



Reintroduction of at-risk forest tree species using biotechnology depends on regulatory policy, informed by science and with public support

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Abstract

Introduced pests (insects and pathogens) have rapidly increased the numbers of at-risk native forest tree species worldwide. Some keystone species have been functionally extirpated, resulting in severe commercial and ecological losses. When efforts to exclude or mitigate pests have failed, researchers have sometimes applied biotechnology tools to incorporate pest resistance in at-risk species to enable their reintroduction. Often erroneously equated solely with genetic engineering, biotechnology also includes traditional and genome informed breeding—and may provide a holistic approach toward applying genomic-based information and interventions to increase tree species' pest resistance. Traditional tree breeding is responsible for successes to date, but new technologies offer hope to increase the efficiency of such efforts. Remarkable recent progress has been made, and for some at-risk species, novel biotechnological advances put reintroduction within reach. The high costs of reintroduction of at-risk species at necessary scale, however, will initially limit the pursuit to a few species. Successful deployment of pest resistant material may require improved species-specific knowledge and should integrate into and leverage existing reforestation systems, but these operations are sometimes rare where pest threats are greatest. While use of some biotechnologies, such as traditional tree breeding, are commonplace, others such as genetic engineering are controversial and highly regulated, yet may be the only viable means of achieving reintroduction of some at-risk species. Efforts to modify policy toward allowing the use of appropriate biotechnology, especially genetic engineering, have lagged. Provided that risk-benefits are favorable, policy is likely to follow with public opinion; in some countries, society is now increasingly open to using available biotechnologies. Continued engagement using the most recent advances in social science to build public trust, combined with a science-based collaboration among land managers and regulators, will generate the collective momentum needed to motivate policymakers to act rapidly given the speed at which forest health threats unfold and the large areas they affect.

Keywords Biotechnology · Forest restoration · Genetic engineering · Invasive species · Resilience · Tree breeding

Urgency to reintroduce at-risk forest trees

Introduced pests (insects and pathogens) threaten forests around the world. Due to population expansion that drove associated market globalization during recent decades, the number of introduced (non-native) pests has increased exponentially in many regions (Aukema et al. 2010; Santini et al. 2013). As a result, introduced pests have had a substantial negative effect on forest ecosystems in some regions. In the United States (U.S.), for example, more than 450 alien pest species are present and although most cause minimal damage to forests, about 15 of these pest species account for a tree mortality rate of 5.53 terragrams of carbon (TgC) per year and threaten future loss of 41% of the total live forest biomass (Fei et al. 2019). Similarly, the total economic cost of common ash (*Fraxinus excelsior* L.) die-back in Britain is estimated to be £14.8 billion over 100 years, with more than half of the total cost (£7.6 billion) expected to occur within the next 10 years (Hill et al. 2019). Introduced pests may also negatively impact biodiversity and have important ecological and societal consequences (Mitchell et al. 2018, 2021). In addition to overall forest productivity and biodiversity declines, introduced pests can cause some native tree species to become “at-risk”, i.e., threatened by possible exposure to population-level damage, and become of special management concern. In the U.S., tree species are at-risk from about 90 invasive pest species (Alien Forest Pest Explorer 2022). The population level damage for at risk species varies from possible extinction, which is rare, to more commonly innocuous (Williamson and Fitter 1996). However, the 15 or so invasive species that cause severe commercial and ecological loss are vexing (Fig. 1).

Well-known examples of severely threatened keystone at-risk forest tree species include American chestnut (*Castanea dentata* Marshall) Borkh.) due to chestnut blight caused by *Cryphonectria parasitica* (Murr.) Barr (= *Endothia parasitica* (Murr.) Anderson & Anderson); butternut (*Juglans cinerea* L.), due to butternut canker disease (BCD) caused by the fungus *Ophiognomonia clavignenti-juglandacearum* (Ocj;



Fig. 1 At-risk native forest tree species of North America showing pest decline, including (from left to right): white ash (*Fraxinus americana* L.) showing larval feeding galleries under bark from the emerald ash borer, American chestnut (*Castanea dentata*) infected with chestnut blight, and stem canker on butternut (*Juglans cinerea*). Photos: DF Jacobs

