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Climate change threatens carbon storage in Europe's urban trees

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ABSTRACT

Urban trees contribute substantially to numerous ecosystem services. Here we quantify the threat to carbon stored by urban trees from increased heat and drought arising from climate change. We use data from tree inventories in 22 European cities, spread across five Köppen-Geiger climatic zones, that record ~1.2 million trees from 188 species. We calculate species' climatic niches using global tree distribution data and estimate species-specific thermal and hydraulic safety gaps and margins for each city in 2050 and 2070 using the RCP 8.5 emissions scenario. This scenario provides the best match for emissions to at least 2050 under current and stated policy plans, and highly plausible emission levels to 2100. We then assess the proportion of current carbon storage at risk from changes in temperature (associated with thermal stress) and precipitation changes (associated with hydraulic stress). By 2070 a substantial amount of the current carbon storage in urban trees is projected to be threatened by climatic stress. Average values (depending on the precise methods used for calculating climatic niches) are: 99.96 % - 99.98 % in the cold semi-arid climate zone; 82.97 % - 92.61 % in the humid subtropical zone, 69.72 % - 72.00 % in the warm Mediterranean zone, 44.18 % - 55.06 % in the humid continental zone and 29.60 % - 43.22 % in the temperate oceanic zone – although within each climatic zone risks are lower in some cities. In each climatic zone the vast majority of this threat is associated with thermal stress, with precipitation changes projected to be a comparatively minor threat. Our analyses highlight individual species which are particularly vulnerable to future climatic conditions, and more resilient species that if rapidly planted on mass could improve resilience of urban tree stocks to climate change. Our findings inform the development of climate-ready urban forestry and planning strategies that will facilitate long term carbon storage capacity of Europe's urban forests, and emphasise the urgency of doing so.

1. Introduction

Urbanisation is rapidly transforming the earth's terrestrial surface. Global urban land is predicted to increase by 140 % between 2012 and 2050, with the majority of the global human population already living and working in urban areas (Zhou et al., 2019). Ensuring sustainable urban development is a key objective of the Sustainable Development Goals (Vaidya and Chatergi, 2020). Maintaining and improving provision of ecosystem services (ESs) will play a key role in this challenge (Endreny et al., 2017). These services are primarily derived from green spaces (Kowarik, 2011). For numerous services (including carbon storage and sequestration, flood mitigation, supporting other biodiversity and human health and well-being) trees contribute more to service provision than any other vegetation type (Mexia et al., 2018).

Urban tree cover is declining in many urban areas globally (Nowak and Greenfield, 2020), with climate change proposed to be amongst the greatest threats in the medium- and long-term (Emilsson and Ode Sang, 2017; Ossola and Lin, 2021). Higher temperatures can result in significant reductions in photosynthetic rates and increased mortality, driving reduced sequestration and increasing carbon losses (Ordóñez Barona, 2015; Meineke *et al.*, 2016). Climate change may also increase drought stress, due to changes in seasonal precipitation patterns (Mishra et al., 2015; Tabari, 2020), for example through drier and warmer summers increasing evaporative losses (David et al., 2018). Urban trees are particularly susceptible to these changes, as impervious surfaces increase surface runoff and decrease water infiltration, thus reducing soil

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moisture (Gillner et al., 2014). Drought can reduce growth rates and tree health (Nitschke et al., 2017), which can rapidly lead to urban tree mortality via decreases in xylem pressure, resulting in the rapid collapse of a tree's hydraulic system (Arend et al., 2021). It may also induce stomatal closure that reduces photosynthetic rates and carbon sequestration (Hoshika et al., 2020), potentially leading to starvation due to insufficient carbohydrate stores (McDowell & Sevanto, 2010; Sala et al. 2010) and reduced carbon sequestration potential (Guo et al., 2024). Climate change can further threaten the survival of urban trees by exacerbating impacts of other stressors including herbivorous insect attack (Dale and Frank, 2017), disease (Tubby and Webber, 2010) and pollution (Locosselli et al., 2019; Hoshika et al., 2020). All of these mechanisms can add to reductions in urban tree cover which arise from the loss of green-space due to continued urban development and densification (Nowak and Greenfield, 2020, Thaweepworadej and Evans, 2023).

