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A silvicultural synthesis of sweet (*Castanea sativa*) and American (*C. dentata*) chestnuts

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ABSTRACT

Sweet chestnut (*Castanea sativa*) and American chestnut (*C. dentata*) have been explicitly linked to ancient, historical, and contemporary cultures while enhancing ecological services in forests in which they occur. Threats that currently face these chestnut species are unprecedented and additive, including global climate change, nonnative pest and pathogen species, land use changes, and lack of scientific knowledge and technologies. In this paper, we provide a synthesis of traditional and novel silvicultural systems for chestnut, focusing on these two important species. We frame the discussion within the context of the species' cultural and ecological significances, scientific knowledge bases, and associated knowledge gaps. Sweet and American chestnuts require divergent strategies to sustain their conservation values due to differing cultural and ecological landscapes and biological stressors. Both species share the need to conduct active forest management to maintain or restore populations in native or naturalized habitats. Even-aged management is the preferred regeneration method for both species. Coppicing that is commonly implemented for sweet chestnut can provide a potential strategy for American chestnut once disease-resistant material becomes widely available. Blight caused by *Cryphonectria parasitica* may limit long rotation timber production of American chestnut, even for resistant material, making short-rotation systems a more attractive management option. Advanced artificial regeneration and breeding strategies have been developed for American chestnut but are largely underdeveloped for sweet chestnut. High forests of sweet chestnut can play an important role in new single or mixed species plantations, naturalized stands, or in naturally regenerated stands for production of medium-large dimension timber. American chestnut will likely be managed as a minor to moderate component of mixed species forests to achieve ecological restoration goals. A close-to-nature silvicultural approach has not been tested for either species and may be difficult to implement due to the threats from changing climate conditions and nonnative pathogens. Traditional and emerging markets of sweet chestnut, such as biomass or carbon markets, may help inform future opportunities around American chestnut for tribal and rural communities. Climate change and other threats call for synergistic partnerships and knowledge sharing to maintain or restore sweet and American chestnuts as part of the global ecosystem.

1. Introduction

Chestnut species belonging to the genus *Castanea* Miller (Fagaceae) evolved nearly 60 million years ago and have provided ecological services and fulfilled human resource needs within a diversity of forest ecosystems and civilizations on three continents for millennia (Europe, Asia, and North America). Chestnut and human civilizations co-evolved, with tree populations becoming more prevalent and widespread during the late Holocene in part due to human spread and cultivation (Delcourt et al., 1998; Mellano et al., 2012; Tulowiecki and Larsen, 2015; Pollegioni et al., 2020). The sweet chestnut (*C. sativa* Mill.) and the American chestnut [*C. dentata* (Marsh.) Borkh.] are distinguished from other

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Castanea species because they are the only two chestnut species that have been managed heavily for wood products (e.g., timber, firewood, small-diameter wood) (Buttrick, 1915; Conedera et al., 2004; Krebs et al., 2022) as opposed to being valued or managed predominately for fruit production.

Sweet chestnut populations grow on more than 2.5 million hectares in southern Europe and western Asia (Conedera et al., 2016), and the American chestnut originally occupied 80 million hectares in eastern North America (Little, 1977) (Fig. 1). Sweet and American chestnuts have been historically valued for rot resistant, fast-growing, and combustible wood and for hard mast that provided a stable and nutritious food source for humans, domesticated livestock, and wild game (Buttrick, 1915; Ziegler, 1920; Conedera et al., 2004; Beccaro et al., 2019) (Fig. 2). The concept of the circular economy (although historically this terminology did not exist) has always been intrinsic to the chestnut given its multiple uses in rural communities. Mutually beneficial relationships between humans and trees have ultimately resulted in expansion of populations of these species and increased their biodiversity over hundreds if not thousands of years (Tulowiecki and Larsen, 2015, Pollegioni et al., 2020).

In addition to their diverse utilitarian values, the sweet chestnut and American chestnut both provide (currently for the former and historically for the latter) important ecosystem services (Fig. 2). Managed coppices (i.e., forests formed from stools that produce sprouts on relatively short rotations) and high forests [i.e., forests originated from seed or from planted seedlings on rotations long enough to produce timber) IUFRO, 2005] of sweet chestnut continue to promote diverse faunal species, reduce wildfire risks, increase wildlife habitat and structural diversity, improve water conservation and soil stabilization, and improve landscape aesthetics (Muster et al., 2007; Patrício and Nunes, 2017; Garfì et al., 2022). Sweet chestnut forests are recognized by the European Union as important habitats for pollinators and constitute stable reservoirs of biological richness (Kudrnovsky et al., 2020). Sweet chestnut may offer silvicultural options for climate change adaptation on sites that are not too water limiting (Conedera et al., 2021).

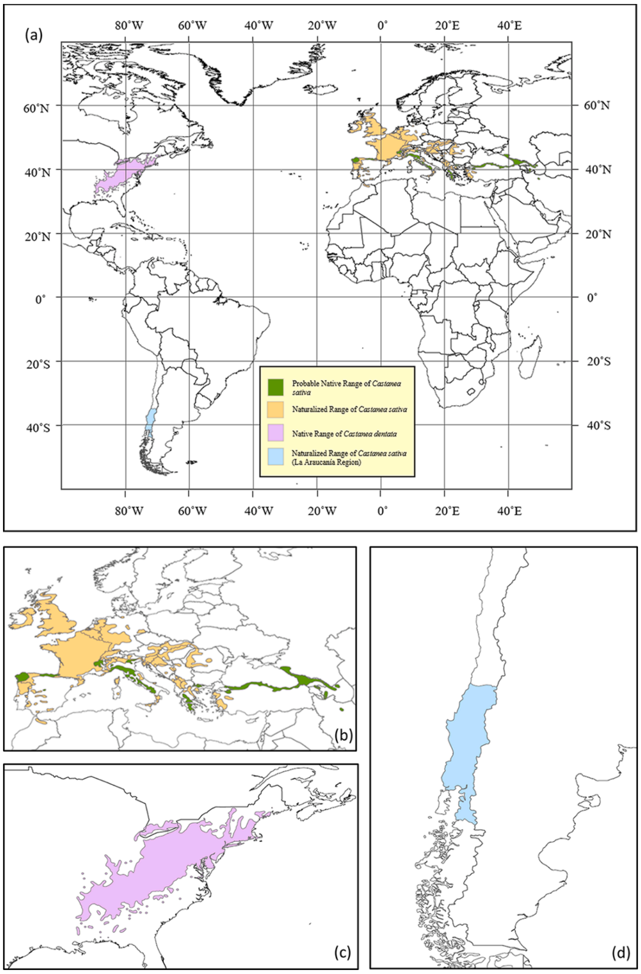


Fig. 1. Geographic areas encompassing American chestnut (*Castanea dentata*) and sweet chestnut (*C. sativa*) species' native ranges (a), sweet chestnut's native and naturalized range in Europe and western Asia (b), American chestnut's range in eastern North America (c), and sweet chestnut's naturalized range in Chile (c).

American chestnut is considered a former ecological foundation species that helped define ecosystems throughout its range (Braun, 1950; Jacobs et al., 2012; Dalgleish et al., 2016). The tree was abundant, especially in the southern Appalachian Mountain region, where it was often the most common tree associate (Russell, 1987). Limited studies suggested American chestnuts produced a preferred nut for certain wildlife species, compared to hickory (*Carya*) and oak (*Quercus*) (Minser et al., 1995; Wright et al., 2022), and the impact from the loss of chestnut to wildlife dynamics was probably profound (Diamond et al., 2000, Dalgleish and Swihart, 2012; Clark et al., 2019a). American chestnut hosted 60 species of Lepidoptera (moths), and seven had the tree as the solitary host (Opler, 1979). Macroinvertebrate populations may have shifted with the American chestnut's demise (Smock and MacGregor, 1988).

More than Asian chestnut species, the sweet chestnut and the American chestnut have been negatively impacted by nonnative pests and pathogens over the last two centuries. An Oomycete that causes Phytophthora root rot (as known in North America) and ink disease (as known in Europe) [causal organisms *Phytophthora cinnamomi* Rands and *P. cambivora* (Petri) Buisman] have led to species contractions and declines in both sweet chestnut and American chestnut, particularly in clayey or poorly drained soils, since the early- to mid-19th century (Anagnostakis, 1995). The chestnut blight fungus [causal organism *Cryphonectria parasitica* (Murrill) Barr.] was initially reported in Italy in 1938, gradually spread throughout Europe, and was found most recently in the United Kingdom (Rigling and Prospero, 2018; Romon-Ochoa et al., 2022). Chestnut blight has reduced timber and nut productivity in sweet chestnut because the species has low to moderate levels of blight resistance (Waldboth and Oberhuber, 2009; Baser and Bozoglu, 2020), butypovirulent strains of *C. parasitica* have successfully reduced the pathogen's virulence (Rigling and Prospero, 2018). The fungus was introduced into North America in the late 19th century and ecologically extirpated the American chestnut by the mid-20th century, reducing the species largely to understory sprouts that rarely reach reproductive maturity (Anagnostakis, 1995; Griffin, 2000).