Nair, Kostichka, & Kuntz); common ash (*Fraxinus excelsior* L.) in Europe due to ash dieback from *Hymenoscyphus fraxineus* (Kowalski) Baral, Queloz & Hosoya (= *H. pseudoalbidus*; basionym *Chalara fraxinea*); ash (*Fraxinus* spp.) in North America due to emerald ash borer, *Agrilus planipennis* Fairmaire; and elms (*Ulmus* spp.) due to the introduction into Europe and North America of the pathogen *Ophiostoma* spp. that causes Dutch elm disease. The list of new, at-risk species continues to expand rapidly (Potter et al. 2019); for instance, whitebark pine (*Pinus albicaulis* Engelm.), a keystone species in the western U.S. was recently listed as threatened, in part because of the introduced pathogen *Cronartium ribicola* A. Dietr. (U.S. Fish and Wildlife Service 2022).

Often these at-risk tree species remain extant (e.g., individually surviving through stump sprouting or regeneration via seedlings or saplings not yet old or large enough to be affected) but are no longer sufficiently abundant and/or of adequate size and stature to reproduce sexually or perform their ecological function(s), rendering them ecologically extinct (McCauley et al. 2015, 2017). Ecological extinction, the sufficient loss of a tree species' ability to influence ecological dynamics (Tilman 2001), is insidious, as obligate species in higher trophic levels become extinct first, causing deleterious, cascade effects to the ecological web (Wardle et al. 2000; Säterberg et al. 2013; Mitchell et al. 2014). These altered ecosystems may experience a lower diversity of plant dispersal and tree recruitment (Redford 1992) that leads to a homogenization of forest ecosystems, which has negative implications for forest resilience to perturbations, including changes in climate. Left unchecked, these at-risk tree species may develop truncated ranges, lose genetic diversity, and face becoming threatened, endangered, or extinct (Potter et al. 2017, 2019).

The well-known historical loss of some foundational tree species has led to novel predictive and prioritization capacity (Potter et al. 2019) for addressing pest threats to at-risk species. Theoretically, the most effective approach should be exclusion or reducing the rate of spread of pests, but this has not been well adopted due to both international and intra-national constraints. For example, despite the early detection of emerald ash borer threats to *Fraxinus* spp. in North America, campaigns and regulations to eliminate inter-state transfer of logs or wood and sanitation removal of infected trees were unsuccessful in stopping the spread of the pest, which is now ubiquitous across much of North America where ash occurs and has decimated ash tree populations (McCullough 2020). With few remaining alternatives to exclude threats to at-risk species of high commercial and/or ecological value, researchers worldwide have implemented disease resistance programs to develop and deploy pest resistant trees back to the landscape (Snieszko and Koch 2017; Woodcock et al. 2018, 2019).

Some of the longest running such programs began between the 1950s–1980s to develop pest resistance in species such as American chestnut, Sitka spruce (*Picea sitchensis* (Bong.) Carrière), American elm, and white pines (i.e., *Pinus monticola* Douglas ex D. Don, *P. strobus* L.) and have shown some success (Snieszko and Koch 2017; Woodcock et al. 2019). Other disease resistance programs, such as for ash in response to emerald ash borer, have developed very recently. A medium to long-term approach and sustained investment are necessary to have potential for operational deployment of resistant trees using traditional tree breeding (Woodcock et al. 2019; Snieszko and Nelson 2022). Recent advances in tree biotechnology, however, have potential to accelerate the pace and breadth of pest resistance to support reintroduction of at-risk species.

Advancements in biotechnology put reintroduction in reach

Biotechnology refers broadly to the use of biology to solve problems (Editors of Encyclopedia Britannica 2022). In the context of at-risk forest tree species, biotechnology to reintroduce species can take many forms (traditional and genome informed breeding and genetic engineering or the synonymous term, genetic modification). Biotechnology is often erroneously equated solely with genetic engineering. Distinguishing among these forms may help to elucidate the multi-faceted nature of biotechnology for incorporating pest resistance and leverage all available biotechnologies to support reintroduction. This approach may provide a holistic framework toward applying genomic-based interventions to increase tree species' pest resistance efficiently and effectively (Snieszko and Liu 2022; Nelson 2023). The need and use of these biotechnologies will depend on context associated with specific at-risk species (Dumroese et al. 2015). Informed and judicious use of biotechnologies can provide an avenue for rescuing at-risk, ecologically extinct species and moving them toward their restoration on the landscape. In addition to the aforementioned facets of biotechnology, other biotechnologies not discussed herein, such as biological control, may be integrated into pest resistance programs.

