), assisted range expansion (moving from the current range to suitable areas adjacent to the current range), or assisted species migration (moving a species far outside its current range) (Pedlar et al., 2012; Williams and Dumroese, 2013; Ferrarini et al., 2016). The target migration distance, along with the purpose of undertaking AM (i.e., preserving economic goods, sustaining ecosystem services, or avoiding species extinction) provide a framework for examining the potential ecological risks and benefits of AM (Aubin et al., 2011; Breed et al., 2013; Iverson et al., 2019; Clark et al., 2022).

Foresters have a long tradition of moving genetic resources through silvicultural operations but mostly with the singular purpose of timber production (Kellison et al., 2013; Bennett, 2015; Myking et al., 2016; Brus et al., 2019; Hirsch et al., 2019), at times to the detriment of the receiving socio-ecological system (Byerlee, 2014; Lyons and Westoby, 2014; Jiang et al., 2016; Malkamäki et al., 2018; Bond et al., 2019). Nevertheless, AM may be used to avoid losses in forest growth and productivity, prevent species extinctions, and sustain ecosystem services and biodiversity (Gray et al., 2011; Benito-Garzón et al., 2013; Dumroese et al., 2015; Clark et al., 2022; Bellis et al., 2023; Gustafson et al., 2023; Mauri et al., 2023). Although assisted migration is not without risks (Pedlar et al., 2012; Breed et al., 2013), climate warming has demonstrably affected many forest ecosystems and arguably, acting is less risky than not acting (Palik et al., 2022).

This special issue on assisted migration in forestry features ten papers with 57 authors from 13 countries that examine various aspects of assisted migration. Most of the papers focused on a single tree species. The commercially and ecologically important *Fagus sylvatica* L. was the topic of three papers (Budde et al., 2023; D'Odorico et al., 2023; Kurz et al., 2023), while other authors focused on *Quercus rubra* L. (Lindback et al., 2023), *Corylus colurna* L. (Šeho et al., 2023 and *Larix decidua* Mill. (Poupon et al., 2023). A review of North American provenance studies (Park and Rodgers, 2023) featured 49 species, mostly commercial conifer species. A newly established assisted migration study, the Desired REgeneration through Assisted Migration (DREAM) project in eastern Canada and the USA (Royo et al., 2023), is evaluating 14 species. Two papers examined other aspects of assisted migration. A simulation study in northern hardwoods (Gustafson et al., 2023) evaluated transition strategies with the LANDIS-II forest landscape model and direct links to climate and atmospheric drivers to see if major forest functional types were maintained under some climate change scenarios with AM strategies. Kusbach et al. (2023) suggested that ecological classification could be used to minimize risks and uncertainty associated with assisted migration. This introduction to the special issue aims to place these papers in a broader context of AM.

2. Provenancing strategies for assisted migration of forest tree species

Although frequently questioned, a long-lasting management paradigm that 'local-is-best' still prevails in collection of forest reproductive material for reforestation and restoration projects worldwide (McKay et al., 2005; Bucharova et al., 2017; Alía et al., 2022). The debate is fueled with findings on non-local provenances outperforming local ones. For example, in a 60-year review of provenance trials in Australia, Harrison et al. (2017) found that although "local provenances tended to be above the median performance, they were no more represented in the upper quartile - nor were they the best performing provenance more often - than would be expected through chance alone." An important issue is the spatial distribution of provenances within the species natural distribution, as the genetic specificity of growth reactions diminishes toward the distributional margins of a given species (Klisz et al., 2019). When debating provenancing, one should consider more than just a tree

https://doi.org/10.1016/j.foreco.2023.121552

Available online 8 November 2023

species performance. Introduction of non-local provenances can disrupt natural patterns and ecological networks (Bucharova et al., 2022).

The usual practice in transfer of reproductive material relies on recommendations of a single provenance seed collection and matching to the planting site. One of the tools to guide climate-smart seed sourcing is dynamic seed zones (Fremout et al., 2021). To reduce the risk of maladaptation of a single provenance to the new conditions, and occurrence of genetic bottlenecks due to low genotypic diversity captured, more strategies in addition to local provenancing are suggested (Table 1).