Chronologically, the latest serious threat to sweet chestnut forests were represented by intensive infestation of Asian chestnut gall wasp (*Dryocosmus kuriphilus* Yasumatsu) (ACGW), originating from Asia. Canopy damage from ACGW has seriously compromised the photosynthetic efficiency of the trees (Gehring et al., 2018a, 2018b) leading to significant reductions in nut and timber production (Battisti et al., 2014; Marcolin et al., 2021). A biocontrol agent (the parasitoid *Torymus sinensis*, introduced as an integrated control system for this pest) has been shown to be effective in reducing the ACGW population density and consequently the damage to the sweet chestnut productivity (Quacchia et al., 2014; Avtzis et al., 2019; Ferracini et al., 2019). In North America, the ACGW was accidentally introduced in 1974 and has been found in many parts of the American chestnut range, and biological control using parasitic wasps, *T. sinensis* (introduced) and *Ormyrus labotus* (native) hold some promise for control in orchard and forest settings (Cooper and Rieske, 2007).

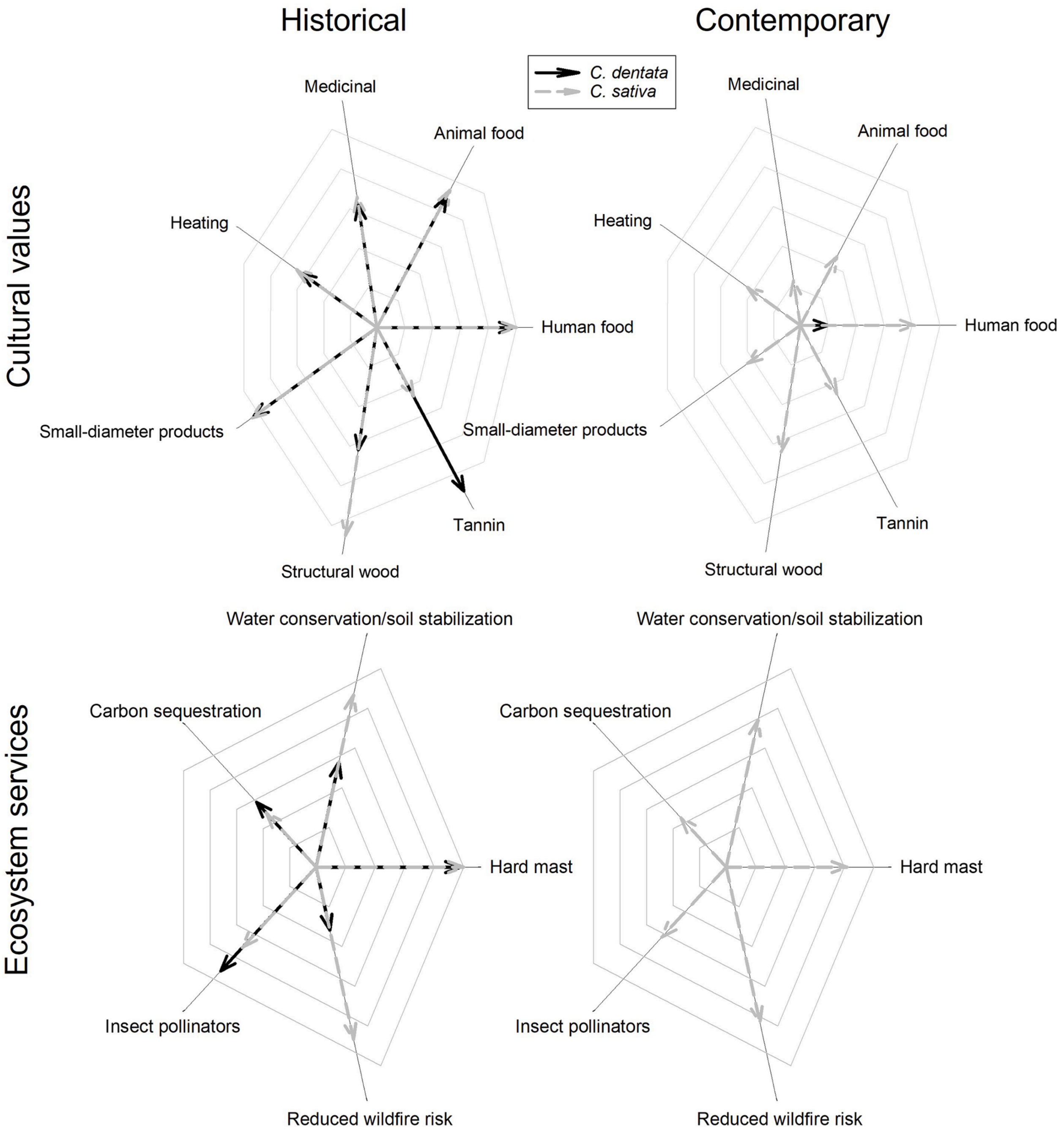


Fig. 2. Conceptual model of relative contributions to cultural values and ecosystem services for historical (*left*, defined as pre-20th century) and contemporary forests (*right*) for American chestnut (*Castanea dentata*) (*solid black*) and sweet chestnut (*C. sativa*) (*hatched gray*). Values range from 0 (minimal contribution) to 5 (maximum contribution) and were approximated based on current knowledge as presented in the article. We recognize that contemporary knowledge on historical values or management systems, particularly those of Indigenous People, are extremely limited and may not be accurately reflected in this figure.

1.1. History of management

Sweet chestnut was cultivated for thousands of years in the temperate and Mediterranean regions of Europe and western Asia through coppicing, high-forest plantings, or as grafted cultivars as a component of agroforestry systems, resulting in a present distribution that is largely naturalized outside of the original native range (Conedera et al., 2004; Krebs et al., 2019). In fact, the long history of sweet chestnut cultivation makes it difficult to identify populations that were naturally established without the influence of human activities (Conedera et al., 2004; Krebs et al., 2022). Utilization and movement of sweet chestnut has been recorded since Roman times, when the wood was used in Roman cremation rituals from the 1st century BCE to the 7th century CE (Costa-Vaz et al., 2020). The sweet chestnut was responsible for the peculiar "civilization of the chestnut" (Gabrielli, 1994; Adua, 1999; Conedera et al., 2004) in the Mediterranean region where the tree's cultivation and products have strongly influenced the basic social fabric of society. Sweet chestnut forests expanded similarly with the cultivation of vineyards (Adua, 1999; Conedera et al., 2004; Monteiro and Patrício, 2007), and it is the only species alongside *Quercus* species accepted for use by the OIV (Organization of Vine and Wine) (Resolution OENO 4/2005). Sweet chestnut wood is also used in the ageing of spirits (Martínez-Gil et al., 2018) due to its excellent flavoring and richness of tannins (Alañón et al., 2013). The sweet chestnut is generally an uncommon natural component in mixed species forests and has become increasingly abandoned in coppice or high-forest plantings. It can produce high-quality timber with good technological and durability characteristics (except for vacuum impregnation) following a tree-oriented silviculture approach based on single-stem selection (Manetti et al., 2014; Giuliarelli et al., 2016; Patrício and Nunes, 2017). Timber products from sweet chestnut include furniture, construction lumber, veneers, flooring, poles, sculptures (Nava and Oliviero, 2021), musical instruments, and cabinets (Borghini and Massafra, 2002).

In contrast to sweet chestnut, the history of human influence on American chestnut populations is not well understood prior to large-scale European colonization in the 18th and 19th centuries. The species was reportedly utilized by Indigenous populations for heating, rot-resistant wood, and for medicine (Moerman, 1986) (Fig. 2), but the historical anthropogenic cultivation and use of American chestnut remains largely unknown. Traditional Ecological Knowledge has been largely lost (Barnhill-Dilling and Delborne, 2019). Following the industrial revolution, the American chestnut was “one of the most promising trees for forest management” in North America (Ashe, 1911; Ziegler, 1920), particularly in the Southern Appalachian region where vast swaths of forests were still on their first harvest rotation (Frothingham, 1924). Wood products included lumber for telegraph poles, furniture, fence posts, and railroad ties, but the species was most valued as a source of tannic acid extract for leather and silk dyes (Buttrick, 1915). Chestnut reproduced easily through sprouting and was maintained through coppice and orchards around rural homesteads for firewood and nut production (Buttrick, 1915). In rural Appalachia, the nuts of American chestnut formed its own currency and were used as a stable food source and an inexpensive feed for livestock (Lutts, 2004).