Traditional tree breeding is a biotechnology that may leverage other biotechnologies, such as use of rooted cuttings, grafting, and somatic embryogenesis to duplicate trees with desired characteristics (Merkle et al. 2023; Nelson 2023; Fig. 2). In traditional tree breeding, genotypes of the at-risk species or of closely related species with desired traits are conserved in vitro or in situ (Engels et al. 2008) and bred for multiple generations using controlled pollination and subsequent selection of resulting progeny having favored characteristics. This leads to combinations of genes that could occur “naturally” toward obtaining the desired resistance. On the one hand, traditional tree breeding has limitations because trees (especially conifers) have extremely large genomes, are slow to reproduce, and often multiple genes and their interactions with the environment are responsible for the desired trait(s) leading to a low heritability and slow accumulation of genetic gain over time (De La Torre et al. 2014). A single breeding cycle often requires a decade or more to complete (Harfouche et al. 2012). Additionally, due to its non-targeted nature, breeding for a desired trait (e.g., disease resistance) may result in accumulation of undesirable traits as well. For instance, growth of American chestnut seedlings bred with Chinese chestnut for blight resistance has not matched that of pure American chestnut in field plantings, despite several generations of backcrossing with American chestnut (Brown et al. 2022). This is likely because backcross hybrid trees selected for blight resistance inherent on average 17% of their genome from Chinese chestnut (Westbrook et al. 2020). On the other hand, traditional tree breeding remains a powerful tool with broad social acceptability to rapidly enable development of resistance, especially for tree species with extensive diversity of resistance mechanisms and high cultural value (Luiz et al. 2023), and recent successes are encouraging (Snieszko and Koch 2017).

Recent and rapid advances in *genomics*, for example, DNA sequencing, genetic marking with molecular markers, and bioinformatics are providing geneticists with novel, powerful, potentially time-saving tools that have potential to assist to reintroduce at-risk species. Genome sequencing of trees provides a basis for better understanding resistance (i.e., frequency, level, distribution, type, durability, stability) toward describing genes with putative disease resistance (e.g., Harper et al. 2016; Stevens et al. 2016; Stocks et al. 2019). Analyzing the RNA transcripts produced by the genome (transcriptomes) has potential to inform levels and mechanisms of resistance within a species as well as species within the