Fagus sylvatica is an important temperate European species suffering from changing and stressful environmental conditions, including crown damage, growth reductions, and increased mortality following recent severe droughts. The closely related *Fagus orientalis* Lipsky, found growing in southeastern Europe, Turkey, the Greater Caucasus region, and the Hyrcanian forest of Iran, has higher drought tolerance and has been suggested for AM. Kurz et al. (2023) examined *F. orientalis* stands across Western Europe, tracing their origin and assessing implications for assisted gene flow from hybridization with *F. sylvatica*. Taking advantage of already introduced *F. orientalis* plantations in Central Europe to assess the impact of gene flow from different *F. orientalis* provenances on neighboring *F. sylvatica* stands was a goal of Budde et al. (2023). In northern Germany, they examined *F. sylvatica* and *F. orientalis* hybridization in a stand more than 100 years old. D'Odorico et al. (2023) demonstrated the potential of leaf spectroscopy to replace resource-intensive genetic analysis and field phenotyping for the discrimination and characterization of these two beech species.

Recent modeling work concluded, however, that seed-sourcing methods based on climate or provenancing yielded results no better than traditional seed-sourcing methods (Notivol et al., 2020). Given that phenotypic plasticity, which can be expressed several ways (Chambel et al., 2005), provides species with a way of coping with environmental perturbations (Gratani, 2014; Chambel et al., 2005; Vitasse et al., 2010) but is still largely unknown (Valladares et al., 2006) and difficult to measure in trees (Chambel et al., 2005), this result is not too surprising. Indeed, high degrees of plasticity have been noted in trees (Vitasse et al., 2010) and this may contribute to tree species occupying a range of environments within a population (Ackerly et al., 2000). While Richter et al. (2011) concluded that phenotypic plasticity can increase a species' resistance to climate change, recent work reveals that plant plastic responses to climate were, however, muted compared to non-climatic factors and that this should be considered when investigating plasticity and climate interactions (Stotz et al., 2021). Thus, no single provenancing strategy is likely to work universally, and selection of provenancing strategies should consider site conditions, species genetic variation, and local adaptation combined with climate projections for the focal site (Ivetić and Devetaković 2016) while being mindful of phenotypic plasticity.

Understanding the response of a species to rapid climate change is important to developing assisted migration strategies. *Larix decidua* is

Table 1
Synopsis on provenancing strategies (updated from Ivetić and Devetaković 2016).

Provenancing strategy	Brief description	Advantages	Disadvantages	Best to use	Source
Local	Collection of seeds vary in the focal site. Risk level depends on original population size.	No risk of maladaptation and outbreeding depression. Low failure rates.	Risk of genetic drift. Low production of new genotypes. Conditions driving local adaptation can change.	Where only local populations remain, and no substantial change of distribution is predicted.	(Broadhurst et al., 2008; Sgrò et al., 2011; Breed et al., 2013)
Site-adjusted	Use of a comprehensive landscape genomic approach to select the best mixture of genotypes for focal site.	Minimize outbreeding depression and at the same time increase genetic diversity and reduce the risk of inbreeding depression.	High costs associated with genomic analyses and the complexity of bioinformatic and statistical analyses.	Restore sites ranging between moderately disturbed and highly degraded.	(Carvalho et al., 2021)
Regional admixture	Seeds are sourced from multiple populations within the same region as the focal site and mixed prior to use.	Increase the genetic diversity, while restricting seed origins to a regional scale will maintain regional adaptation.	Risk of outbreeding depression. Conditions driving local adaptation can change.	When risk of non-local provenances to disrupt natural patterns of within-species biodiversity exists and will affect ecological networks.	(Bucharova et al., 2022)
Composite	Mimic natural gene flow patterns by use of seed mixture from populations at various distances to the focal site.	Encourages production of new genotypes, potentially facilitating rapid adaptation to novel conditions.	Using seed from distant sources may result in maladaptation to local conditions. Outbreeding depression risk.	Where no significant range shifts are predicted, and only small local populations remain.	(Broadhurst et al., 2008; Breed et al., 2013)
Admixture	Collection of seeds from wide array of provenances, capturing a wide selection of genotypes from various environments with no spatial bias towards the focal site.	Build evolutionary resilience by introduction of more additive genetic variation.	Risk of introducing invasive genotypes. High risks of introducing maladapted seed. Substantial risk of outbreeding depression.	Where drastic changes are confidently predicted, growth data is lacking.	(Breed et al., 2013)
Predictive	Use of genotypes that are determined to be adapted to projected conditions. Requires data on local adaptation of many populations. Requires climate projections for the target species and planting site.	Low risk of maladaptation, inbreeding depression, and outbreeding depression. Low risk of failure if seed source is matched well with predicted environments.	Substantial risk of failure if seed source is poorly matched with predicted environments. Lack of data on local adaptation for most species. Uncertainty of climate change predictions.	For species expressing local adaptation to environmental variables.	(Sgrò et al., 2011; Breed et al., 2013)
Climate-adjusted	Combine genetic diversity and adaptability, targeting projected climate change directions. Collection of seeds biased toward the direction of predicted climatic change, but not exclusive to it.	Enhance climate-resilience of planting material by mixing genotypes from a climatic gradient, including local genotypes as well.	Risk of outbreeding depression. Risk of disruption of local adaptation to non-climatic factors. Lack of future climate-matching populations.	Where data on inter-population genetic variation are available.	(Prober et al., 2015)

