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OPINION

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Resilient trees for urban environments: The importance of intraspecific variation

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Societal Impact Statement
Trees in urban environments provide us with shade, heat mitigation, flood abatement, noise and pollution reduction, pollination, beauty, and much more. However, many of these benefits are strongly connected to tree size and vitality, with larger, healthier trees providing ecosystem services more effectively, which means that selecting the right tree for site and function is crucial in order to gain all benefits from our urban trees.

Summary
Trees play a major role in the Earth's biogeochemical processes, influencing soil production, hydrological, nutrient and carbon cycles, and the global climate. They store about 50% of the world's terrestrial carbon stocks, and provide habitats for a wide range of other species, supporting at least half of the Earth's known terrestrial plants and animals. Trees are not only found in forests and other natural ecosystems, but also in urban environments. Most of the human population is concentrated in cities, towns and villages, so urban trees are critical to meet on-going and future social, economic and environmental challenges. However, many urban tree populations are strongly challenged by a changing climate, outbreaks of pests and pathogens and an urban development with increasingly dense cities and a high proportion of impermeable surface materials. The importance of intraspecific variation needs to be better acknowledged in this context, since poor matching of trees and the local climate and growing conditions can lead to extensive loss of valuable trees. By using the right genetic plant material for the challenging urban environments, a more resilient tree population with a greater diversity and higher capacity for delivering ecosystem services can be gained. Here, we wish to discuss the need to consider intraspecific variation when planning resilient tree populations for urban environments and how seed banks and botanical garden play important roles in efforts to improve the matching of genetic plant material for future environmental challenges. Strategies to enrich urban tree diversity and increase resilience are outlined.

KEYWORDS
biodiversity, climate change, tree selection, urban environment, urban trees

1 | INTRODUCTION

About 30% of the over 70,000 known tree species worldwide are likely under threat of extinction (Cazzolla Gatti et al., 2022). The main threats to tree diversity are forest clearance due to agriculture and urbanisation, direct exploitation for timber and other products, and pressures arising from climate change and biosecurity risk (Newton, 2021). Over the past 300 years, global forest area has decreased by about 40% and 29 countries have lost more than 90% of their forest cover (FAO and UNEP, 2020). From 2000 to 2020, the world experienced a net loss of over 100 million hectares (c. 2.4%) in tree cover (FAO and UNEP, 2020). Trees are of immense ecological importance as they define and form the major structural components of forest ecosystems, which cover approximately 31% of the world's land surface. Forests play a major role in the Earth's biogeochemical processes, influencing soil production, hydrological, nutrient and carbon cycles, and the global climate. They contain about 50% of the world's terrestrial carbon stocks, while over 75% of the world's accessible freshwater is obtained from forested catchments (Newton, 2021). Forests provide habitat for a wide range of other species apart from trees, supporting at least half of the Earth's known terrestrial plant and animal species (Rivers et al., 2022). Conversely, trees are not only found in forests, but also occur on savannahs, shrubland and grasslands, in deserts, wetlands, coastal and rocky ecosystems, and urban environments. In cities, towns and villages, trees are vitally important to meet on-going and future social, economic and environmental challenges. Today, 55% of the world's population (4.2 billion people) lives in urban areas, a figure which is set to rise to 70% by 2050 (Callaghan et al., 2021). Urban trees are therefore essential to the lives of most of the human population.

1.1 | Urban environments and trees

Trees in urban environments offer multiple contributions to people including regulating, cultural, provisioning and supporting services, all of which are critical for sustainable urban development and human well-being (Cimburova & Pont, 2021) (Figure 1). Many of these benefits are strongly connected to tree size and vitality, with larger, healthier trees providing ecosystem services more effectively (Gomez-Muñoz et al., 2010; Hand et al., 2019).

Increasingly dense cities with a large proportion of paved and impermeable surfaces create challenging conditions for urban trees to develop successfully (Table 1). With climate change, multiple stressors such as heat waves, drought and temporary flooding will increasingly limit tree growth in urban environments and lead to higher tree mortality, and the potential loss of crucial ecosystem services. In a global study, Esperon-Rodriguez et al. (2022) found that the capacity to tolerate the projected conditions in urban environments has already been exceeded for 56–65% of the trees in 164 cities across 75 countries. It has been recommended that for long-term stability of urban forests, trees resilient to climate change must be chosen, so that they can survive and thrive (McPherson et al., 2018). Moreover, global movement of goods and people has enhanced the spread of invasive pests and pathogens worldwide (Aide & Grau, 2004; Crowl et al., 2008). Critically, climate change is allowing plant pests and pathogens to establish themselves in regions that previously had an unsuitable climate, increasing the mortality of common urban tree species. The combination of shifting climate compatibility interacting with novel biotic threats will limit the range of tree species that can deliver crucial ongoing resilience to the ecosystem services provided by the urban forest.

FIGURE 1 Ecosystem services provided by trees in urban environments divided in four classes of services: provisioning, regulating, supporting, and cultural.

TABLE 1 List of current and future challenges that can affect urban trees.

Climate change	
	Drought - many regions of the world will experience more frequent long periods of drought.
	Heat **-** many regions of the world will experience more frequent heat waves.
	Flooding – In connection with more frequent extreme weather, heavy and prolonged periods of rain will become a challenge for urban trees in specific regions with hypoxic conditions as a result.
	Storms – Some regions of the world will experience more storms with intensively high winds
	Wildfires – Because of a warmer and drier climate intense wildfires will become more frequent and threaten urban settings
Pests & Pathogens	
	Pests and pathogens will affect many urban trees globally with extensive tree loss likely. These biotic threats will limit the number of species that can be introduced into urban environments. A changing climate will also aid the establishment of pests and pathogens in new regions. Such expansions of pest or pathogen distributional ranges, can lead to these threats becoming much more widely spread within both natural and urban tree environments.
Urban development	Through an increasing densification of urban environments, the space for trees above as well as below ground is limited. The dense settlement of cities results in an 'urban heat island' that will increase evapotranspiration, tree water use, and water stress. The paved inner-city environments of many cities combined with very efficient drainage make the growing conditions extremely challenging with dry and/or hypoxic conditions.