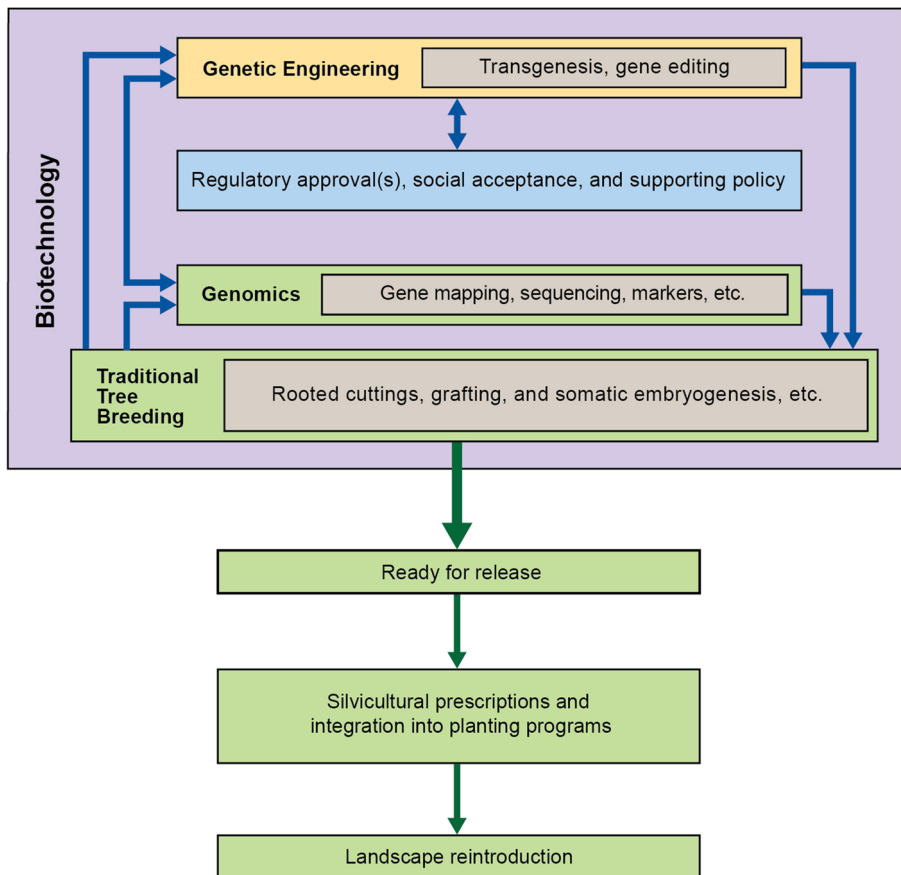


Fig. 2 Biotechnology may take many forms, with varying regulatory frameworks, and provides a holistic approach toward applying genomic-based interventions to increase tree species' pest resistance. Deployment of pest resistant material achieved through biotechnology to support landscape-scale reintroduction is dependent on capacity to integrate into operational tree planting programs, silvical knowledge, societal acceptance, and public policy

genus (Sniezko and Liu 2022). Genetic mapping and marker-assisted selection can assist in identifying genes conferring major resistance, complexes of genes that together provide elevated quantitative resistance, and describe genes that contribute to increased pest susceptibility (Engelhardt et al. 2018; Sniezko and Liu 2022, 2023). This information can be leveraged toward stacking multiple genes into a single genotype (i.e., pyramiding) to improve the durability of resistance (Sniezko and Liu 2022, 2023). Moreover, all these techniques can be used to further evaluate characteristics of the pest, rendering information on the mechanisms used, and potential adaptation of those mechanisms, by the pest (e.g., Rigsby et al. 2015; Duan et al. 2017). These biotechnological techniques offer promise for more rapid and robust selection of genotypes for inclusion into traditional tree breeding programs. Achieving the full potential of these techniques will depend on overcoming social, biological, and economic constraints (Whetten et al. 2023).

As discussed previously, *genetic engineering* is often erroneously equated with biotechnology yet is in fact simply a set of specific tools within biotechnology. We consider

genetic engineering as “any technique that uses recombinant, synthesized, or amplified nucleic acids to modify a genome” (Nelson 2023) and any plant derived with such modified nucleic acids, be they cisgenes or transgenes, to be a genetically engineered organism. Notably, however, this field is moving rapidly in response to regulatory and policy changes. In the U.S., an emphasis on mechanisms of action rather than gene insertion methods or specific insertions is increasingly determining whether or not the result of genetic engineering could have been achieved through traditional tree breeding (Federal Register 2020), which affects the regulatory process. The revolutionary use of CRISPR/Cas9 (clustered regularly interspaced short palindromic repeats) gene editing technology, which can accurately and relatively easily insert and alter DNA with targeted specificity, has intriguing implications for the pyramiding of resistant genes as well as removal of genes associated with elevated levels of susceptibility (Gorash et al. 2021). While application of CRISPR was recently achieved in European chestnut (*Castanea sativa* Mill.) (Pavese et al. 2021), technical and societal obstacles to its near-term use remain. These obstacles include a lack of knowledge to guide gene editing for traits of complex inheritance, difficulty of transformation in many important genotypes, and complexity of application in breeding programs (Strauss et al. 2022). Additionally, field trials are highly regulated in most countries and recombinant DNA-modified trees are not allowed in key forestry certification programs (Strauss et al. 2022).