1.2. *Justification and objectives*

Sustainability, conservation, or restoration concerns surround both sweet and American chestnuts, but success of these efforts depends partially on improving *Phytophthora* and *C. parasitica* resistance coupled with appropriate silvicultural or management techniques. Strategies and institutional frameworks for development and distribution of disease-resistant American chestnut have been advanced over decades through collaborations among citizen scientists, government agencies, and non-profit organizations (Anagnostakis, 2012; Powell et al., 2019). A similar model for sweet chestnut does not yet exist, but population declines of sweet chestnut have been attributed to cultural factors in addition to nonnative diseases and pests (Conedera et al., 2016), necessitating different approaches than those for American chestnut. Resistant phenotypes, genotypes and specific markers for resistance to *Phytophthora* (Costa et al., 2011; Santos et al., 2017; Westbrook et al., 2019) and *C. parasitica* (Westbrook et al., 2020; Fernandes et al., 2022) have been identified, but fully disease-resistant chestnuts have yet to be realized. Hypovirulence has been successfully utilized as a biological control method for sweet chestnut, but this method has generally failed in North America for American chestnut due to the highly heterogenic vegetative compatibility (*v-c*) types (Milgroom and Cortesi, 2004; Rigling and Prospero, 2018). A large-scale traditional breeding approach that backcrosses Asian chestnut genes into the American chestnut genome has been developed over the last 100 years to produce hybrid American chestnut trees (Burnham et al., 1986; Steiner et al., 2017). Breeding programs for sweet chestnut are comparatively underdeveloped (Fernandes et al., 2022). Genetic transformation is an approach to control pathogens using transgenes or cisgenes currently being pursued for both sweet and American chestnut (Newhouse and Powell, 2021; Fernandes et al., 2022), but social factors, legislation, and broad market barriers have inhibited the use of transformed trees in Europe (Chang et al., 2018). American chestnuts transformed with a wheat gene (oxalate oxidase (OxO), Powell et al., 2019) are currently under federal review in the United States, and approval would allow unregulated distribution of genetically modified trees on private lands. Potential distribution of genetically modified trees has elicited concerns among some scientists, Indigenous groups, and the public (Petit et al., 2021; Diehm 2022), particularly around environmental justice (Barnhill-Dilling et al., 2020). Disease resistance and mitigation measures require substantial long-term commitment of resources (Clark et al., 2014a; Newhouse and Powell, 2021), which necessitates silvicultural strategies incorporating biocontrol, breeding, or genetic transformation be as successful as possible.

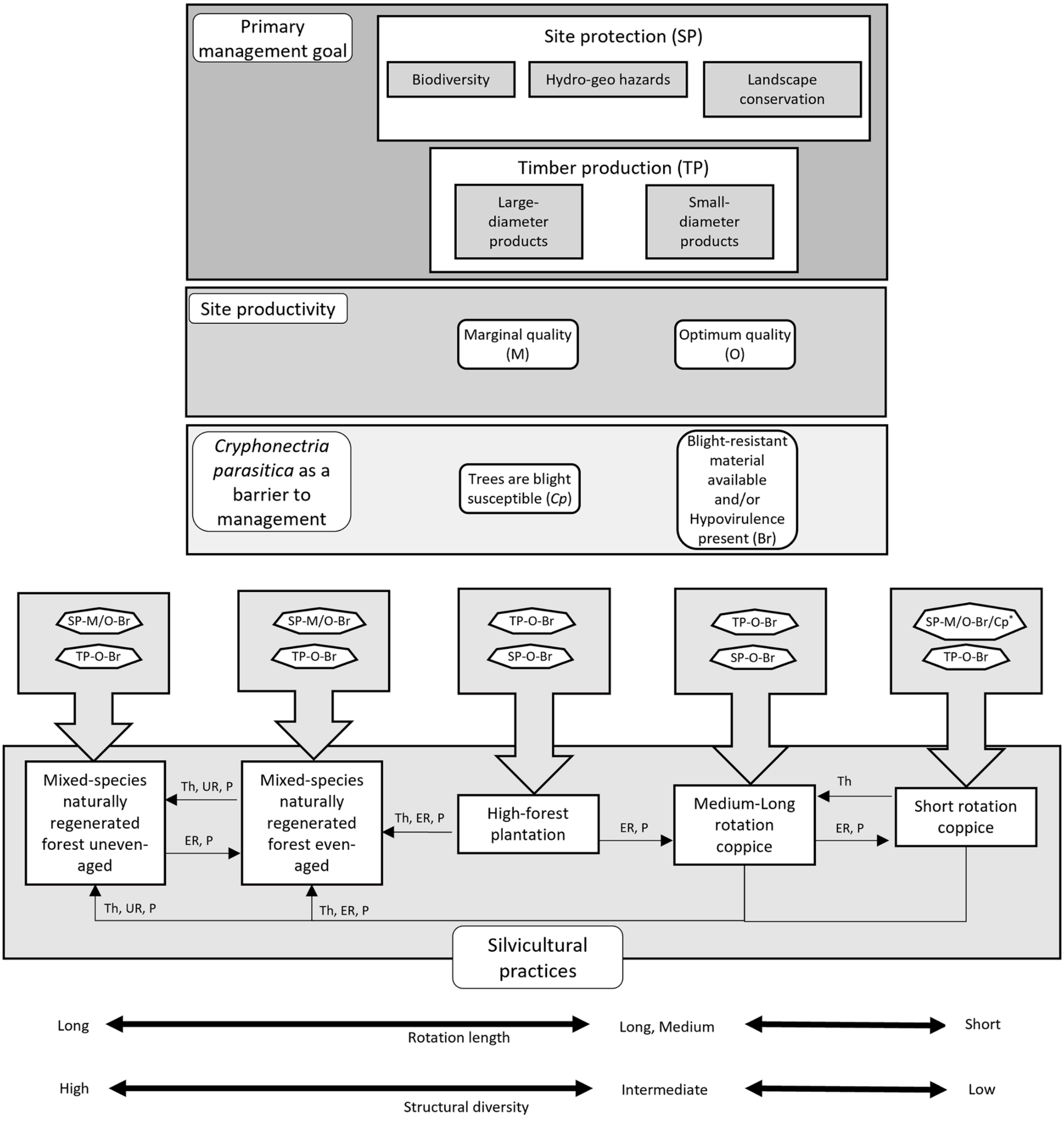
The conservation and management strategies of sweet and American chestnuts may have important commonalities and differences that have not before been adequately described or discussed across the genera, particularly in a silvicultural context. Review or synthesis papers on chestnut species have often focused on narrowly defined ecological parameters or management concerns, such as timber productivity (Manetti et al., 2001), biogeography (Fei et al., 2012), pests and pathogens (Fernandes et al., 2022), or public lands restoration (Clark et al., 2014a), and are often species specific (Jacobs, 2007; Jacobs et al., 2012). One paper examined the reproductive dynamics, pathology, and distribution of sweet chestnut in comparison to American chestnut with a narrow geographic focus (Pridnya et al., 1996). International collaborations and research integration are becoming increasingly important as our forest ecosystems face common threats and challenges (Parrotta, 2019). Thus, we formed a new chestnut working party within the Silviculture Division of the International Union of Forest Research Organizations (IUFRO) (Working Party 1.01.13) to collaborate at a global scale, facilitate information exchange, and develop new synergistic approaches that can help solve conservation and management problems.

The objective of this paper is to synthesize commonalities and divergences in silvicultural approaches for sweet and American chestnuts that may help mitigate future challenges faced by both species. We restrict our discussion of sweet chestnut to silviculture in coppice, high forests, and mixed species forests, and we limit the discussion of orchard fruit production. We provide a historical and contemporary context for silvicultural strategies of sweet and American chestnut, and we also propose future considerations and new opportunities for forest management for these two species.

2. Management and silvicultural strategies

Differing cultural landscapes, biological stressors, and specific extant population dynamics have resulted in divergent management goals between sweet and American chestnuts, but both species require similar silvicultural practices to sustain genetic diversity and economical and ecological values (Fig. 3). The most striking interspecies divergence is that sweet chestnut remains more cultivated than the American chestnut, while also being less susceptible to blight. Sweet chestnut was intensively managed primarily through coppice for small and large diameter wood production (Conedera et al., 2016; Krebs et al., 2022) but sometimes from abandoned orchards or agroforestry systems initially designed for nut production (Camus, 1929; Gabrielli, 2002; Conedera et al., 2004). Ecosystem services, such as watershed protection, carbon sequestration, and biodiversity are being increasingly considered in modern calculations of the value of sweet chestnut coppice and high forests (e.g., Lopes and Cunha-e-Sá, 2014), but the primary current motivation for sweet chestnut silviculture remains utilitarian.

American chestnut was historically managed primarily as an undomesticated canopy dominant in mixed-species stands on intermediate to productive sites or in pure forests on lower quality or heavily cut-over sites (Ashe, 1911; Frothingham, 1924). American chestnut management was historically focused on economic timber production (Frothingham, 1924), but contemporary management goals have shifted toward species restoration to improve ecosystem function, resilience and genetic conservation (Jacobs et al., 2015). The recent motivations of American chestnut restoration comes from public and private collaborations that work under policy or administrative frameworks of environmental protection, conservation, and stewardship (Jacobs et al.,



*non-resistant trees could be used in very short rotations depending on the degree of infection and tree vigor

Fig. 3. Conceptual model for silvicultural practices for sweet and American chestnut for two primary management goals considering site and disease conditions. Abbreviations in the bottom panel are: even-aged regeneration harvest (ER), planting as an optional enrichment practice (P), thinning (Th), and uneven-aged regeneration harvest (UR).

2012; Clark et al., 2014a; Steiner et al., 2017).