To create resilience to present and future challenges, where the exact consequences of future scenarios cannot be predicted in advance, a commonly proposed solution is to cultivate a large diversity of trees, that is, increase tree diversity at many taxonomic levels, including infraspecific variation. However, this will require substantial changes in national, regional and local policy as urban tree inventories often comprise of few species that dominates in many urban tree populations, many of which in Europe and North America are at risk from outbreaks of serious pests and diseases such as the Asian long-horned beetle *Anoplophora glabripennis*, the emerald ash borer *Agrilus planipennis*, Ramorum disease *Phytophthora ramorum*, and the ash die-back fungus *Hymenoscyphus fraxineus* (e.g., Cowett & Bassuk, 2020; Sjöman & Östberg, 2019; Tubby & Webber, 2010; Yan & Yang, 2017). A clear example of a very limited diversity of urban trees is Helsinki, Finland, where almost 44% of all trees in public spaces are represented by *Tilia* spp. with a significant threat if these trees should be attacked by a serious pest or pathogen outbreak (Sjöman & Östberg, 2019).

Achieving an increased diversity of urban trees to improve the resilience of urban forests to future conditions is likely to involve greater use of non-traditional tree species, particularly in regions with relatively few native species, such as western and northern Europe. Current literature guiding urban planners, landscape architects and garden designers about tree selection (e.g., Tabassum et al., 2023) relates to individual species. Such guidance does not adequately acknowledge the adaptive variation that results from the processes of natural selection found in more challenging climate conditions and stressful growing environments (Sjöman & Nielsen, 2010). Intraspecific variation, consisting of genetic and phenotypic diversity within and between populations of wild and domestic organisms, plays a critical role in regulating ecological processes in the face of adverse and often unpredictable stressors.

1.2 | Intraspecific variation and effects of its loss

There is growing evidence of large intraspecific variation within many tree species in response to different growing conditions, such as gradients in water availability. For example, drought-adaptation traits in tree species such as *Acer grandidentatum*, *Acer rubrum*, *Acer saccharum*, *Betula pendula*, *Fraxinus Americana*, *Quercus ilex* and *Quercus rubra* have been shown to differ across environmental gradients, relating to habitat type and precipitation (e.g., Alder et al., 1996; Bauerle et al., 2003; Hannus et al., 2021; Marchin et al., 2008; Schuldt et al., 2016; Sjöman et al., 2015). A robust body of biogeographical literature links some of this intraspecific variation to local adaptation (Temunović et al., 2012; Zohner et al., 2020). This is also apparent when comparing precipitation and temperature regimes throughout distribution ranges.

Intraspecific variation in traits is reported to be most common among species with a large natural distribution, as these species can occur in many different types of climates and growing environments (Royer et al., 2009). A species' capacity to tolerate an increasingly stressful situation may rely strongly on beneficial variants already present in the stressed population, rather than on new variants arising through genetic mutation (Orr & Unckless, 2008; Teotónio et al., 2009). Indeed, it has been suggested that an effective evolutionary response is positively related to the amount of standing genetic variation (Blows & Hoffmann, 2005; Lynch & Lande, 1993). Thus, the ability to cope with changing and stressful environmental conditions depends largely on how well individuals can adjust phenotypically to the altered conditions, and on the genetic variation present in the population upon which selection can act (Bijlsma & Loeschcke, 2012). The genetic variation that can be lost in a single generation when converting forests to agriculture through clearcutting may take hundreds of generations to restore, which for long-lived organisms such as trees could mean thousands of years. In the face of rapid climate change – with marked changes documented at the scale of years or decades – there is a twin need to both safeguard genetic variation to mitigate tree diversity loss and to retaining its potential for urban landscapes and horticulture (Leigh et al., 2019).

The list of tree species likely to show long-term resilience to serious pathogens and pests in urban environments in many parts of the world is very limited. It is, therefore, of great importance to find additional genetic material of these species with the capacity to cope with future climate conditions and resilience to known pests and pathogens. In the selection of future urban trees, good genetic matching for urban environments is essential in order to maximize the longevity and benefits of the trees (Figure 2). Today, urban tree nurseries, which supply most city trees worldwide, have very limited to non-existent awareness of intraspecific variation which may be a low interest priority for nurseries (Sjöman & Watkins, 2020). This indicates that the ornamental perspective has been prioritized in cultivar selection, at the expense of finding genetic material that has a higher tolerance for, e.g., drought. As a consequence, trees purchased for urban planting may not be genetically well suited to developing successfully in these challenging environments. There is thus a strong risk that many trees planted in towns and cities today will not develop into large, healthy trees with the capacity to deliver crucial ecosystem services.

Because of the current pace of habitat loss worldwide (in part due to urbanisation), there is a risk of losing valuable wild genotypes in many species of trees, compromising their ability to adjust to future challenges both in nature and when used in cities and horticulturally. In addition, fragmentation of habitats leads to small, isolated populations that are subject to genetic erosion, as populations of normally outcrossing species come to show decreased levels of genetic variation and a decrease in fitness because of inbreeding depression (Nickolas et al., 2019). To make things worse, the magnitude of inbreeding depression generally increases considerably under stressful environmental conditions, such as extreme climatic events including heat waves and seasonal droughts (Armbruster & Reed, 2005). This makes inbred populations more vulnerable to environmental stressors. For urban forests, genetic matching to future urban environments in a region is important to develop more resilient plant material (Sjöman et al., 2019). For instance, importing genotypes from warmer regions (e.g., lower latitudes) of a species distribution can improve the ability of the local population to cope with ongoing climate change by promoting genes of more distant and (slightly) different habitats within the species range (Leigh et al., 2019).