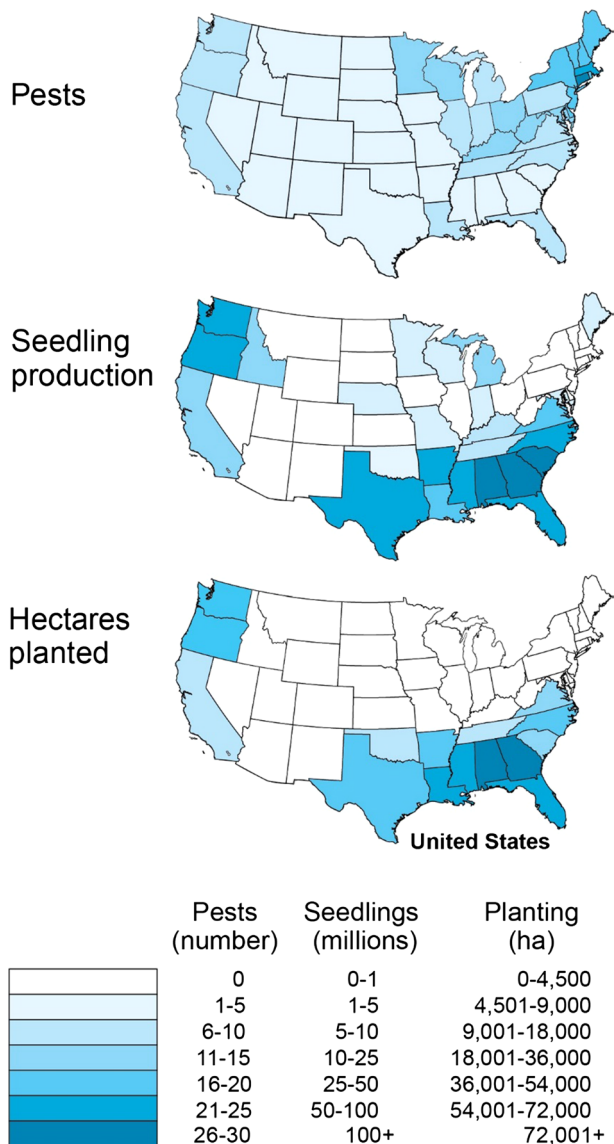
Leveraging or refining silvicultural systems to accept pest resistant trees

To successfully deploy pest-resistant germplasm to reintroduce at-risk forest tree species, planting of nursery-grown seedlings will be needed to artificially regenerate these species. An understanding of the biology and ecology of these species is needed to ensure successful artificial regeneration that may lead to re-establishment of pest resistant populations with potential to naturally regenerate across the landscape (Jacobs 2007; Jacobs et al. 2013). This species-specific foundational information can be drawn upon to guide seed collection, nursery seedling propagation, site preparation and planting techniques, as well as to manage regeneration after its reintroduction into forests. The existing knowledge base varies among species, often depending on the length of time that a given species has been extirpated from the landscape. For instance, American chestnut and American and European elms were functionally eliminated from forests decades before the development of modern principles of forest ecology (Paillet 2002) and only recently has field-based research been directed toward informing restoration efforts (Jacobs et al. 2013; Wang et al. 2013; Martín et al. 2019). Other species, such as ash in North America or Europe (Pautasso et al. 2013; McCullough 2020), have more recently been threatened by pests and therefore may already have well-established methods, including planting requirements, to draw from. For some other recently threatened forest tree species, however, regeneration has mainly been accomplished naturally and prescriptions for planting establishment of such at-risk species may still be poorly developed, yet this knowledge is needed to successfully deploy pest-resistant material.

In addition to establishing a sound knowledge base to facilitate reintroduction of at-risk forest tree species, deployment of pest-resistant germplasm through artificial regeneration could logically be accomplished by integrating into and leveraging existing systems of tree planting operations. However, >90% of forest regeneration in the U.S. is accomplished

naturally (Oswalt et al. 2014) and at-risk species in need of reintroduction may be lacking the capacity for operational nursery production and planting in respective regions of high priority for deployment. In the case of the continental U.S., for example, the highest occurrences of pests (i.e., threats) are sometimes located in regions with the lowest rates of tree seedling production in forestry nurseries as well as total land area planted (Fig. 3). This trend is most notable in the northeastern U.S., which as a global hub for trade imports has historically high risk of pest introduction (Fei et al. 2019), yet its forest management relies nearly entirely on natural regeneration for stand establishment (Bataineh et al. 2013). The southeastern U.S. has by far the highest rates of seedling production and planting

Fig. 3 The cumulative number of pests by state putting forest trees at-risk in the coterminous United States (Alien Forest Pest Explorer 2022), annual forest tree seedling production, and subsequent land area planted (Haase et al. 2021)



associated almost exclusively with commercial pine plantations (Fox et al. 2007), but relatively lower forest pest occurrences. Although reforestation systems in the southeastern U.S. rarely target at-risk forest tree species, the existing nursery and planting infrastructure could more easily accommodate such a shift than in the northeastern U.S. This presents a dilemma to solve to ensure that pest resistant material can be successfully deployed across the landscape.