2.1. Natural regeneration management systems

The two species are competitive across a wide range of temperature and moisture gradients (as reviewed in Jacobs et al., 2012), although cold tolerance can be a limiting factor (Griffin, 2000; Schaberg et al., 2022), particularly for sweet chestnut (Freitas et al., 2021). Both species prefer deep well-drained acidic soils (Russell, 1987; Conedera et al., 2016; Tulowiecki, 2020) and have relatively fast growth in full-sun conditions on good soils. Seedlings from seed exhibit intermediate levels of shade tolerance (Wang et al., 2013). These silvical characteristics allow for relatively wide flexibility in managing natural regeneration, but the majority of management was historically and remains largely even-aged. Both sweet and American chestnut trees have silvical characteristics that facilitate a rapid response to managed disturbances such as even-aged regeneration harvesting in mature forest stands or coppicing in relatively young forest stands.

Silvicultural research and management of both species are limited to varying degrees by impacts from nonnative pests and pathogens (Fig. 3), and both species are largely dependent on sprouting abilities for natural regeneration. The future of American chestnut restoration, however, will involve planting disease-resistant material in nearly all management scenarios (Jacobs, 2007; Clark et al., 2014), while sweet chestnut can depend on natural regeneration if stocking levels are sufficient. Sweet and American chestnut seeds can be scattered by birds and mammals (Wright et al., 2022), and natural regeneration from seedlings may increase the complexity and adaptability of forests to a wide range of conditions (Puettmann et al., 2009).

2.1.1. *Coppice-forest management*

Sweet chestnut coppice forests, even from older trees, remain the primary regeneration method used to produce small-diameter wood products, high-quality timber, fuelwood, and several secondary products (e.g., honey, litter, mushrooms). Management goals and timber quality will vary depending on site productivity, stand age, rotation time, and sources of regeneration (e.g., wild seed versus planting) (Conedera et al., 2001; Fonti et al., 2002; Manetti et al., 2019) (Fig. 3.). Biomass fuels and other wood products (e.g., vineyard poles) can be produced in short/medium rotations (20–30 years) on marginal sites, while high-quality timber production is possible to obtain by lengthening rotations (40–45 years) in productive stands by selecting one shoot per stump (Bourgeois, 1992; Bourgeois et al., 2004; Manetti et al., 2006; Patrício et al., 2020) (Table 1). Short-rotation coppices are typically single species, but coppice with standards can increase tree biodiversity and floristic composition (e.g., early-stage species of understory).

Even-aged management of American chestnut was historically conducted with longer rotations than is deemed optimal with sweet chestnut, and short-rotation coppice was largely restricted to poor quality (i.e., drier) sites where sawtimber quality was relatively low (Ashe, 1911). Early American foresters found that a 60-year rotation was the optimum age in both northern and southern forest sites to produce cordwood used for tannic acid extract (Mattoon, 1909; Ashe, 1911). Shorter rotation coppice forests of American chestnut were utilized for fuel wood for charcoal, mine poles, and railroad ties, while quality sawtimber was found mostly in uneven-aged forests of seedling origin (Ashe, 1911). Coppice systems near rural farms, small towns, and homesteads produced small-diameter wood products in 30–40 years (Buttrick, 1915). Pre-blight management of American chestnut in what is now called the “wildland-urban interface”, had similarities to that of the historical and contemporary sweet chestnut in Europe and western Asia.

Deer browse may represent a growing threat to sweet chestnut coppice and to American chestnut reintroduction sites, particularly if deer densities remain high or browse is not mitigated with fencing (Bottero et al., 2022; Pinchot et al., 2022). Perhaps the most profound threat to natural regeneration of both species, however, is related to changes in land use and decreases in active management. Rural land abandonment in the last century has affected sweet chestnut with serious repercussions on genetic diversity, ecosystem services, rural economies, as well as the ability to manage chestnut stands (Arnaud et al., 1997; Piussi, 2006; Wall et al., 2021). Sweet chestnut stands managed by coppicing for centuries are now left unstable, with profound structural changes and transformations that increase wildfire (Garfì et al., 2022) and hydrogeological risks (Zlatanov et al., 2013; Vergani et al., 2017; Unrau et al., 2018). Forest abandonment increases the normal rotation-time, in many cases doubling it, yielding excessive density of old stools (often coupled with high mortality of stools, see Conedera et al., 2001; Vogt et al. 2006) that are more difficult to manage. The large root biomass and the increasing competition with other species caused a reduction in growth and loss of vitality of the older stools (Conedera et al., 2001; Vogt et al., 2006) (Fig. 4). Smaller sized chestnuts (below 50 cm in DBH), showed increased vulnerability to pathogens and a high mortality rate when in suppressed positions due to lack of management (Conedera et al., 2021). Alternatives to traditional coppice management using medium-long rotations is needed for sweet chestnut (Bourgeois, 1987; Amorini et al., 2000; Cutini, 2001; Marcolin et al., 2020; Patrício et al., 2020), and treatment of overaged coppices represent emerging research involving thinning, planting for enrichment, or regeneration harvests (Figs. 3 and 4) (Marcolin et al., 2020; Patrício et al., 2020). These land use changes also have a high potential to affect the future of American chestnut restoration, as decreases in the forest land base is predicted to continue over the next 40 years (Keyser et al., 2014).

Fig. 4. Sweet chestnut coppice management, including simple coppice management in Switzerland (*top*; image courtesy provided by M. Conedera), coppice with standards in northern Italy (*middle*), and an example of stool's uprooting in an abandoned coppice (*bottom*).

Table 1
Silvicultural options for sweet chestnut coppices for wood or timber production. Based on Manetti et al., 2017.

	Short	Medium	Long
Approximate rotation length (years)	16 – 25	28 – 35	50
Number of thinnings	1	3 – 5	5 – 8
Target stem diameter (cm)	12–15	> 20	> 30
Products	Poles	Poles, beams	Poles, beams, boards

2.1.2. *High-forest or mixed-species forest management*

Management of non-coppice forests (e.g., high forests) is comparatively less common than the coppice forest system for sweet chestnut (Conedera et al., 2016), and generally is formed from planting seedlings. Harvesting in sweet chestnut high forests ordinarily converts to a coppice system, which facilitates a natural regeneration method of propagation usually without the need to replant (Fig. 3.), limiting the high forest to the first rotation. In contrast, American chestnut restoration will generally be conducted by enriching a mixed species forest site by planting blight-resistant trees into thinned or naturally regenerated forests with chestnut as a minor to moderate component, depending on future management decisions (Jacobs, 2007; Clark et al., 2020). American chestnut will probably remain less cultivated compared to sweet chestnut high-forest systems in Europe or naturalized stands in South America. Mixed broadleaved chestnut forests of both species represent important sources of germplasm for genetic or breeding programs (Fernandes et al., 2022) in addition to their timber and non-timber values.

High-forest management could be an alternative to traditional coppice management for sweet chestnut depending on the environmental, economic, social, and management objectives (Bourgeois, 1987; Amorini et al., 2000; Cutini, 2001; Marcolin et al., 2020; Patrício et al., 2020) (Fig. 3). The high-forest system can produce high-quality timber in productive stands with similar rotations lengths as the coppice system, but this has not been the option in many countries due to the lack of past appropriate silvicultural practices and the risk of serious damage from pests and diseases. High forest systems contribute to a sustainable multifunctional forest that provide periodic revenues, while at the same time promote ecosystem services such as biodiversity conservation, carbon sequestration and storage, soil and water conservation and landscape preservation. A study in Spain found that sweet chestnut formed advance regeneration in unmanaged secondary oak forests, suggesting that the species may persist through gap-phase dynamics with the ability to form mixed stands in more natural forest settings (Silla et al., 2018). Natural regeneration also provides the benefit of increasing genetic diversity and structural diversity, which is considered relatively low in coppice systems (Fernández-López and Alía, 2003).

The productive potential of sweet chestnut in high-forest systems was studied in the only mature chestnut stands known in northern Portugal (Patrício, 2006) (Fig. 5). The observed site index (SI) ranged from 14 to 26 m of dominant height for a reference age of 45 years (Fig. 6). Potential for quality timber production of large dimensions was found at SI $>$ 22, and the optimal range of stand density for single-stem selection on a tree-by-tree basis (tree-oriented silviculture) had a relative spacing between 32% and 26% of growing stock for producing high-quality timber (Patrício and Nunes, 2017).

In North America, the 'high-forest' system does not currently exist for any native Fagaceae species, as hardwood plantings are typically done to enrich a site dominated by naturally regenerating tree species (Dey et al., 2008). Once resistant material becomes available, American chestnut trees would be best maintained to enrich mesic or submesic forest sites where sunlight is not limiting and blight control is highest (Griffin, 2000). If not impeded by nonnative diseases, gap-forming processes through silvicultural management (e.g., patch clearcuts or small tree gaps) could develop desired horizontal and vertical structural heterogeneity and facilitate chestnut recruitment (Zlatanov et al., 2015), similar to the idea of 'close-to-nature' silviculture (see section 3.1.1), but this approach has gone largely untested. A recent study on seedling ecology of a rare naturally regenerated American chestnut stand at the northern edge of the species range supported a management strategy that favors competition control in the first two to three years of seedling development along with creating gaps to facilitate rapid growth (Dalgleish et al., 2023).