1.3 | The role of seed banks and botanical gardens in the face of environmental challenges

Evidence shows that we are facing a sixth mass extinction of species, if those species at risk today do in fact disappear (Barnosky et al.,

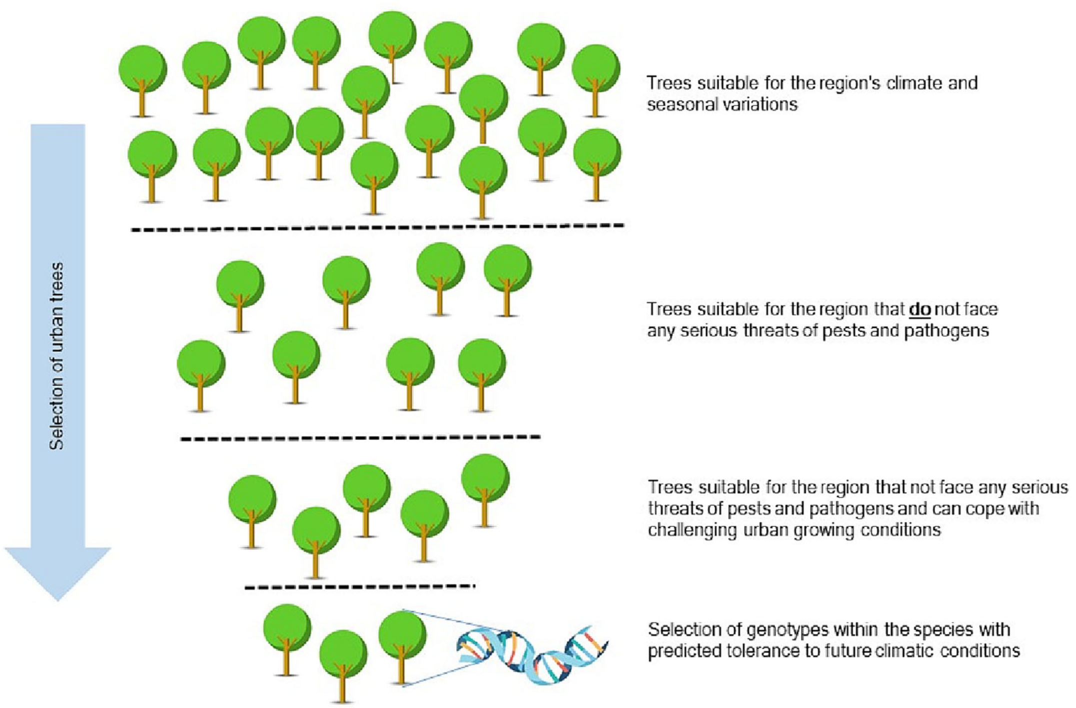

FIGURE 2 Filters that should be applied when selecting urban trees for a future climate. It is crucial to not only consider aspects such as resilience to pests and pathogens but also how the genetic material matches inner city environments in a future climate. The number of species that are not at risk of being affected by serious diseases and pathogens, and have the capacity to handle the local climate and tolerance for the growing conditions on site is usually very limited, especially in a more northern climate. This means that the few species that can handle the mentioned challenges should be of a genetic material that can also handle a future climate, which makes knowledge of the genetic variation within different tree species and its suitability for a future climate absolutely crucial.

2011; Brooks et al., 2019; Ceballos et al., 2017). In plants, two in five species are likely to be threatened (Antonelli et al., 2020; Nic Lughadha et al., 2020). This loss of diversity is unacceptable, especially since diversity is key for ecological resilience to future challenges. Averting dramatic loss of diversity and associated loss of ecosystem services is still possible through intense conservation actions, but the window of opportunity is rapidly closing. Moreover, many existing conservation programmes are mainly directed towards preventing tree losses at the species level and seldom acknowledge loss of variation within species, despite the rate of loss of intraspecific variation being many times greater than the rate of species loss (Hughes et al., 1997; Leigh et al., 2019; Mimura et al., 2017). Indeed, diversity below the species level remains severely under-evaluated in global surveys (Laikre et al., 2020).

As political and social pressure to increase tree planting intensifies (Forest Commission, 2019), a golden rule for successful reforestation projects is to 'choose the right tree for the right place' (Di Sacco et al., 2021). Burley et al. (2019) identify two key components for the urban forestry sector in selection of trees for a future climate. First, selection of species based on hierarchical filters using climate as the pivotal biophysical limiting factor would improve outcomes for cities. Second, species that may have been resilient in horticultural plantings under previous or current conditions may be unreliable in the future, while new opportunities will emerge as suitable climate space appears beyond the current range of species. However, even these identified factors reflect the pattern followed in the plant-guided literature, with the focus of attention firmly placed on species – as if they were ecologically homogeneous units – rather than genotypes which clearly shows a limited exchange of knowledge between science and practice. As global temperatures continue to rise in the 21st century and beyond, urban forestry and planning efforts should identify ecotypes and pools of genotypes within species that are most likely to thrive in future climates, in order to maximise planting success and provide a return on investment in the long term (Watkins et al., 2021).

Botanical gardens around the world have long worked on identification and conservation of biological diversity, but even in that context variation within species has been under-prioritised compared with variation between species. Many botanical gardens in the northern hemisphere have also attempted to identify trees that can grow in a more challenging cold climate by looking for cold-hardy plant genetic material growing at the northernmost limit of the species distribution. However, there have been very few recent botanical expeditions with the objective of finding genotypes of common species that are more exposed to heat and drought within their natural distribution, and thus possibly better adapted to a future with a warmer and periodically drier climate (Sjöman et al., 2019). An example of recent conservation efforts with the aim of collecting and storing important genetic material is the joint work of the Millennium Seed Bank Partnership coordinated by the Royal Botanic Gardens, Kew. At the Millennium Seed Bank in West Sussex, England, over 2.4 billion seeds from more than 40,000 species collected all over the world are banked to conserve them for the future, with a focus on species that are economically important, threatened, or narrowly distributed. Important questions concerning this type of conservation effort are whether the seed material currently held in seed banks can already provide sufficient genetic material for a future climate, to what extent seeds from various ecotypes for different species are included, and how much of the whole distribution of each species is represented in the seed collection. These and related questions are now shaping agendas for seed banks and botanical gardens (Mounce et al., 2017). It has also become clear that conservation seed banks need to be complemented by seed banks focused on supplying seeds for habitat restoration, including tree planting initiatives (Breman et al., 2021; Goodale et al., 2023).

To explore these issues in practice, we considered four tree species with a very large natural distribution in the northern hemisphere, and with different rainfall and temperature regimes throughout their distribution: *Acer platanoides*, *Acer rubrum*, *Betula pendula* and *Carpinus betulus*. We then compared these with the provenances of the species found in the Millennium Seed Bank. This comparison shows that banked seeds have a very limited gene pool and lack provenances with natural growing conditions matching those found in urban environments in major European cities (Figure 3).