Societal perception and policy remain weakest links

Moving forward with policy that supports using biotechnology (ranging from selective breeding to genetic engineering) to reintroduce at-risk tree species will be challenging. The ensuing discussions and ultimate decisions will need to consider, meld, and communicate across a spectrum of science disciplines, a disparate public with a continuum of personal values, knowledge, and perceptions toward the topic, regulators having important responsibilities to the public, and policymakers keen to satisfy constituents. Traditional, long-standing, and widely used tree breeding to produce disease resistant trees for reintroduction is characterized by general acceptance among the public and relatively few policy regulations in their use. Nevertheless, social acceptability of deploying specific products derived from traditional tree breeding, such as use of hybrids or backcross trees, is not entirely resolved as some uncertainty and reluctance among land managers and the public remains (Brennan et al. 2023; Jacobs et al. 2013). Using genetic engineering to reintroduce at-risk tree species is much less well accepted, although regional and demographic variation exists (Brennan et al. 2023; Jepson and Arakelyan 2017a, b; Marzano et al. 2019). For example, younger generations appear to be more open to use of genetically engineered trees in natural woodlands and forestry plantations (Jepson and Arakelyan 2017a, b; St-Laurent et al. 2018). Here, we focus the discussion on the challenges and opportunities of framing the use of all forms of biotechnology to reintroduce at-risk tree species.

The public perception of and associated policy regulations of using genetic engineering in plants is primarily focused on food crops and is complex and contentious (Hallman et al. 2003; Costa-Font et al. 2008; Frewer et al. 2013; Jepson and Arakelyan 2017a; Marzano et al. 2019). On one hand, the public may more readily support the use of genetically engineered trees because trees are valued for reasons beyond food, such as for watershed protection, wildlife habitat, carbon sequestration, and conservation (Merkle et al. 2007; Gamborg and Sandøe 2010; Brister and Newhouse 2020). On the other hand, the public may be more hesitant to accept genetically engineered trees because trees are longer-lived and therefore have longer-term ecological implications (Williams 2005; Hall 2007; Merkle et al. 2007; Gamborg and Sandøe 2010). Indeed, public acceptance of using genetic engineering to reintroduce at-risk tree species may be lacking because the intention is to have heritable results that persist across generations. This contrasts with other biotechnologies, such as with human medications, that limit effects to an individual and enjoy widespread public favor (Aucott and Parker 2021).

Whether the topic is climate change, microplastics, reclaimed water, genetically modified organisms, or just about anything else, humans often form opinions based on little scientific data and a range of perceptions (e.g., Wunderlich and Gatto 2015; Ricart and Rico 2019; Catarino et al. 2021). These opinions are constructed on values that lie on a continuum from egoistic (concern for self), to altruistic (concern for community), to biospheric (concern for non-human species) (Stern 2000). Not surprisingly, environmental values also lie on a continuum, with support for pro-environmental policies generally thought to

increase with movement from egoism to biospherism (Vaske and Donelly 1999). This simplistic approach becomes murky, however, because people perceive aspects of the environment, such as nature, naturalness, wildness, and health, through a localized prism that also includes community values and culture (Hull et al. 2010). Thus, for example, an egocentric individual could support a pro-environment policy perceived to provide local benefit to the person or community, whereas a biocentric individual, who believes that forests have an intrinsic value regardless of value to humans, may oppose a pro-environment policy that is perceived to challenge the notion that “nature knows best” and can “self-heal” (Hull et al. 2010). This distinction can be more fluid because an individual could, depending on circumstances, express all three values and be pro-environment (Snelgar 2006). Such value orientations, once expressed, can be slow to change (Hiroyasu et al. 2019).

Many popular opinions are made based on little scientific knowledge, and increasingly influenced and reinforced through social media. However, public knowledge concerning a particular topic or policy also runs a continuum from vague or general awareness to more specific, detailed knowledge (Trevethan 2017). Similar knowledge continuums are also evident among professionals within disciplines. For example, within the U.S. Department of Agriculture (USDA), Forest Service, land managers often have a different working knowledge (and perceptions) concerning climate change amongst themselves (Rodriguez-Franco and Haan 2015) and compared to agency scientists actively researching the topic. And, within the science community engaged in exploring genetically modified organisms, other continuums exist. For example, research molecular biologists may approach non-knowledge (defined as the absence of knowledge) from a control-oriented perspective (unknowns can be explored in the controlled atmosphere of the laboratory) whereas research ecologists do so from an uncertainty-oriented perspective because unknowns are often characterized by complex systems with high spatial and temporal heterogeneity that span diverse disciplines (Böschchen et al. 2006).