2.2. Artificial regeneration and plantations

Both the sweet and American chestnuts have been cultivated and planted artificially through seeding, seedling production, and clonal production such as grafting, but the history, primary methods and purposes of this cultivation differ among chestnut genera. Historically, the cultivation of sweet chestnut is much longer than the American chestnut, beginning as early as the Early Bronze Age (Krebs et al., 2019), with the onset of arboriculture in Europe (from 2750 to 1900 BP). The first evidence of active selection and clonal propagation by grafting of sweet chestnut was in the 15th century CE (Pollegioni et al., 2020), but

Fig. 5. Different stand development phases and management intensities of sweet chestnut in a high forest in Portugal including a young stand (<15 years) of chestnut in northeastern Portugal (left), a 45-year-old chestnut stand that has been poorly managed (not tended or properly thinned) in Serra de Bornes, northern Portugal (middle), and a 60-year-old forest recruiting natural regeneration of sweet chestnut in Serra da Padrela, northern Portugal (right).

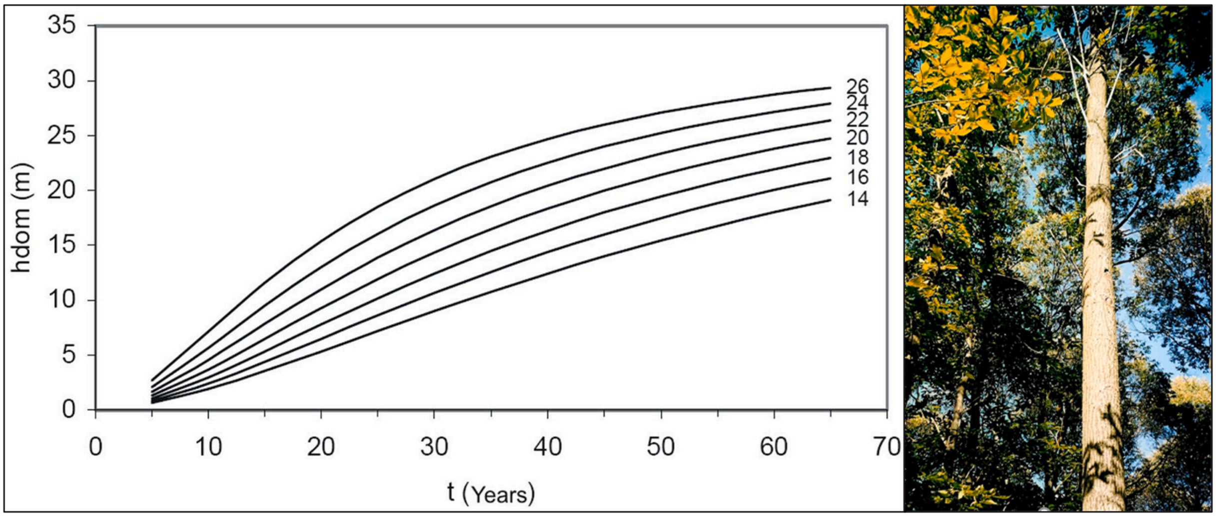


Fig. 6. Site index curves for high-forest stands of sweet chestnut in northern Portugal (*left*). Potential for high-quality crop trees was found at SI > 22 (base age 45) (*right*). hdom = dominant average height of the 100 largest trees per hectare; t, the age of the stand (years).

could have been as early as the 1st century BCE (Conedera et al., 2004). American chestnut was historically not planted, at least in modern times, but the species was used as rootstock for grafts of sweet chestnut in the 1770 s for nut production, notably by Thomas Jefferson at his home in Monticello (Anagnostakis, 1995). There was virtually no mention of planting chestnut in historical forestry literature, and Traditional Ecological Knowledge is largely missing.

For silvicultural purposes, sweet chestnut plantings are typically done to create high-forest stands within their native range (Fig. 3) or as part of naturalized stands (Balandier and Dupraz, 1999; Bourgeois et al., 2004). Planting is not often required to regenerate sweet chestnut, instead relying on sprouting from existing stumps, a concern for future genetic conservation and in general for species diversity in chestnut stands (Mason and Macdonald, 2002; Gondard et al., 2006; Mattioni et al., 2008). Planting sweet chestnut as a primary species in mixtures has improved growth, timber quality (Loewe-Muñoz et al., 2023), and stem form when planted with conifers (Bourgeois et al., 1991). When planted as a secondary species, sweet chestnut provides an intermediate revenue.

Sweet chestnut has been included in many pure and mixed plantations in Italy to provide high-value timber production (Buresti-Lates and Mori, 2009). The same planting scheme was used in Portugal and other countries, where there was a strong investment in planting of this species, mainly under the European Community Support Frameworks (Bourgeois et al., 1991; Patrício, 2006; Patrício and Nunes, 2017). The success of these funds is demonstrated by the sweet chestnut's contemporary afforestation rate in Portugal, northern Spain and France, estimated at 4,500 ha year^{-1} (Alvarez-Alvarez, 2004). Sweet chestnut has been included among the eight most important species for high-value timber production in the UK (Kerr and Evans, 1993) given its ease of establishment, fast growth rate, readiness to coppice, and marketability of small or large wood and production (Everard and Christie, 1995). Regarding initial plantation density, up to 1,200 plants per hectare have been recommended in France for timber production, leaving 200 trees per hectare at the end of the rotation (40–50 years) (IDF, 1990). Similar densities are recommended and used in Portugal in new plantations (Patrício, 2006) and in Chile (Benedetti-Ruiz et al., 2023).

Unlike the sweet chestnut, American chestnut will require artificial regeneration using blight-resistant material for most silvicultural practices. Planting would probably not be a profitable enterprise for the foreseeable future and would be conducted primarily for research or restoration programs required for reintroducing the species into diverse, mixed-species forest ecosystems that are naturally regenerating (Hebard, 2001; Jacobs, 2007; Anagnostakis, 2012; Clark et al., 2014a) (Fig. 7). Artificial regeneration can also provide information on performance of various breeding lines or germplasm that can complement breeding orchard tests (Hebard et al., 2014) or biocontrol tests using hypovirulent *C. parasitica* strains (Tagliaferri et al., 2002). Planted pure American chestnut seedlings showed fast growth in even-aged timber harvests and thinnings, but inferences are limited because of differences in genetic diversity and seedling quality among studies (McCament and McCarthy, 2005; Rhoades et al., 2009; Clark et al., 2012a, 2014b). Tests of traditionally bred material with varying levels of blight resistance planted into silvicultural treatments are relatively rare and short-term but do indicate positive responses to disturbances such as prescribed fire and harvesting (Griscom and Griscom, 2012; Thomas-Van Gundy et al., 2017; Brown et al., 2022; Clark et al., 2016, 2019b, 2023; Pinchot et al., 2017, 2020). Backcross hybrid seedlings have shown fast growth and good competitive ability following planting, depending on genetics and site productivity (Clark et al., 2016, 2023; Brown et al., 2022; Pinchot et al., 2020). The only planting study to date of transgenic American chestnuts planted in silvicultural tests mirrored studies using traditionally bred material; trees exhibited relatively fast growth under more open light regimes (Evans et al., 2023). Initial favorable growth is important because repeated stand entries will probably be limited by administrative restrictions or costs of non-commercial treatments, similar to oak plantings (Dey et al., 2008).

Diverse and properly sourced seed remains an important aspect for forestry and reintroduction programs for both species. Sweet chestnut seeds rarely come from scarce wild populations and are usually collected from coppice stands or from orchards, as has been shown in Iberian Peninsula afforestation programs (Ciordia et al., 2012). Orchard stands, however, showed less genetic differentiation than coppices and old high-forest stands (Seabra et al., 2001). American chestnut reintroduction at a landscape scale will require seeding or planting seedlings from open-pollinated blight-resistant trees that are locally adapted (Steiner et al., 2017) and can be economically mass produced (Clark et al., 2014a).

Artificial regeneration offers opportunities to improve ecosystem services for both species. Planting could ameliorate losses from sweet chestnut forest abandonment that, along with drought, have increased fire frequency, and reduced wildfire protection, soil stabilization, and water conservation (Zlatanov et al., 2013; Vergani et al., 2017; Unrau et al., 2018; Garfì et al., 2022)). In addition to potentially providing a more stable mast producer to eastern North American forests (Diamond et al., 2000), American chestnut reintroduction provides potential

Fig. 7. American chestnut restoration in the Southern Appalachians of the United States involves planting large 1–0 bare root nursery seedlings of interspecific backcross hybrids (*top*) into newly established even-aged regeneration harvests (*bottom left*). Planted seedlings were capable of obtaining 11 m in height and 13 cm in diameter at breast height in 10 years (*bottom right*).

afforestation benefits on mine reclamation sites (Skousen et al., 2018) or other degraded lands where perhaps trees are easier to manage than in forest conditions (Jacobs and Severeid, 2004; Jacobs et al., 2012). Afforestation also affords additional opportunities for state or federal cost-share funding in the United States.