Apart from seed banks, living collections also preserve genetic material from extinction in the wild, with large botanical gardens and arboretums being critical organisations in this pursuit. However, recent research shows that most taxa within these collections are well below the genetic conservation targets, which means that existing collections of trees constitute a very small percentage of the available genetic variation (Hoban et al., 2020). One obvious reason for this is that many botanic gardens and arboretums lack the space to include large numbers of tree individuals with different genetic backgrounds in order to ensure that they have a broad representation of a particular species in their collection. Another reason is that, for economic, legal and logistic considerations, curators liberally share seeds and other propagating material between gardens, instead of making new acquisitions from wild populations, which means that many collections now have similar genetic material (Flower et al., 2018; Kashimshetty et al., 2017; Khoury et al., 2019). A telling example of this is *Acer griseum* from China, highly valued as an ornamental, for which all specimens in commercial cultivation and in botanical collections originate from Ernest H. Wilson's collection of the species in 1901, meaning that the species is represented by a very narrow genetic base (Aiello et al., 2020). In the wild this species occurs in many types of climates, although due to habitat loss, logging and wood harvesting it is formally classified in the IUCN Red List as Endangered, (Aiello et al., 2020). This distinction between the genetic base of plants in cultivation and those in the wild highlights the importance of in situ conservation of wild populations in protected areas and shows a need for propagation and ex situ preservation of trees in unprotected areas.

1.4 | The way forward in conserving genetic diversity for urban forests

A search for long-term sustainable plant material for local urban environments is needed to prevent loss of resilience of urban

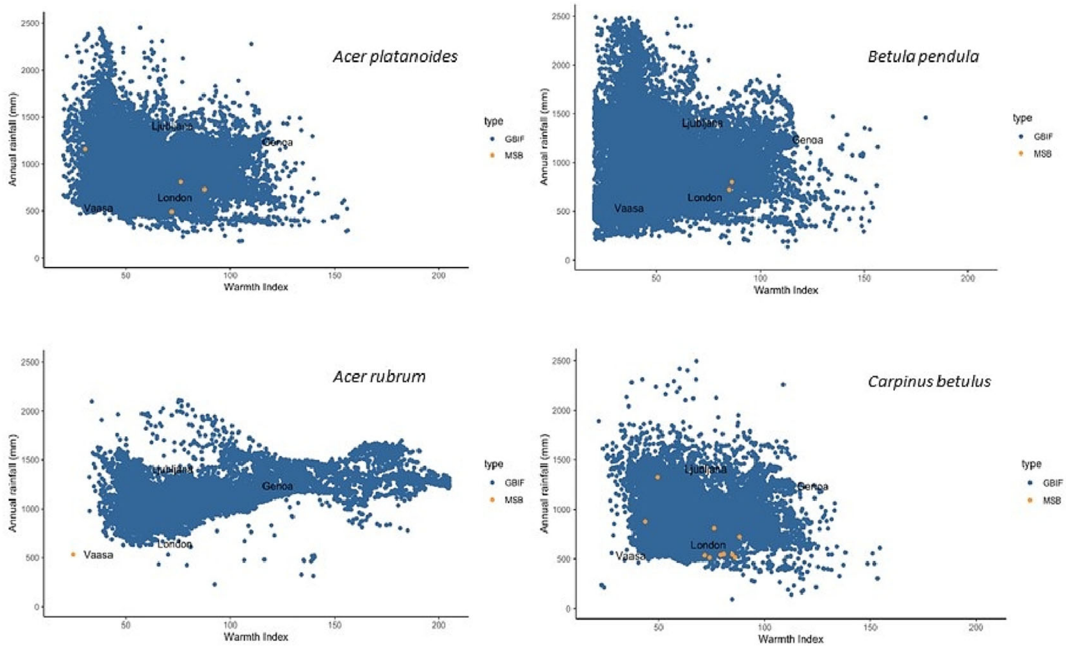

FIGURE 3 Representation of provenances of four common tree species with a large natural distribution, including a large variation in climates, where genetic materials used in the study which are from the Millennium Seed Bank (MSB) are marked in orange, compared with their whole natural range (based on warmth index and annual precipitation) marked in blue. Figures modified from Sjöman and Watkins (2020) where distribution data is sourced from GBIF (Global Biodiversity Information Facility).

environments to future challenges and to maintain the supply of important ecosystem services. The outcome will be crucial for the growing human population living in urban environments worldwide.

In order for researchers, urban planners and other practitioners to identify these future trees, we need to immediately stop considering species as a uniform mass, without acknowledging the genetic variation they contain. We also need to collectively start applying concepts such as ecotypes or genetic origin (provenance), and focus on those that are adapted to the current and modelled future environmental conditions in the target location for their cultivation.

This means that extensive conservation efforts are required even for species that are not at risk of global extinction, but for which ecotypes with the greatest potential for urban environments are being lost regionally or locally. These rescue operations will require increasing both in situ and ex situ efforts. The in situ work will involve identifying areas where unique ecotypes of promising urban tree species have evolved to possess characteristics that make them valuable for urban environments in other regions. Actions in support of conservation of the genetic diversity within species need to be mandated through policies and legislation from local to international scales to reduce the risk of losing highly valuable ecotypes that could help urban environments to manage future challenges. In order to rescue valuable genotypes, ex situ activities are critical and should aim at collecting as much of the species geographic distribution as possible, in order to obtain a broad representation of the existing genetic material to be stored in seed banks or living plant collections such as botanical gardens. There is a particular challenge for ex situ collections of species that are very difficult to cultivate (Fant et al., 2016). While seed banks are an efficient genetic safeguard for many plant species, about 20% of plant species have recalcitrant seeds (those that cannot survive in standard seedbank conditions) or other sampling or storage challenges (Wyse et al., 2018). Although cryopreservation is often an option (although not always; see e.g., Wyse et al., 2018), it is very expensive, and consequently ex situ conservation efforts of species with recalcitrant seeds are usually limited to living plants in collections.

A key challenge for ex situ collections is capturing high genetic diversity in as few individuals as possible. A botanic garden might have resources to maintain a few to a few dozen (sometimes hundreds) of individuals of some priority species, but not the thousands that seed banks can or need to preserve (Hoban et al., 2020). Another limitation in ex situ collections is the increasing restrictions on material exchange imposed by global regulations on access, benefit sharing, and biosecurity. The purpose of these regulations is to protect the genetic material of one country from being exploited by other countries or organisations, but they have also made collection permits difficult to secure for conservation and especially for commercial horticultural use (Sirakaya, 2019). If the use of specific genetic material is restricted to non-commercial academic purposes, botanic gardens risk hosting potentially useful plant material that is unavailable for commercial cultivation and more widespread use in the urban landscape.