Understanding of the magnitude of climate change threats to the provision of urban ecosystem services derived from trees is still limited. The impacts will vary with exposure, i.e. the magnitude of climatic change in the focal area, and vulnerability, i.e. species' traits including climatic niche breadth that determine their ability to tolerate climatic variations (Pacifici et al., 2015; Esperon-Rodriguez et al. 2024). In Europe, at high latitudes, increasing temperatures may enhance growth rates of urban trees (Pretzsch et al., 2017), whilst trees in warmer and drier cities may experience thermal and hydraulic stress that reduces growth rates and increases mortality (Anderegg et al., 2019; Burley et al., 2019; Zeppel et al., 2013; Kunstler et al., 2020). Here, we provide the first large-scale assessment of how climate change will impact carbon storage in European urban trees. Our approach focuses on assessing the extent to which future climatic conditions will lie outside species' climatic tolerances. Carbon storage and many other ecosystem services and functions scale with tree size in a manner that is similar to the allometric relationship between tree biomass and carbon (Nowak et al. 2008; Anderson-Teixeira et al. 2015; Trlica et al. 2020). Consequently, whilst we focus on carbon storage our results provide some indication of how other urban ecosystem services, such as local climate regulation (cooling) and flood alleviation, may be impacted by climate change stress on urban tree assemblages.

We first calculate species thermal and hydraulic niches using a bioclimatic approach based on species global distributions. We then calculate the carbon stored by each species in each of 22 European cities (located within the five largest climatic zones in Europe) and calculate species' climatic safety gaps and margins for each city by 2050 and 2070 (i.e. the extent to which future climates are within or outside each species' thermal and hydraulic niches). This enables us to assess the likely risk from climate change for each species and each urban location, and thus i) provide an estimate of the proportion of carbon stored in urban trees within each climate zone that is likely threatened by climate change, and ii) assess the relative roles of changes in temperature and precipitation. Furthermore, we highlight tree species whose contributions to carbon storage are particularly threatened by, or resilient to, climate change. Our findings inform and emphasise the urgency of developing climate-ready urban forestry and planning strategies that will facilitate the long-term carbon storage capacity of Europe's urban forests.

2. Materials and methods

2.1. Data collection

In February 2021 we searched the Global Urban Tree Inventory (GUTI; Ossola et al., 2020) for data from European urban areas (hereafter referred to as cities) and identified 55 such inventories. When original data were not available via GUTI we approached the organisations and authors responsible for data collection to obtain raw data. These 55 inventories were screened to meet our minimum criteria of providing i) species binomial names, ii) data on the diameter of individual trees, and iii) data from at least 3000 tree stems to ensure that inventories provided sufficiently robust representations of each city's tree assemblage. Twenty inventories met these criteria. Additional literature searches were performed in March 2021 to check for more recent tree inventories not included in GUTI. Searches used Google Scholar, with the search terms "urban" and "city" and "tree" and "inventory". Two additional datasets were obtained using this approach. We checked the description of the locations included in each inventory to ensure all sites were urban, example descriptions include: Fingal county - 'all urban trees in Fingal county'; Hamburg – 'street/roadside trees' and Budapest 'park and street trees' (Table S4). For the 11 inventories that provided geo referenced locations we used satellite imagery from google maps to check that the surveyed region contained sufficient impervious surface to be classified as an urban area, e.g. Bonnington et al., 2014 classifies urban 1 km^2 grid cells as those with at least 25 % impervious surface cover (Fig S4). Finally, inventory data were combined, creating a dataset that included species occurrence records from 22 cities across Europe (Fig. 1), with a total of ~1.8 million tree records (Table S1, S4).