Cultural protocols for production of bare-root hardwood species have been developed to improve success following planting for oak species (Kormanik et al., 1994; Clark et al., 2000; Dey et al., 2008), but only limited research on chestnut has been conducted to refine the planting process. Nut size affected nursery seedling development of sweet chestnut (Tumpa et al., 2021), but the effect of nut or seedling size has not been adequately studied in agroforestry or forest systems. Nut size, seedling quality and interactions with genetic family or seed source were shown to affect outcomes for American chestnut and interspecific hybrids (Clark et al., 2012b, 2016; Pinchot et al., 2015). American chestnut nursery seedlings were reported to be highly variable in quality regardless of heritage but could obtain relatively large sizes (>1.5 m) in one year, the largest of which have been shown to be competitive with fast-growing shade-intolerant species (Brown et al., 2022; Clark et al., 2016, 2019b, 2023) (Fig. 7).

The relationships between soil microbes and planted chestnut seedlings have also been tested. Ectomycorrhizal fungi inoculations were recommended for sweet chestnut to not only to improve mineral nutrition but also to protect roots from fungal diseases (Crawford, 1995); the inoculation with edible *Boletus edulis, B. pinicola, B. aereus,* and *Morchella conica* showed to improve seedling quality (González et al., 2010), and other fungal species are also feasible, including some truffles (*Tuber* spp) (Crawford, 1995). In North America, the research is sparse, but different chestnut species and backcross hybrids recruited divergent rhizobiomes in a commercial nursery which was theorized to affect their seedling performance in the field (Reazin et al., 2019); however, subsequent analysis indicated fungal communities had no effect on seedling growth (Brown et al., 2022). Soil microbial communities of American chestnuts were found to reduce conspecific growth and survival potentially because of *Phytophthora* root rot disease, but American chestnut soils had neutral effects on heterospecific growth in other forest species (Coughlin et al., 2021).

2.3. Naturalization

Naturalization, defined as self-sustaining populations of trees outside of their native range (c.f., Gallagher et al., 2015), is more common for sweet chestnut than for American chestnut. Sweet chestnut was planted in South America (Argentina, Chile, and Uruguay), Australia, and New Zealand, outside of its native range, as early as the 1800 s for nut and timber production (Fig. 8). In Chile, it has become naturalized (Fig. 8.). Low genetic variability may have important implications to future species conservation in naturalized habitats (Loewe et al., 2008), both in pure and mixed plantations. Over 350 ha of pure forest plantations have been established in southern areas of Chile (Benedetti et al., 2005) mostly at high densities (3x3 m) and extensively managed. Plantations are currently between 20 and 80 years-old with estimated productive cycles of 30–35 years (Benedetti et al., 2018), shorter than in Europe (Kerr and Evans, 1993). Average annual diameter growth ranges from 1.0 to 1.5 cm in non-managed trees in a wide geographic distribution (Loewe et al., 1994). Mixed plantations have been established in over 600 ha with conifers such as *Pinus radiata*, *Pseudotsuga menziesii* and *Cupressus torulosa* (Loewe and González, 2006). These mixtures yield straight, smooth, cylindrical stems with natural pruning, improving their timber quality (Loewe et al., 2005) (Fig. 8). Positive results have also been obtained when sweet chestnut was grown in association with several broadleaves, including *Quercus robur, Q. rubra, and Prunus avium*

Fig. 8. Chilean pure non-managed chestnut plantations , adult (*top left*) and young (*bottom left*). Mixed plantation associated with *Cupressus torulosa* (*top right*), and windbreak (*bottom right*).

(Loewe-Muñoz et al., 2023) and native species such as *Nothofagus alpina*. Species cropping is especially attractive for small and medium-size landowners, providing the possibility to annually produce nuts and to obtain quality timber at the end of the rotation, particularly with low planting densities (500–650 plants per hectare) (Loewe et al., 1994). Conducting surveys of existing germplasm to identify individuals with the best fruit, forest or mixed-species characteristics would make it possible to improve the income and living conditions of socioeconomically depressed sectors.

Naturalization of American chestnut outside of its native range was historically rare and occurred in northern and western areas just outside the native range (Brewer, 2005; Dalgleish et al., 2016). One successful population has been thoroughly studied, located on a farm approximately 600 km from the western edge of the native range (Gilland et al., 2012). Less than a dozen American chestnut seedlings were originally transplanted from an east coast source. The planted trees matured, reproduced and chestnuts naturally spread to become a substantial portion of the dominant species of the stand (Paillet and Rutter, 1989), displacing native species in less than 80 years (McEwan et al., 2006). Blight cankers were detected in the 1980 s and biological control has been partially maintained since 1992 (Double et al., 2018). Interspecific chestnut hybrids and cultivars are limited to orchards for nut production or planted as ornamental trees in North America and do not generally spread into native forests (Schlarbaum et al., 1994).

3. Future considerations for chestnut management

Conservation of forests are a global concern, and more values are increasingly placed on multifunctional forests (Taye et al., 2021). Sweet chestnut and American chestnut (if blight-resistant varieties become available) forests provide a variety of ecological services and economic benefits to rural communities even when grown as monocultures. Concerns for the future of chestnut management and conservation from a silvicultural perspective include answering knowledge gaps, understanding the potential species' benefits and challenges related to climate change, and better control of timber quality to increase economic outputs. Multifunctional management perspectives will be an added value for non-timber benefits for sweet and American chestnut forests in the future.

3.1. Silvicultural knowledge gaps

Sweet and American chestnut both have important silvicultural knowledge gaps that will affect long-term management of chestnut resources in dynamic and often novel forest conditions. For sweet chestnut, current knowledge gaps revolve around reinvigorating and recovering coppice forests (e.g., by natural regeneration, Marcolin et al., 2020) to produce quality wood on productive sites, for multifunctionality, and to increase the genetic and structural diversity. For American chestnut, silvicultural research is limited, and tests need to incorporate a diversity of disease-resistant progeny to better select genotypes for particular environmental conditions. For both species, a return to historical conditions is not possible owing to land-use and human demographic pressures and nonnative species like ACGW, chestnut blight, and *Phytophthora* diseases (Keyser et al., 2014).

Management decisions should first be guided by two preliminary assessments: i) the ecological eligibility of the site (Fig. 3), and ii) land ownership considerations. For the first point, managers should consider the adequacy of site fertility/productivity or adequate minimum stools or natural regeneration density (for sweet chestnut). An important metric for sweet chestnut is the minimum site index (height of the dominant shoots at 10 years age) under which it is not worth producing timber (Lemaire, 2008). Density of natural seed-regeneration that is typically present in chestnut coppices should be in sufficient numbers to replace dead stools and to increase the final density of the coppice stand (Manetti et al., 2018; Marcolin et al., 2020). For American chestnut, sites of moderate productivity probably offer the best opportunities as they were historically the most chestnut dominated (Frothingham, 1924), provide a balance between tree growth and associated competition (Pinchot et al., 2020), and may have the best potential for blight control (Griffin, 2000). Habitat suitability models developed for American chestnut indicate the species prefers well-drained, sandstone derived soils with limited agricultural activity (Fei et al., 2007; Henderson et al., 2023). For point ii, considerations may include questions around available resources to invest in management activities, accessibility and viability for management actions such as coppicing (for sweet chestnut) and logging to clear planting spots (for American chestnut), as well as aptitude for different activities.

If these points have been satisfied, then the process of recovery in sweet chestnut coppice forests can begin by cutting remaining individuals to stimulate sprouting. The specific silvicultural practice will depend on the primary management goals (ecological or economic focused objectives) and desired structural diversity (Fig. 3). However, many knowledge gaps remain, including specifics of the thinning regime, rotation length, and climate change responses (i.e., areas with traditional chestnut cultivation are experiencing high levels of drought during spring and summer). In a preliminary study, dendrochronology revealed that growth in coppices under ordinary management was better in the 30–40 years prior to present, but the causes of these differences have not been investigated (Marcolin, unpublished data). Future investigations could test temporal differences in wood production in other parts of the species native or naturalized range.

3.1.1. Close-to-nature silviculture

Regeneration systems such as uneven-aged systems or variable-density thinning are being increasingly considered as part of a 'close-to-nature' silviculture (CNS) system in Europe (Remeš, 2018) and in North American (Keyser and Loftis, 2013; Kern et al., 2017). Different basal area reductions (thinning or regeneration harvesting) have been tested in overaged or abandoned coppices of sweet chestnut leading to development of multi-layered structures, promoting natural regeneration, and enhancing biodiversity (Amorini et al., 2000; Marcolin et al., 2020). Regular thinning cycles and even-aged cuttings in short to medium rotations can provide revenue streams while increasing species richness, emulating forest gaps across a larger temporal and spatial scale (Mattioli et al., 2016). Older high-forest stands can recruit advance regeneration (Fig. 5), and gap-forming silvicultural practices favor structural heterogeneity and species self-replacement (Silla et al., 2018).