We suggest two strategies in order to enrich urban tree diversity and resilience: 1) widespread genetic screening of existing tree collections in botanical garden and arboretums, to assess the degree of intraspecific variation/number of distinct ecotypes captured within collections for a given species. This will allow further evaluation and comparison of different genetic materials functional traits and their capacity for future climate scenarios in different plant collections (Hirons et al., 2021) (Figures 4 and 2) identifying natural habitats with matching climate and growing conditions for those species within urban environments (nationally and internationally). This step will require climate modelling to identify specific regions and habitats that may include valuable genetic material with the capacity to tolerate challenging urban environments for the region. This latter direction can detect areas of a species distribution that are not existing in ex situ collection but have a good matching to urban environments in a future climate.

Moreover, for many countries with an exceptionally rich tree flora, it is possible to evaluate and use the native tree species to a much greater extent than today when many exotic species dominate urban plantations as seen in regions such as eastern Africa (Dharani, 2011). However, because of a very limited understanding of many native species capacity for urban horticulture, it is crucial to first thoroughly evaluate their usefulness and potential for substituting the dominating exotic species. For regions with a limited native tree flora, it is inevitable to use species from other parts of the world that can handle the city's challenging environments and deliver important ecosystem services while not becoming invasive threats (Sjöman et al., 2015).

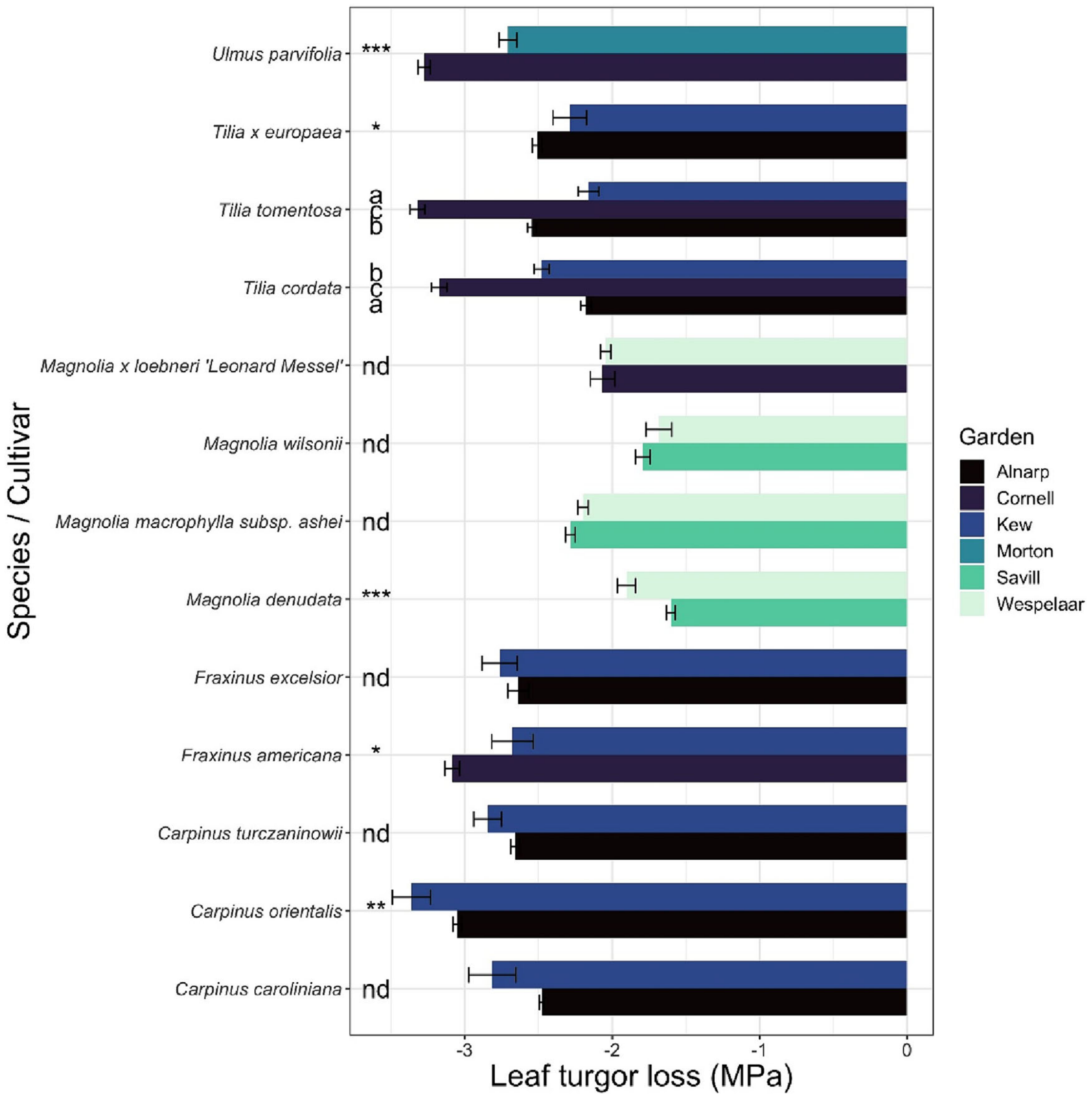

FIGURE 4 Estimation of drought tolerance through evaluation of water potential at leaf turgor loss (TLP) of selected tree species taken from different botanical collections, including different genetic types within same species. An increased negative value in MPa indicates a higher level of drought tolerance. Where two gardens are compared, the significance level is indicated by *$p < .05$, **$p < .01$, and ***$p < .001$. Letters of heterogeneity indicate differences where three gardens are compared. nd = no significant difference. The error bars represents the standard error of collected TLP data (Hirons et al., 2021).