Cities were classified by their Köppen-Geiger (Köppen) system, which is based on threshold climatic values and seasonality of monthly air temperature and precipitation, using 1 km resolution Köppen classification maps (Beck et al., 2018). Three cities (Girona, Bolzano and Budapest) at the boundary between climate zones were assigned to a Köppen zone based on the largest climatic zone within the city boundary, defined by a polygon of urban landcover determined using Google Maps imagery (obtained in April 2021), using R 4.0.3. The 22 European cities cover the five largest Köppen climate zones within Europe, with smaller climatic zones or those that occupy regions with limited urban development (such as the far north of Europe) not being represented within our dataset (Fig. 1). Twelve of our cities are located in the temperate oceanic zone (mild summers, cool winters and small annual temperature ranges), three in the humid subtropical zone (long, hot, humid summers and cool to mild winters), four in the humid continental zone (warm, often hot and humid, summers and cold winters with large seasonal temperature differences), two in the semi-arid zone (receives precipitation below potential evapotranspiration, but not as low as a desert climate) and one in the warm Mediterranean zone (dry summers and mild wet winters).

2.2. Taxonomic standardisation

A list of 5425 unique species binomials was extracted from the combined inventories. These raw records required standardisation due to inclusion of cultivar information, misspellings and other errors in name formatting and punctuation. We assigned correct species binomials to each tree record using the methodology of Burley et al. (2019). Briefly, subspecies, cultivar and hybridisation information was removed from each species binomial. For example, *Malus domestica* ''Garden Sun Red'' was renamed as *Malus domestica*. Some hybrids (e.g. *Platanus x acerifolia*) were retained as they are considered horticultural species and occurrence records are available in GBIF. Next, taxonomic checks were performed on species binomials using the *Taxonstand* package in R (Cayuela et al., 2012), which uses The Plant List (TPL) for its taxonomy backbone (http://www.theplantlist.org/). Unique binomials were checked against TPL to attribute the current valid binomial name to each entry. For example, *Abelia koreana* was corrected to *Abelia biflora*. *Taxonstand* re-attributed correct binomials to ~80 % of uncleaned species binomials. To assign correct binomials to the remaining species, punctuation and special characters etc. were manually removed because they prevented recognition by *Taxonstand*. Four species of palms were removed (following Chave et al., 2009) as these are not 'true' trees and thus do not have a dry wood density estimate available via the DRYAD dry wood density database (Chave et al., 2009). Finally, records without species information, for example