Close-to-nature silviculture remains entirely unexplored with American chestnut owing to lack of disease-resistant material, but uneven-aged experiments with related North American oak species (*Quercus* in the family Fagaceae) have largely failed. The desired species composition and richness were not achieved with single-tree selection in oak forests because of recruitment of undesirable shade-tolerant species (Schuler, 2005; Keyser and Loftis 2013). Young American chestnut resprouts from stools are adapted to low light environments, persisting for decades in the absence of a disturbance (Paillet, 1982), but shade tolerance diminishes over time (Mattoon, 1909). Thus, sprouts or germinant seedlings would need to be released prior to long-term suppression (Ashe, 1911) as their survival and growth is limited by conspecific and heterospecific competitors in the first three years of life (Dalgleish et al., 2023). Intensive management that falls outside the CNS approach may be required for sweet and American chestnut because of their disturbance-dependent and shade-intolerant silvical characteristics. Natural forest dynamics and protection from land degradation has been ascribed to CNS (Schütz, 1999; Piussi, 2006), but these practices may not improve resiliency and health of trees or forests constantly challenged by novel threats such as climate change or nonnative pests or pathogens (O'Hara, 2016).

Non-chestnut species displacement is a potential ecological and economic concern, particularly for American chestnut restoration (Jacobs et al., 2012). Silvicultural treatments to increase the chestnut component could alter existing food webs, soil nutrients and microbiomes, and suppress other tree species. After centuries of cultivation and management, however, sweet chestnut remains a minor component in naturally regenerated forests, excluding the agroforestry system. Direct evidence for species displacement in American chestnut stands is primarily limited to one naturalized stand in midwestern North America where chestnuts were replacing oak and hickory regeneration (Paillet and Rutter, 1989), but this study has limited applicability within the native range. American chestnut restoration might displace competing vegetation species over multiple generations according to a population model in the northcentral portion of the species' range (Gustafson et al., 2017). For both species, silvicultural management decisions will need to be refined to maintain high species diversity if so desired.

3.1.2. *Artificial regeneration*

American chestnuts can be planted using disease-resistant seedlings, once available, but managers face questions around silvicultural prescriptions, local site conditions, and long-term durability of disease resistance (Jacobs, 2007; Clark et al., 2020). Perhaps more important than for sweet chestnut, management decisions for American chestnut will need to yield successful outcomes because of the considerable investments required to produce and plant blight-resistant seedlings (Clark et al., 2014a). This represents a challenge because planted American chestnut trees from breeding programs have only been tested in relatively narrow ranges of ecological and management conditions for a short period of time (Clark et al., 2016, 2023; Thomas-Van Gundy et al., 2017; Pinchot et al., 2020, 2022; Brown et al., 2022), and genetically engineered trees have received even more limited field testing (but see Evans et al., 2023), due to current regulations. Augmenting silvicultural research with breeding or genetic tests further increases complexity, costs, and commitments, and may require sacrificing more basic genetic questions such as climate adaptation or disease resistance (Schaberg et al., 2022). To date, silvicultural research using American chestnut or traditionally bred material has focused on planting in even-aged regeneration harvests or in shelterwood underplantings, which have been largely successful (e.g., Clark et al., 2016, 2019, 2023; Pinchot et al., 2017, 2020; Schaberg et al., 2022; Evans et al., 2023), but testing seedlings planted into other regeneration or tending treatments are needed (Clark et al., 2020). An additional challenge for American chestnut planting will be implementing commercial timber harvests on public lands. Competing priorities, lack of available harvest areas, and funding for non-commercial activities would probably limit activities (Clark et al., 2020). Unlike the sweet chestnut, planting on private lands can be risky because private lands have less stable ownership without environmental protections (e.g., conservation easements), and they will likely not reap economic returns favored by many landowners. Public investments and legislation to assist in tree planting and associated activities are increasing, however, which may affect future restoration efforts (Balloffet and Dumroese, 2022; Gwaze, 2022).

Development of high-quality seed or seedlings for planting using the target plant concept framework (c.f., Dumroese et al., 2016) has not yet been fully developed for any chestnut species. Considerable progress has been made on understanding the importance of seedling quality for American chestnut or their associated backcross hybrids (Clark et al. 2012a, 2016, 2023; Pinchot et al., 2015), but similar research has been limited for sweet chestnut. Planting sweet chestnut is currently not a priority for maintenance of the species as it is for American chestnut, but new seedlings are required to restore the density of stools to a suitable number (Manetti et al., 2022) or to initiate high-forest stands. Additionally, changes in current forest conditions from threats such as climate change or nonnative pests and pathogens may necessitate planting, as has been shown for the American chestnut.

3.1.3. *Prescribed fire*

Fire effects on chestnut have gone largely untested. The associations between sweet chestnut and fire are ancient, while the historical relationship between fire and American chestnut is mostly unknown. Controlled fires were extensively used by Romans to foster sweet chestnut establishment. During the late Middle Ages fire use declined because of biomass removal, landscape fragmentation and specific fire bans to protect the cultivated chestnut stands (Agnoletti, 2018). In sweet chestnut coppice or orchards, fire has received limited use to burn litter and rehabilitate the trunk of old and hollow trees. Prescribed fire can damage trees, degrading timber quality.

In the last few decades, abandonment of sweet chestnut forests along with warmer and drier years than average conditions, led to an increase in fire frequency (Morales-Molino et al., 2015) reducing ecosystem services (Garfì et al., 2022) (Fig. 2.). Only one study has been conducted to examine prescribed fire effects on planted American chestnut seedlings, and they found fire had no effect on survival or growth although it did increase browsing by deer (Clark et al., 2014b). Early American foresters disfavored fire due to damage to the thin-barked American chestnut (Ashe, 1911), but these views were largely influenced by a culture of fire suppression.

3.2. *Climate change*

Climate change is predicted to have varying effects on distributions of sweet and American chestnuts among and within species. Threats to regeneration, recruitment and growth, timber productivity, and provision of ecosystem services are of primary concern (Thiffault and Pinno, 2021). Pests and pathogens (native and nonnative) may also become more or less severe as climate changes affect host vulnerabilities or pathogen dynamics (Finch et al., 2021).

Sweet chestnut and American chestnut are expected to severely decline in southern regions of the Northern Hemisphere (Sarıkaya and Orucu, 2019; Barnes and Delborne, 2019; Noah et al., 2021). The current distributions of chestnut species were strongly correlated to thermal and moisture variables (Fei et al., 2012), and their historical distributions have shifted with global climate fluctuations such as the Little Ice Age (Conedera et al., 2021). The mean annual temperature gradients for the species' current distributions are relatively wide, 7.4–16.9° C for American chestnut and 8.0–15.0° C for sweet chestnut (Fei et al., 2012; Freitas et al., 2021). Both species are limited to varying degrees by cold tolerance (Freitas et al., 2021; Schaberg et al., 2022), which can also impact conservation efforts if climate change brings more extreme cold events.

Changes in the moisture regime is a concern for both species, as drought may push sweet chestnut management away from some Mediterranean regions (Camisón et al., 2020; Freitas et al., 2021). The consideration of sweet chestnut as a 'future-proof' tree in the face of global climate change because of its wide adaptability and large range (Häne, 2018) has recently been challenged (Conedera et al., 2021). The sensitivity of recalcitrant seeds to drought conditions means that they are at greater risk of regeneration failure under many climate change scenarios than non-recalcitrant seeds (Pritchard et al., 2022). Sweet chestnut trees appear to be particularly prone to increasing water stress (Conedera et al., 2021). Similarly, climate change is expected to restrict populations of American chestnut on drier, sandier soils (Noah et al., 2021).

Management of sweet chestnut populations or reintroduction of American chestnut might be best targeted for areas predicted to be unfavorable to *Phytophthora* diseases based on predicted climatic and edaphic conditions (Gustafson et al., 2022), such as sites with high soil porosity and limited drought stress (Menéndez- Miguélez et al., 2015). American chestnut populations in the northern part of the range, however, may become progressively more susceptible to Phytophthora root rot under a warming climate (Balci et al., 2007). Effects of climate change on blight remains unknown, but temperature or drought stress will likely decrease host resistance (Finch et a., 2021). The impact of nonnative pests such as the ACGW that impacts both sweet and

American chestnut is likely to be affected by climate change, as the insect population dynamics changes along elevational gradients (Bonsignore et al., 2019).

Assisted migration would move chestnut species into higher elevations or latitudinally north to reduce threats from drought or extreme temperatures (Freitas et al., 2021; Noah et al., 2021). Testing sweet chestnut seed sources or genetic varieties across climatic gradients has been largely conducted from a nut production viewpoint (Freitas et al., 2021). Common garden, assisted migration, and genetic studies revealed high genetic diversity (Martín et al., 2012), potential for high adaptability and plasticity to drought or heat stress (Ciordia et al., 2012; Dorado et al., 2023), and superior genetic families were identified based on a multi-trait system including timber production (Alvarez-Alvarez, 2004; Míguez-Soto and Fernández-López, 2015). Similarly, American chestnut from moderate temperature zones planted in the northern part of the range exhibited superior adaptability and cold tolerance in the short term (Schaberg et al., 2022). Young American chestnut seedlings also outperformed other species in an assisted migration trial at approximately 44° latitude (Clark et al., 2022). Genomic studies have identified distinct populations of sweet and American chestnut that could serve as conservation units for climate change mitigation strategies (Martín et al., 2012; Sandercock et al., 2022). Adaptability will be especially important in areas where dramatic climatic change effects are expected (Eriksson et al., 1993) such as the Iberian Peninsula in Europe (Ramírez-Valiente et al., 2009) or the southern end of the American chestnut range (Barnes and Delborne, 2019; Noah et al., 2021).