2 | CONCLUSIONS

Trees are among our best allies in the fight against climate change and biodiversity loss. Although we often think of them in forests, most of our interactions with trees take place in urban environments, where they provide us with shade, heat mitigation, flood abatement, noise and pollution reduction, pollination, beauty, and much more. However, to maintain and increase those manifold benefits we urgently need to rethink tree selection for urban environments, to include those species and provenances most suitable for the environmental conditions and stresses posed by a rapidly changing and unpredictable climate, spreading pests and emerging plant diseases. Major efforts now must take place to increase representation of future urban trees in living collections and seed banks, alongside genetic screening of potentially suitable genetic plant material for cultivation. With growing recognition of the current and future values of trees to our societies, we now have to realise these great opportunities.

AUTHOR CONTRIBUTIONS

Henrik Sjöman: Conceptualization; methodology; investigation; formal analysis; writing—original draft writing—review and editing. **Harry Watkins:** Conceptualization; methodology; investigation; writing—review and editing. **Laura J. Kelly:** Writing—review and editing. **Andrew Hirons:** Writing—review and editing. **Kent Kainulainen:** Writing—review and editing. **Kevin Martin:** Writing—review and editing. **Alexandre Antonelli:** Conceptualization; methodology; investigation; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

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 STATEMENT

Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

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REFERENCES

Aide, T. M., & Grau, H. R. (2004). Globalization, migration, and Latin American ecosystems. *Science*, *305*, 1915–1916. https://doi.org/10.1126/science.1103179

Aiello, A. S., Bachtell, K. R., Dosman, M. S., & Wang, K. (2020). *Acer griseum*, the paperbark maple. In *International Dendrology Society yearbook 2020*. International Dendrology Society.

Alder, N. N., Sperry, J. S., & Pockman, W. T. (1996). Root and stem xylem embolism, stomatal conductance, and leaf turgor in Acer grandidentatum populations along a soil moisture gradient. *Oecologia*, *105*(3), 293–301. https://doi.org/10.1007/BF00328731

Antonelli, A., Smith, R. J., Fry, C., Simmonds, M. S., Kersey, P. J., et al. (2020). *State of the World's plants and fungi, Royal Botanic Gardens (Kew)*. Sfumato Foundation.

Armbruster, P., & Reed, D. H. (2005). Inbreeding depression in benign and stressful environments. *Heredity*, *95*(3), 235–242. https://doi.org/10.1038/sj.hdy.6800721

Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O. U., Swartz, B., Quental, T. B., Marshall, C., McGuire, J. L., Lindsey, E. L., Maguire, K. C., Mersey, B., & Ferrer, E. A. (2011). Has the Earth's sixth mass extinction already arrived? *Nature*, *471*, 51–57. https://doi.org/10.1038/nature09678

Bauerle, W. L., Whitlow, T. H., Setter, T. L., Bauerle, T. L., & Vermeylen, F. M. (2003). Ecophysiology of Acer rubrum seedlings from contrasting hydrologic habitats: Growth, gas exchange, tissue water relations, abscisic acid and carbon isotope discrimination. *Tree Physiology*, *23*(12), 841–850. https://doi.org/10.1093/treephys/23.12.841

Bijlsma, R., & Loeschcke, V. (2012). Genetic erosion impedes adaptive responses to stressful environments. *Evolutionary Applications*, *5*(2), 117–129. https://doi.org/10.1111/j.1752-4571.2011.00214.x

Blows, M. W., & Hoffmann, A. A. (2005). A reassessment of genetic limits to evolutionary change. *Ecology*, *86*(6), 1371–1384. https://doi.org/10.1890/04-1209

Breman, E., Ballesteros, D., Castillo-Lorenzo, E., Cockel, C., Dickie, J., Faruk, A., … Ulian, T. (2021). Plant diversity conservation challenges and prospects—The perspective of botanic gardens and the millennium seed Bank. *Plants*, *10*(11), 2371. https://doi.org/10.3390/plants10112371

Brooks, T. M., Pimm, S. L., Akçakaya, H. R., Buchanan, G. M., Butchart, S. H. M., Foden, W., Hilton-Taylor, C., Hoffmann, M., Jenkins, C. N., Joppa, L., Li, B. V., Menon, V., Ocampo-Peñuela, N., & Rondinini, C. (2019). Measuring terrestrial area of habitat (AOH) and its utility for the IUCN red list. *Trends in Ecology & Evolution*, *34*(11), 977–986. https://doi.org/10.1016/j.tree.2019.06.009

Burley, H., Beaumont, L. J., Ossola, A., Baumgartner, J. B., Gallagher, R., Laffan, S., Esperon-Rodriguez, M., Manea, A., & Leishman, M. R. (2019). Substantial declines in urban tree habitat predicted under climate change. *Science of the Total Environment*, *685*, 451–462. https://doi.org/10.1016/j.scitotenv.2019.05.287

Callaghan, A., McCombe, G., Harrold, A., McMeel, C., Mills, G., Moore-Cherry, N., & Cullen, W. (2021). The impact of green spaces on mental health in urban settings: A scoping review. *Journal of Mental Health*, *30*(2), 179–193. https://doi.org/10.1080/09638237.2020.1755027

Cazzolla Gatti, R., Reich, P. B., Gamarra, J. G., Crowther, T., Hui, C., Morera, A., Bastin, J. F., De-Miguel, S., Nabuurs, G. J., Svenning, J. C., & Serra-Diaz, J. M. (2022). The number of tree species on earth. *Proceedings of the National Academy of Sciences*, *119*(6), e2115329119.

Ceballos, G., Ehrlich, P. R., & Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences*, *114*, E6089–E6096. https://doi.org/10.1073/pnas.1704949114

Cimburova, Z., & Pont, M. B. (2021). Location matters. A systematic review of spatial contextual factors mediating ecosystem services of urban trees. *Ecosystem Services*, *50*, 101296. https://doi.org/10.1016/j.ecoser.2021.101296

Cowett, F. D., & Bassuk, N. L. (2020). Street tree diversity in Massachusetts, USA. *Arboriculture & Urban Forestry*, *46*(1), 27–43. https://doi.org/10.48044/jauf.2020.003

Crowl, T. A., Crist, T. O., Parmenter, R. R., Belovsky, G., & Lugo, A. E. (2008). The spread of invasive species and infectious disease as drivers of ecosystem change. *Frontiers in Ecology and the Environment*, *6*(5), 238–246. https://doi.org/10.1890/070151

Dharani, N. (2011). *Field guide to common trees & shrubs of East Africa*. Penguin Random House South Africa.