widely planted and Poupon et al. (2023) quantified the genotype × environment interaction (GxE) of a larch provenance using factor analytic (FA) modeling to correlate growth variables (mean annual height and diameter increments, and wood density) with site variables. They concluded that the FA methodology is a valuable tool for selecting suitable genotypes adapted to specific environmental conditions.

Establishing mixed forests with an admixture of other tree species (e.g., conifers with scattered broadleaves) has been proposed as mitigation and adaptation responses to climate change (Jandl et al., 2015; Bauhus et al., 2017). *Corylus colurna* is adapted to difficult environmental conditions and has been promoted as a valuable alternative tree species in some European regions (Albrecht and de Avila, 2018). Overexploited in its natural distribution in Asia Minor, the Caucasus, and the Balkan Peninsula because of its valuable wood, *C. colurna* is found only in small and isolated populations. Šeho et al. (2023) examined its genetic structure and variation in trees of 25 populations from throughout its natural distribution. They found medium to high levels of genetic variation, with somewhat lower values in Georgia and Türkiye compared to Balkan populations, suggesting separate refugia and migration pathways during the Holocene. Since 2018, provenance trials for *C. colurna* have been installed in Germany (mostly Bavaria and Baden-Württemberg) with provenances from the Balkans and Türkiye (Liesebach et al., 2021).

3. A framework for assisted migration decision making

Strategies for adapting to climate change have been described as incremental, anticipatory, and transformational (Stanturf, 2015) or similarly as resistance, resilience, and facilitation (Millar et al., 2007). These three strategies are, respectively, forestalling impacts and protecting valuable resources, improving the capacity of ecosystems to return to desired conditions after disturbance, and actively facilitating the transition of ecosystems from current to new conditions. The non-management or passive response (Jandl et al., 2019) is incorporated in the incremental/resistance strategy. Current conditions and anticipated magnitude of change (low, medium, or high) dictate the appropriate management response (Millar and Stephenson, 2015). Assisted migration and provenancing strategies are included in the climate change adaptation strategies (Table 2).

In deciding on an AM strategy, four initial questions are (1) which species need to be moved; (2), where should the species be moved to; (3) how soon should the species be moved; and (4) is a species being considered because it is at risk from climate change or is it a candidate for moving because it could replace an at risk species? Generally, a species is more likely to be at risk if it is at the trailing edge of its distribution, e.g., where warmer and possibly drier future conditions are likely. Species at the leading edge of the distribution may be good candidates for assisted population migration or assisted range expansion. Candidates for replacing at risk species may be relatively near (range expansion) or far away (assisted species migration). Although the current climate models are of insufficient resolution for many management decisions, they are improving and becoming more generally available and tractable for resource managers, particularly dynamically down-scaled regional climate models (e.g., Jacob et al., 2020; Kotamarthi et al., 2021; Liu et al., 2021).

Table 2
Adaptation, assisted migration, and provenancing strategies.

Activity Adaptation[1]	Strategy Incremental/ Resistance	Anticipatory/ Resilience	Transformational/ Facilitation
Provenancing[2]	Local Site Adapted	Regional Admixture Composite Predictive	Admixture Predictive Climate Adjusted
Assisted Migration[3]	Assisted Population Migration	Assisted Range Expansion	Assisted Species Migration

[1] Adapted from Stanturf (2015) and Millar et al. (2007).
[2] Adapted from Ivetić and Devetaković (2016).
[3] Adapted from Williams and Dumroese (2013).