3.3. *Timber quality*

Both sweet chestnut and American chestnut have wood defects that degrades their timber value. Sweet chestnut is prone to ring shake within its native range, particularly in high-forest conditions where large diameter timber is produced (Fonti and Sell, 2003; Spina and Romagnoli, 2010) or on old coppice stumps. The ring shake afflicts only a small proportion of trees within a coppice stand (Fonti et al., 2002), and is affected by management intensity and rotation length (Everard and Christie, 1995; Manetti et al., 2022). Ring shake in the Northern Hemisphere is the most frequent cause of economic losses (Manetti et al., 2001; Fonti and Macchioni, 2003), but this defect is not present for naturalized populations in Chile where chestnut timber is of excellent quality. The geographic origin of the seed and individual tree genetics are important factors affecting ring shake, indicating there is a potential breeding solution . A dedicated tree improvement program does not yet exist to address this problem.

The chestnut wood industry in Chile demands defect-free logs of a minimum of 40 cm in diameter and 140 cm in length (Loewe-Muñoz et al., 2023). Sweet chestnut dry sawn timber prices have increased steadily in the last three decades in Europe (Loewe and Benedetti, 2007; Loewe-Muñoz, unpublished data). These trends highlight the economic relevance of the species, and confirms the demand for high-quality sweet chestnut timber and the potential for managing stands to improve timber quality and productivity.

Ring shake defects have not been reported in American chestnut, but a decrease in wood quality related to the chestnut timber worm (*Melittoma sericeum*), the cause of 'wormy chestnut', was historically cited (Ashe, 1911). This defect is now highly valued in contemporary markets for recovered chestnut wood and may affect future pricing from restoration plantings. Wounds from chestnut blight may relegate the species to short-rotation wood products or non-timber forest products, such as nuts, or fuel wood. Chestnut blight wounds have been reported on even the most resistant backcross hybrid seedlings tested to date (Clark et al., 2019a, 2019b, 2023), and it is unclear how wounding on genetically transformed trees would affect wood quality (see pictures of blight wounds in Newhouse and Powell, 2021).

4. New opportunities for chestnut management to benefit the bioeconomy

Chestnut species have the potential to deliver a range of benefits in local economies if environmental and social aspects receive adequate attention in multifunctional management. Optimizing actively managed chestnut forest ecosystems by valuing their ecosystem services may be advanced with new policies and funding mechanisms such as the Horizon Europe program. Bioenergy presents a relatively new market opportunity that could assist in the management of poor-quality unmanaged coppice of sweet chestnut or perhaps in future American chestnut plantings. Biomass residues can be manufactured into pure pellets (Gündüz et al., 2016) or pellets blended with biomass of other species such as pines (Gil et al., 2010). By tapping into the carbon markets, landowners in Europe and North America can earn income for carbon offsets created by their sustainable chestnut forest management (ecosystem service valuation). High forests and coppices managed for high-quality timber have the benefit of maximizing the proportion of harvested wood that goes into long-lived carbon-stable products, using only residual wood for bioenergy and providing greenhouse gas emissions (GHG) mitigation benefits (Birdsey et al., 2018). Timber and nut-oriented chestnut plantations were found to be good carbon sinks, even at low densities (Menéndez-Miguélez et al. 2023). American chestnut compared similarly to co-occurring species in carbon sequestration models, indicating it might play a role in mitigating climate change (Gustafson et al. 2017).

American chestnut, when restored, could be considered for coppice management where the species can be maintained through short to long rotations (Fig. 3), depending on the desired economic product or ecological service. In fact, repeated cutting of second-growth mixed species stands was promoted in the United States prior to the introduction of chestnut blight for conversion to even-aged coppice forest for multi-use wood products (Ashe, 1911); coppice management was common in rural pastoral settings (Buttrick, 1915). This may be particularly important for Indigenous communities and rural communities that rely on self-sufficient goods and services to augment or fulfill food, fuel, or wood product needs on a short rotation. Additionally, local short-rotation coppice could help reduce the threat of nonnative pest spread from movement of firewood (Solano et al., 2021). American chestnut returning as an important saw timber tree on long rotations remains questionable because trees will probably contract *C. parasitica*, even if blight-tolerant, creating wounds that will degrade wood quality.

American chestnut offers an opportunity for management focused on improving habitat for wildlife on state game lands, federal wildlife reserves, or private hunting leases where the tree can provide an important source of hard mast for game species like black bear (*Ursus americanus*), turkey (*Meleagris gallopavo*), and deer (*Odocoileus virginianus*). Afforestation to reclaim mine sites and abandoned agricultural land represents a relatively large opportunity for blight-resistant American chestnut trees (Jacobs, 2007), and this type of planting also affords opportunities for cost-share programs from federal and state sources without necessarily an emphasis on wood production. Repeated planting into regeneration harvests of mixed species forests may be required to maintain the American chestnut long-term (Fig. 3).

Non-traditional uses of sweet chestnut forests have gained importance, including tourism, educational and recreational activities. The development of valuable products from wood, fruit residues and other components of the tree are an increasing trend. Sweet chestnut fruit pericarp and integument were found to be a source of interesting biocompounds such as tocopherols, pigments and polyphenols (de Vasconcelos et al., 2010). Further research could point at economically valuable and sustainable production for both sweet and American chestnut.

In several areas of Europe, such as Italy, timber quality is usually low despite its durability, given its poor shape, presence of ring shake and abundant knots. Important traditional uses as poles for agriculture uses (traded in Italy at € 150–200 per m^3), have decreased by substitution with pre-stressed concrete or galvanized steel (Blanc et al., 2021). Consequently, research on innovative uses such as Oriented Strand Board (OSB), compensated and lamellar panels has been developed (Locatelli et al., 2021), representing potential new markets for chestnut species.

5. Summary

Sweet chestnut has been domesticated and cultivated since Roman times, providing a diversity of wood and non-timber products. In contrast, American chestnut's traditional and historical values have been largely lost because chestnut blight and Phytophthora root rot coincided with massive timber extraction, along with the loss of Indigenous peoples' cultures. Historical and contemporary silvicultural approaches of sweet and American chestnut have been largely even-aged, but the specific regeneration systems diverge among species. Coppice management within an agroforestry system has been the primary mode of regeneration for sweet chestnut, while coppice of American chestnut was historically restricted to forest sites with lower productivity or near rural homesteads. Land abandonment is the main silvicultural concern for sweet chestnut coppice forests and represents an impending threat to American chestnut restoration once disease-resistant material is reintroduced. New silvicultural management practices of sweet chestnut coppices (medium-long rotations) and proper management of high-forest systems have made it possible to improve production and wood quality, envisaging favorable potential in the timber market (Manetti et al., 2006; Manetti et al., 2016; Patrício et al, 2020). Traditional timber products will probably be restricted due to damage from blight for American chestnut, even for resistant material (Steiner et al., 2017). Short-rotation systems, as used in Europe, might be a more attractive management option for American chestnut.

As climate change and land use pressures increase, so will the need to manage stands with alternative regeneration systems and practices, such as adaptive silviculture or CNS (Achim et al., 2022), but these systems have gone largely untested for either species. Sweet and American chestnut have varying degrees of climate adaptation potential, and genetic conservation units have been identified to guide assisted migration (Martín et al., 2012; Sandercock et al., 2022). Chestnut populations are expected to contract in hotter and drier forest types such as Mediterranean forests for sweet chestnut or southern North American populations for American chestnut (Noah et al., 2021).

Programs and policies are being developed that constitute important milestones for forests in general, and more specifically for chestnut forests in Europe, which can also serve as an important framework for other countries. New opportunities for markets are opening such as biomass residues, and biocompounds from nuts and other components of the tree for the sweet chestnut, while mine reclamation and afforestation could accelerate American chestnut restoration potential. American chestnut has a well-developed framework for genetic improvement and species reintroduction throughout the former range, largely derived from programs co-developed by private non-governmental organizations (e.g., The American Chestnut Foundation), the United States Department of Agriculture, and state and university cooperators. This type of framework could be used as a model to help guide development of similarly threatened or declining species, like the sweet chestnut (Jacobs et al., 2012).

International teams like the IUFRO working party (1.01.13) and meetings like the International Chestnut Symposiums are important for building synthesis and forging new collaborations across continents to help answer important ecological and management questions. Collaborative networks that integrate disciplines and large geographic areas necessary to advance species silvicultural management are rare for any tree species. Ultimately, all management is species- and placed-based and will require connections between local, rural, or tribal communities and professional foresters informed by the latest science.

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CRediT authorship contribution statement

Stacy L. Clark: Conceptualization, Resources, Writing – original draft, Writing – review & editing. **Enrico Marcolin:** Conceptualization, Writing – original draft, Writing – review & editing. **Maria Sameiro Patrício:** Conceptualization, Writing – original draft, Writing – review & editing. **Verónica Loewe-Muñoz:** Conceptualization, Writing – original draft, Writing – review & editing.

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.

Data availability

No data was used for the research described in the article.

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