Di Sacco, A., Hardwick, K. A., Blakesley, D., Brancalion, P. H., Breman, E., Cecilio Rebola, L., Antonelli, A., et al. (2021). Ten golden rules for reforestation to optimize carbon sequestration, biodiversity recovery and livelihood benefits. *Global Change Biology*, *27*(7), 1328–1348. https://doi.org/10.1111/gcb.15498

Esperon-Rodriguez, M., Tjoelker, M. G., Lenoir, J., Baumgartner, J. B., Beaumont, L. J., Nipperess, D. A., Power, S. A., Richard, B., Rymer, P. D., & Gallagher, R. V. (2022). Climate change increases global risk to urban forests. *Nature Climate Change*, *12*, 950–955. https://doi.org/10.1038/s41558-022-01465-8

Fant, J. B., Havens, K., Kramer, A. T., Walsh, S. K., Callicrate, T., Lacy, R. C., Maunder, M., Meyer, A. H., & Smith, P. P. (2016). What to do when we can't bank on seeds: What botanic gardens can learn from the zoo community about conserving plants in living collections. *American Journal of Botany*, *103*, 1541–1543. https://doi.org/10.3732/ajb.1600247

FAO and UNEP. (2020). *The state of the World's forests 2020. Forests, biodiversity and people*. Rome.

Flower, C. E., Fant, J. B., Hoban, S., Knight, K. S., Steger, L., Aubihl, E., Royo, A. A., et al. (2018). Optimizing conservation strategies for a threatened tree species: In situ conservation of white ash (*Fraxinus americana* L.) genetic diversity through insecticide treatment. *Forests*, *9*(4), 202. https://doi.org/10.3390/f9040202

Forest Commission. (2019). Government supported new planting of trees in England. Report for 2019–20.

Gomez-Muñoz, V. M., Porta-Gándara, M. A., & Fernández, J. L. (2010). Effect of tree shades in urban planning in hot-arid climatic regions. *Landscape and Urban Planning*, *94*(3–4), 149–157. https://doi.org/10.1016/j.landurbplan.2009.09.002

Goodale, U. M., Antonelli, A., Nelson, C. R., & Chau, M. M. (2023). Seed banks needed to restore ecosystems. *Science*, *379*(6628), 147. https://doi.org/10.1126/science.adg2171

Hand, K. L., Doick, K. J., & Moss, J. L. (2019). *Ecosystem services delivery by large stature urban trees*. Research Report-Forestry Commission.

Hannus, S., Hirons, A., Baxter, T., McAllister, H. A., Wiström, B., & Sjöman, H. (2021). Intraspecific drought tolerance of *Betula pendula* genotypes: An evaluation using leaf turgor loss in a botanical collection. *Trees*, *35*(2), 569–581. https://doi.org/10.1007/s00468-020-02059-7

Hirons, A. D., Watkins, J. H. R., Baxter, T. J., Miesbauer, J. W., Male-Muñoz, A., Martin, K. W., Bassuk, N. L., & Sjöman, H. (2021). Using botanic gardens and arboreta to help identify urban trees for the future. *Plants, People, Planet*, *3*(2), 182–193. https://doi.org/10.1002/ppp3.10162

Hoban, S., Callicrate, T., Clark, J., Deans, S., Dosmann, M., Fant, J., … Griffith, M. P. (2020). Taxonomic similarity does not predict necessary sample size for ex situ conservation: A comparison among five genera. *Proceedings of the Royal Society B*, *287*(1926), 20200102. https://doi.org/10.1098/rspb.2020.0102

Hughes, J. B., Daily, G. C., & Ehrlich, P. R. (1997). Population diversity: Its extent and extinction. *Science*, *278*, 689–692. https://doi.org/10.1126/science.278.5338.689

Kashimshetty, Y., Pelikan, S., & Rogstad, S. H. (2017). Effective seed harvesting strategies for the ex situ genetic diversity conservation of rare tropical tree populations. *Biodiversity and Conservation*, *26*(6), 1311–1331. https://doi.org/10.1007/s10531-017-1302-3

Khoury, C. K., Amariles, D., Soto, J. S., Diaz, M. V., Sotelo, S., Sosa, C. C., Jarvis, A., et al. (2019). Comprehensiveness of conservation of useful wild plants: An operational indicator for biodiversity and sustainable development targets. *Ecological Indicators*, *98*, 420–429. https://doi.org/10.1016/j.ecolind.2018.11.016

Laikre, L., Hoban, S., Bruford, M. W., Segelbacher, G., Allendorf, F. W., Gajardo, G., Rodríguez, A. G., Hedrick, P. W., Heuertz, M., Hohenlohe, P. A., Jaffé, R., Johannesson, K., Liggins, L., MacDonald, A. J., OrozcoterWengel, P., Reusch, T. B. H., Rodríguez-Correa, H., Russo, I. R. M., Ryman, N., & Vernesi, C. (2020). (2020). Post-2020 goals overlook genetic diversity. *Science*, *367*, 1083–1085. https://doi.org/10.1126/science.abb2748

Leigh, D. M., Hendry, A. P., Vázquez-Domínguez, E., & Friesen, V. L. (2019). Estimated six per cent loss of genetic variation in wild populations since the industrial revolution. *Evolutionary Applications*, *12*(8), 1505–1512. https://doi.org/10.1111/eva.12810

Lynch, M., & Lande, R. (1993). Evolution and extinction in response to environmental change. In P. Kareiva, J. G. Kingsolver, & R. B. Huey (Eds.), *Biotic interactions and global change* (pp. 234–250). Sinauer.

Marchin, R. M., Sage, E. L., & Ward, J. K. (2008). Population-level variation of *Fraxinus americana* (white ash) is influenced by precipitation differences across the native range. *Tree Physiology*, *28*(1), 151–159. https://doi.org/10.1093/treephys/28.1.151

McPherson, E. G., Berry, A. M., & van Doorn, N. S. (2018). Performance testing to identify climate-ready trees. *Urban Forestry & Urban Greening*, *29*, 28–39.