Common garden studies are useful for evaluating which populations are best suited for climatic conditions at range limits. For example, *Q. rubra* is an important eastern North American forest species with an adaptation lag, i.e., climate is shifting the potential suitable range faster than *Q. rubra* can migrate. Lindback et al. (2023) established two common gardens to evaluate twelve populations representing the current range. The goal was to determine which populations were best suited for climatic conditions at the range limits in the northeastern and central USA. They observed aboveground growth, phenology (senescence, budburst), and frost damage for three years and found that southern seed source populations from warmer and wetter locations showed greater relative growth rate at the central range site but were susceptible to frost damage in the spring and autumn. Northern seed sources, from colder, drier locations, had earlier budburst and were able to utilize early growing season snow melt and higher solar radiation and grew better at the northern range site and senesced earlier, avoiding autumn frosts.

Range-wide knowledge of the interplay between climate, growth, and ecophysiology is incomplete for many species (Valladares et al., 2014; Díaz et al., 2022). As Park and Rodgers (2023) recommended, growth and performance of potential migrants should be assessed against climate variables, other than general climatic means, that are linked to ecophysiological processes governing growth, survival, and phenology, such as temperature extremes, frost and drought indices, or growing-season duration. Particular notice should be given to extreme weather, likely to be a key determinant of long-term tree health and persistence (Sang et al., 2021; Zeng et al., 2022; Lindback et al., 2023).

Some guidance may come from bioclimatic envelope models (BEM) to delineate current and projected distributions (Pearson and Dawson, 2003; Araújo and Peterson, 2012; Wang et al., 2012). Bioclimatic envelope models associate current and/or past climate and species' occurrences to identify favorable regeneration and persistence conditions using various statistical approaches. These models have several uses but in AM, they are applied to identifying suitable habitat under future climate. Use of BEM has progressed from using just one or two models to multiple models in ensembles (Araújo and New, 2007). Although many BEMs only consider climate factors, recent work has incorporated terrain, soil, and other environmental factors on species distribution (Hamid et al., 2019; Wang et al., 2023). For example, Brunton et al. (2023) used bioclimatic variables and topographic factors, regression (GLM) and Random Forest (RF) distribution models with an ensemble of three CMIP6 climate models and four emission scenarios to model spatial dynamics of *Fontainea australis* Jessup & Guymer and *Fontainea oraria* Jessup & Guymer in Australia. Kusbach et al. (2023) suggested another approach, using ecological classifications that incorporate vegetation dynamics to characterize sending and receiving site conditions.

Projecting future habitat suitability based on current or past occurrence requires consideration of how much of the species distribution has been sampled for presence/absence (Araújo and Peterson, 2012) including whether the complete environmental range has been characterized. Because of phenotypic plasticity and dispersal limitations, the realized niche that is sampled may underrepresent the fundamental niche. That is, an area may be biotically suitable under current climate, but the species of interest is not present due to competition, dispersal limitations, or past management (Thuiller et al., 2008; Araújo and Peterson, 2012; Valladares et al., 2014; Pacifici et al., 2017; Norberg et al., 2019).

When to implement AM is an ongoing question; changing climatic and landscape conditions in its current range and in possible receiving locations also will affect risk status. Uncertainty about future climate conditions in potential receiving areas affects decisions about where and how far to move a species. Projections of future climate are uncertain at the temporal and spatial scales relevant to AM but overall, projections paint a picture of a variable but potentially warmer and drier climate with increased frequency of extreme weather events (IPCC, 2023; Park et al., 2023). The spatial and temporal uncertainties of future climate (where, when, and by how much climate changes) suggest that many decisions could be maladaptive if a species is introduced too soon or to an improper receiving environment (Fisichelli et al., 2016; Anderegg et al., 2020). The challenge is for an introduced species or population to not only be adapted to future climate, but robust and able to persist under current climate.

Of particular concern is the possibility of a novel climate developing, that is, climatic conditions without modern analogs, characterized by high seasonality of temperature and spatially variable shifts in precipitation (Williams and Jackson, 2007; Williams et al., 2007; Mahony et al., 2017). Among the multiple existing metrics (Garcia et al., 2014), the velocity of climate change, representing the rate of movement of climatic isopleths across a landscape (Loarie et al., 2009) is widely used in conservation planning (Brito-Morales et al., 2018) and may be useful in AM decisions. Assisted migration may not be a near-term concern in regions where ecosystems are projected to change little over time; in such cases, incremental adaptation may be the prudent course. In regions likely to experience rapid climatic shifts, or where great uncertainty prevails, AM may be, however, a useful tool in a portfolio of management actions aiming to create a diverse landscape that reduces the risk of socio-ecological losses (Wang et al., 2012).