As noted above, acceptance and support of forest management activities are influenced by an individual's values; often the public focus on historical or static forest conditions precludes acceptance of novel or unconventional approaches perceived to be unnatural and therefore riskier or unethical (Park and Talbot 2012; St-Laurent et al. 2018). Value-based decisions are tempered, however, with the amount of knowledge one has and the level of trust one has in that information (McFarlane et al. 2006; Hajjar and Kozak 2015; Gregory et al. 2016). Public opinion must be respectfully considered and integrated because adoption and implementation of any forest management activity depends on public trust (McFarlane et al. 2012; Greenberg 2014), and levels of trust fluctuate with levels of knowledge and experience. As an individual increases their knowledge and experience with a topic, the basis of decision-making shifts from trust in perceived experts who can make informed decisions to a greater reliance on personal judgement (McFarlane et al. 2012).

Developing trust in the message is vital, and scientists and environmental groups are perceived with the highest public trust on other contentious forestry topics, such as assisted migration, with the federal government, industry representatives, and politicians perceived less so (St-Laurent et al. 2018; Solano et al. 2022). Trust in scientists may translate to less perceived risk and more acceptance of interventions, but the delivery of data may or may not be helpful. Schuler (2004) concludes that for food GMOs, public perceptions, and not science, were paramount in framing the discussion, and although information can shift perceptions, it is not easy, nor the only factor (Satterfield et al. 2009).

Understanding that communication is foundational to success is much simpler, and much different, than actual, effective communication with the public that garners, for example, support for using biotechnology to reintroduce at-risk species. Given the complex

nature of the debate, and the wide spectrums of values and knowledge across a disparate group of actors, how might scientists converse with others toward obtaining social acceptance to safely, ethically, appropriately, and holistically use tools in the evolving biotechnology toolbox?

Listening to concerns and engaging the public are paramount for building trust. In western Canada, impacts from insects and diseases were perceived to be most detrimental to the well-being of forest-dependent communities (Hajjar and Kozak 2015; St-Laurent et al. 2018). Building on this, thoughtful dialogue with the public about how introduced insects and diseases put native tree species at risk, and how biotechnology may be part of a holistic approach to reintroduce those species, should begin immediately and be ongoing (Clark et al. 2002; Powell et al. 2019). Members of the public are more prone to agree with others who share their values; thus, to be successful the messaging must be delivered from a broad spectrum of advocates, thereby positively influencing their disparate factions. A major challenge is finding the correct spokesperson(s) because who delivers science-based information is critical (Kahan 2010). Moreover, the message from the spokesperson must be true and truthfully (without hidden bias) presented (Andersson et al. 2006). The likelihood of a single message coalescing from diverse advocates is, however, unlikely (Sylvester et al. 2009). Even so, the responsibility likely falls to government to forge a coalition toward development of the public process to transparently, and in balanced fashion, discuss critical issues to assess the use of biotechnology, and thereby avoid, or begin to address, non-science-based opinion (Cobb and Macoubrie 2004).

While the public trusts federal government less than scientists (St-Laurent et al. 2018), a federally supported initiative that leads with scientists and leverages its partners and stakeholders around a central theme that addresses and provides for diverse values may be an effective strategy. For example, the USDA Forest Service, which has a long tradition of managing forests to meet multiple use objectives, could lead communications in the United States. The agency has a cadre of scientists and university partners focused on molecular biology, genetics, ecology, and restoration, as well as NGO partners, who together could provide information (pros and cons) that the public trusts. The agency currently supports environmental, industrial, NGO, and other partners toward successfully obtaining mutually agreed upon diverse management objectives, such as biodiversity, rural community development and sustainability, recreation, clean water provision, and healthy, resilient forests. Thus, a message from scientists and a trusted locally based spokesperson could speak to how all of the various facets of biotechnology may (or may not) serve as a tool to reintroduce populations of at-risk trees.