Mimura, M., Yahara, T., Faith, D. P., Vázquez-Domínguez, E., Colautti, R. I., Araki, H., Javadi, F., Núñez-Farfán, J., Mori, A. S., Zhou, S., Hollingsworth, P. M., Neaves, L. E., Fukano, Y., Smith, G. F., Sato, Y. I., Tachida, H., & Hendry, A. P. (2017). Understanding and monitoring the consequences of human impacts on intraspecific variation. *Evolutionary Applications*, *10*, 121–139. https://doi.org/10.1111/eva.12436

Mounce, R., Smith, P., & Brockington, S. (2017). Ex situ conservation of plant diversity in the world's botanic gardens. *Nature Plants*, *3*(10), 795–802. https://doi.org/10.1038/s41477-017-0019-3

Newton, A. C. (2021). *Ecosystem collapse and recovery*. Cambridge University Press. https://doi.org/10.1017/9781108561105

Nic Lughadha, E., Bachman, S. P., Leão, T. C., Forest, F., Halley, J. M., Moat, J., Walker, B. E., et al. (2020). Extinction risk and threats to plants and fungi. *Plants, People, Planet*, *2*(5), 389–408. https://doi.org/10.1002/ppp3.10146

Nickolas, H., Harrison, P. A., Tilyard, P., Vaillancourt, R. E., & Potts, B. M. (2019). Inbreeding depression and differential maladaptation shape the fitness trajectory of two co-occurring *eucalyptus* species. *Annals of Forest Science*, *76*(1), 10. https://doi.org/10.1007/s13595-018-0796-5

Orr, H. A., & Unckless, R. L. (2008). Population extinction and the genetics of adaptation. *The American Naturalist*, *172*(2), 160–169. https://doi.org/10.1086/589460

Rivers, M., Newton, A. C., Oldfield, S., & Global Tree Assessment Contributors. (2022). Scientists' warning to humanity on tree extinctions. *Plants, People, Planet*, *2022*, 1–17.

Royer, D. L., Meyerson, L. A., Robertson, K. M., & Adams, J. M. (2009). Phenotypic plasticity of leaf shape along a temperature gradient in *Acer rubrum*. *PLoS ONE*, *4*(10), e7653. https://doi.org/10.1371/journal.pone.0007653

Schuldt, B., Knutzen, F., Delzon, S., Jansen, S., Müller-Haubold, H., Burlett, R., Leuschner, C., et al. (2016). How adaptable is the hydraulic system of European beech in the face of climate change-related precipitation reduction? *New Phytologist*, *210*(2), 443–458. https://doi.org/10.1111/nph.13798

Sirakaya, A. (2019). Balanced options for access and benefit-sharing: Stakeholder insights on provider country legislation. *Frontiers in Plant Science*, *10*, 1175. https://doi.org/10.3389/fpls.2019.01175

Sjöman, H., Hannus, S., Bellan, P., Barblishvili, T., Darchidze, T., & Sikharulidze, S. (2019). Hunting for a larger diversity of urban trees in Western Europe–a case study from the southern Caucasus. *Arboriculture & Urban Forestry*, *45*(5), 221–235. https://doi.org/10.48044/jauf.2019.018

Sjöman, H., Hirons, A. D., & Bassuk, N. L. (2015). Urban forest resilience through tree selection—Variation in drought tolerance in *acer*. *Urban Forestry & Urban Greening*, *14*(4), 858–865. https://doi.org/10.1016/j.ufug.2015.08.004

Sjöman, H., & Nielsen, A. B. (2010). Selecting trees for urban paved sites in Scandinavia–a review of information on stress tolerance and its relation to the requirements of tree planners. *Urban Forestry & Urban Greening*, *9*(4), 281–293. https://doi.org/10.1016/j.ufug.2010.04.001

Sjöman, H., & Östberg, J. (2019). Vulnerability of ten major Nordic cities to potential tree losses caused by longhorned beetles. *Urban Ecosystems*, *22*(2), 385–395. https://doi.org/10.1007/s11252-019-0824-8

Sjöman, H., & Watkins, J. H. R. (2020). What do we know about the origin of our urban trees? – A north European perspective. *Urban Forestry & Urban Greening*, *56*(2020), 126879, ISSN 1618-8667. https://doi.org/10.1016/j.ufug.2020.126879

Tabassum, S., Beaumont, L. J., Shabani, F., Staas, L., Griffiths, G., Ossola, A., & Leishman, M. R. (2023). Which plant where: A plant selection tool for changing urban climates. *Arboriculture & Urban Forestry (AUF)*, *49*(4), 190–210. https://doi.org/10.48044/jauf.2023.014

Temunović, M., Franjić, J., Satovic, Z., Grgurev, M., Frascaria-Lacoste, N., & Fernández-Manjarrés, J. F. (2012). Environmental heterogeneity explains the genetic structure of continental and Mediterranean populations of *Fraxinus angustifolia* Vahl. *PLoS ONE*, *7*(8), e42764.

Teotónio, H., Chelo, I. M., Bradić, M., Rose, M. R., & Long, A. D. (2009). Experimental evolution reveals natural selection on standing genetic variation. *Nature Genetics*, *41*(2), 251–257. https://doi.org/10.1038/ng.289

Tubby, K. V., & Webber, J. F. (2010). Pests and diseases threatening urban trees under a changing climate. *Forestry: an International Journal of Forest Research*, *83*(4), 451–459. https://doi.org/10.1093/forestry/cpq027

Watkins, H., Hirons, A., Sjöman, H., Cameron, R., & Hitchmough, J. D. (2021). Can trait-based schemes be used to select species in urban forestry? *Frontiers in Sustainable Cities*, *3*, 654618. https://doi.org/10.3389/frsc.2021.654618

Wyse, S. V., Dickie, J. B., & Willis, K. J. (2018). Seed banking not an option for many threatened plants. *Nature Plants*, *4*(11), 848–850. https://doi.org/10.1038/s41477-018-0298-3

Yan, P., & Yang, J. (2017). Species diversity of urban forests in China. *Urban Forestry & Urban Greening*, *28*, 160–166. https://doi.org/10.1016/j.ufug.2017.09.005

Zohner, C. M., Mo, L., Sebald, V., & Renner, S. S. (2020). Leaf-out in northern ecotypes of wide-ranging trees requires less spring warming, enhancing the risk of spring frost damage at cold range limits. *Global Ecology and Biogeography*, *29*(6), 1065–1072. https://doi.org/10.1111/geb.13088

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