4. Implementing assisted migration

Rather than rejecting AM outright as too risky, researchers and practitioners are implementing AM in small-scale, experimental fashion to gain the knowledge for broader-scale implementation desired by land managers (Breed et al., 2013; Bucharova, 2017; Breed et al., 2018; Karasov-Olson et al., 2021; Sáenz-Romero et al., 2021; Palik et al., 2022). For example, the DREAM project (Royo et al., 2023) provides a framework for establishing an assisted migration study that combines basic and applied research to reduce uncertainties and derive climate-informed planting approaches. DREAM proceeds in step-wise fashion by sourcing seed in a climatically informed manner, experimentally testing this sourced stock to probe for physiological maladaptation under controlled settings, growing the stock in the field under a range of silvicultural scenarios, and forecasting long-term outcomes using models parameterized from the controlled- and field-tests. Included in the field testing are treatments that include levels of browsing pressure by local herbivores and intraspecific competition that will co-regulate seedling success. The project is implemented at two experimental sites: one in Quebec, Canada and another in Wisconsin, USA.

The DREAM approach exemplifies the increased emphasis on the role of microenvironments, herbivory, and intraspecific interactions as covariates that can explain substantial variation in seedling establishment and survival (Park and Talbot, 2018). A fair test of a provenance or species in an AM trial must ensure that high-quality seedlings are outplanted well, and the direct effects of climate are separated from other factors such as herbivory and competing vegetation (Champagne et al., 2021a; Champagne et al., 2021b; Soubeyrand et al., 2023). As Royo et al. (2023) found, seed procurement and seedling production for AM seedlings were challenging because of administrative constraints, low availability of seed sources, and nursery managers lack familiarity with growth requirements of species from outside their region. These are widespread difficulties for reforestation and restoration globally (Haase and Davis, 2017; Bannister et al., 2018; Acevedo et al., 2021; Fargione et al., 2021; Graudal et al., 2022; Kindt et al., 2023).

Hopefully, the seedlings will experience the expected extreme climatic events during the life of the experiment. Accounting for ecosystem legacies (Johnstone et al., 2016; Jõgiste et al., 2017), especially from past land use management, is important, and the receiving ecosystem must be receptive to the assisted climate migrants. For assisted species migrations in particular, increased attention to the holobiont (Vandenkoornhuyse et al., 2015; Li et al., 2023) may require microbial symbionts to be augmented in the nursery if they are lacking in the receiving ecosystem (Aghai et al., 2019; Jauri et al., 2023).

Moving AM from a theoretical exercise to broad implementation is not unlike the current conversation concerning the use of biotechnology to save at-risk tree species from introduced pests (Jacobs et al., 2023). Successful implementation will require a multi-pronged approach that considers, melds, and communicates across a variety of disciplines and engages the general public, land managers, policy makers toward removing barriers (i.e., perceptions, polices, and regulations). As noted by Jacobs et al. (2023), this can be a complex, ongoing process requiring science-based data transparently provided clearly without bias and jargon. Building trust across an inclusive public spectrum that includes a range of knowledge and values is paramount (Jacobs et al., 2023). Indigenous communities must be included in participatory processes (Peterson St-Laurent et al., 2018; Palik et al., 2022; Royo et al., 2023). And while risk is indeed an important discussion point, so also is a focus on ecological and societal benefits (Jacobs et al., 2023). Stakeholders, especially land managers, must be accepting of the need for assisted migration, which can be an impediment if they are non-receptive to the need, hesitant to change, or risk averse to one or the other adaptation modes (Lieffers et al., 2020; Brennan et al., 2021; Findlater et al., 2022). For scientists engaging land managers, this can be further challenging because land managers often have different levels of working knowledge and perceptions (Rodriguez-Franco and Haan, 2015) and their willingness to employ climate change adaptation strategies, such as AM, is based on their confidence that implementing innovative approaches will be successful (Lenart and Jones, 2014). Managers must be confident that transformational adaptation using AM is "better" than a less radical departure from business as usual. Modeling approaches, such as the one used by Gustafson et al. (2023), can evaluate different transition strategies and compare outcomes in terms of goods and services.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank all the reviewers involved with the ten accepted manuscripts and Maria Elena Fernández, Editor-in-Chief at Forest Ecology and Management, for assisting with the preparation of this special issue. Financial assistance for manuscript preparation was provided in part by the USDA Forest Service, Rocky Mountain Research Station. The findings and conclusions presented are those of the authors and should not be construed to represent any official USDA or U.S. Government determination or policy.

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