In creating dialogue concerning at-risk trees, a focus on ecological and societal benefits rather than risk management may be prudent (Hiroyasu et al. 2019), as is providing opportunities for the public to participate in decisions concerning research and development (Burri and Bellucci 2008; Barnhill-Dilling et al. 2021). It will also be essential to operationalize on-going communication across governmental agencies that ultimately share responsibility for regulating and implementing the use of biotechnology. While a land management organization may promote the ecological and social benefits more than risk management per se, regulatory organizations, with their fiduciary responsibilities to society, namely a “do no harm” approach to implementation of genetic engineering, must necessarily focus on risks (Martín et al. 2019; Pierce et al. 2023); a regulatory process that balances safety, development, and use could prevent unintended ecological consequences without severely limiting use (Gordon et al. 2021). These two approaches need not be antagonistic; realistic discussion associated with ecological processes along with perceived benefits must be supported with data and provide a clear pathway for resolving bias based

on popular opinion. Acknowledging that tree breeding programs are complex and that researchers must consider unintended consequences are important for building public trust (Martín et al. 2023). The use of forecasting (e.g., simulation models that evaluate potential outcomes of reintroduction prior to deployment) may afford a better discourse about potential trade-offs associated with using biotechnology, especially across scales and including opportunity costs (including ecosystem services) associated with or without implementation (Mozelewski and Scheller 2021). Recent work confirms that public and cultural attitudes about perceived benefits and risks are strong drivers of acceptance of trees genetically engineered for resistance to introduced pests (Barnhill-Dilling et al. 2020; Petit et al. 2021; Brennan et al. 2023).

The message shared, especially concerning genetic engineering, must be presented with concrete rather than vague or abstract language; eliminating jargon (e.g., Plaxco 2010) and providing specific examples (Tallapragada et al. 2021) improves delivery effectiveness. For instance, when St-Laurent et al. (2018) surveyed western Canadians about the generic, undefined use of genetically engineered trees in reforestation, the result was poor support for the practice. When more nuanced, specific, described applications of biotechnology in reforestation in the central U.S. were communicated, including genetic engineering, it garnered high levels of support among land managers (Brennan et al. 2023). Provision of scientific knowledge delivered by a trusted locally based spokesperson allows individuals to make more nuanced decisions (Hiroyasu et al. 2019), which may be important for the topic of rescuing at-risk trees using genetic engineering where emphasizing ecological benefits may be paramount to acceptance, and for developing necessary grassroots support that influences policy makers (Daniels et al. 2012). Research is clear that engaging the public and increasing awareness have generated support for other contentious forest management practices, such as increasing the use of prescribed fire (e.g., Loomis et al. 2001) and assisted migration (St-Laurent et al. 2018). It is also clear that public awareness and perceptions are critical to land manager willingness and ability to implement management practices (Archie et al. 2012).

The literature shows that the information deficit model of simply educating the public (Nisbet and Scheufele 2009) is no longer the sole solution to garnering support for use of biotechnology when and where appropriate. While scientist engagement with the public is paramount and can ensure a scientifically ethical approach, equally important are science delivery and deliberate, collaborative dialogue among land managers, regulators, and policy makers (Barnhill-Dilling et al. 2021; Harfouche et al. 2021). Natural scientists likely need to re-evaluate their approach(es) to public engagement, recognizing that it is not just a lack of information, but rather their lack of commitment to be enablers of broader, direct public engagement and dialogue that is counterproductive to the needed effort (e.g., Besley and Nisbet 2011).

There is a need to identify and implement ways to inclusively weave diverse stakeholders into the decision-making process (especially at the local level; Kofler et al. 2018), from research priorities to citizen science opportunities to policy advocacy (e.g., NASEM 2017, 2019; Barnhill-Dilling et al. 2021). The solution should no longer be based on the pretense that scientists should “give the public more information so that they can rationally agree with us,” but rather to foster conversations that include and respect diverse perspectives, creating broad support that can result in long-term support for complex tree breeding programs for at-risk species. During the last decade, the biology and science related to biotechnology approaches in tree breeding has made remarkable progress. Efforts to affect policy toward allowing the use of biotechnology have, however, lagged. While investing resources into the biological side of biotechnology is essential, a concomitant investment

by natural scientists into the social science side of biotechnology may be even more important. Support across the full spectrum of the public (i.e., scientists, land managers, stakeholders, regulators) will hopefully motivate policymakers to react (Daniels et al. 2012).

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Author contributions DFJ and RKD wrote the main manuscript text and prepared the figures. All authors reviewed the manuscript.

Declarations

Conflict of interest The authors declare no conflicts of interest.

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