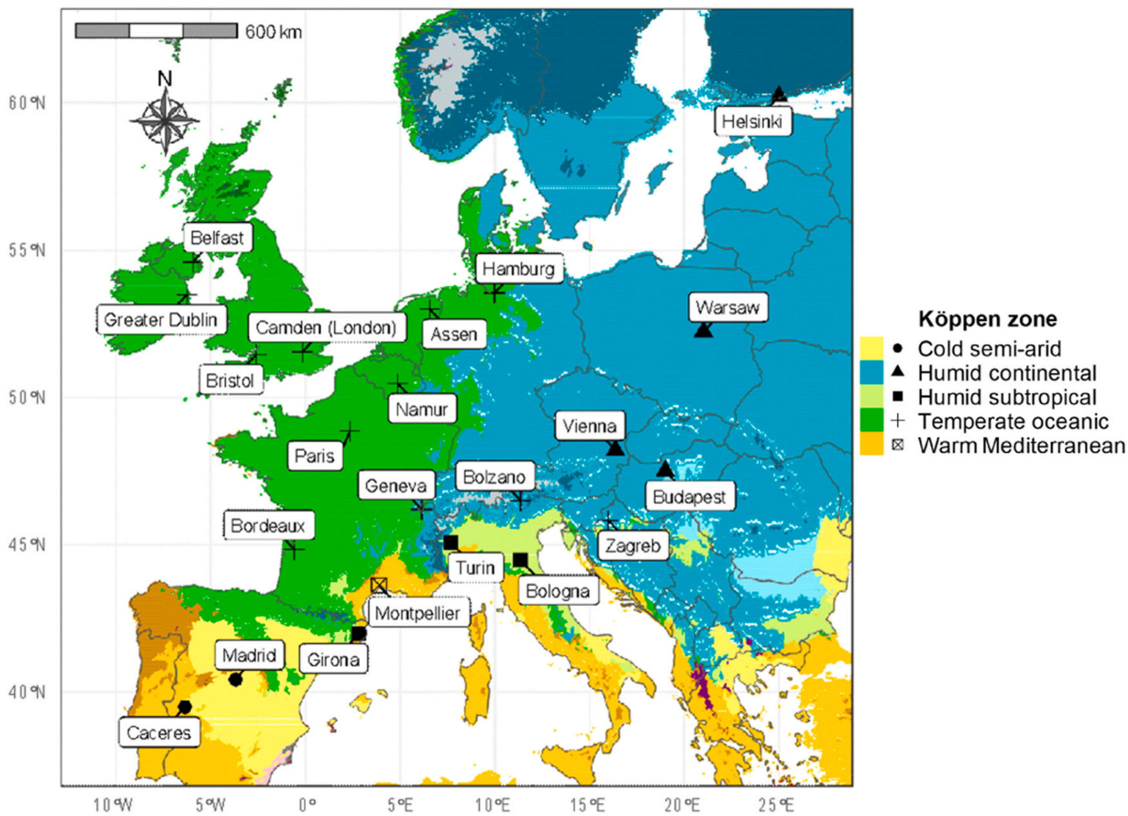

Fig. 1. Location of the 22 study cities coloured by Köppen-Geiger climate zone (as defined by Beck et al., 2018). Cities located at the edges of climatic zones were assigned to the zone that covered the largest proportion of the focal urban area (see methods).

'Non-specified', 'Undetermined species', 'Yet to be collected', 'Tree stump' were removed. This process produced taxonomically validated binomials for 1720 tree species, which were re-attributed to each of the respective raw tree records. When only genus level names were given in inventories, these records were removed as we could not calculate robust climatic niches based on genera.

2.3. Data standardisation

Urban tree inventories typically exclude records for tree saplings, defined for example as ≤25 mm DBH in the commonly used methodology proposed by Nowak et al. (2008). We also exclude records with size data that were likely to represent data collection or inputting errors, or where extreme management of trees (such as pollarding) generated a trunk shape that would invalidate the use of allometric equations to estimate carbon storage. We did this by applying exclusion thresholds based on diameter to height ratios, calculated as [DBH (mm)/height (m)] *100. We excluded trees when this value was ≤ 50 as such trees are implausibly tall for their diameter, e.g. a value of 50 equates to a tree with a DBH of 1 mm and a height of 2 m, or a DBH of 10 mm and a height of 20 m. We also excluded trees when this value was ≥ 2000 as such trees represent those with extremely large diameters given their height, e.g. a value of 2000 equates to a tree with a DBH of 1000 mm and height of 5 m. Application of these criteria removed 45,835 stems (3.3 % of original records), creating a dataset of 1700 species and 1.37 million tree records. We only included species with > 250 records (cumulated across all our focal cities) in our analyses, this follows Ossola et al. (2020), as many tree species are extremely rare in urban areas and contribute negligibly to carbon storage. This reduced the total records to 1.21 million trees across 188 species and maintained on average 95 % (SD ±4.6, $n = 22$) of the trees in each original inventory.

2.4. Calculating carbon storage

Various methods have been used to estimate how much carbon is stored in trees, including iTreeEco and the CUFR Tree Carbon Calculator (Aguaron and McPherson, 2012). However, these methods often use equations derived from natural forests (Nowak et al., 2008), so may be unsuitable for urban trees, given there is evidence that using equations from natural forests, even if they are species specific, may cause significant over or under estimation of carbon storage in urban areas (Yoon et al., 2013; Tanhuanpää et al., 2017). Therefore, urban and species-specific equations and parameters were used, as these better account for differing tree structure and growth characteristics in urban forests. Urban trees for example may have wider crowns due to more open space and different management techniques, or may grow larger due to reduced competition (McHale et al., 2009). We used an allometric equation derived from McPherson et al. (2016) to calculate above ground biomass (Equation 1). Above ground biomass was then multiplied by 1.28 to incorporate below ground biomass, and then multiplied by 0.5 to estimate total carbon storage (McPherson et al., 2016).

$$\textit{Aboveground biomass} = X * D^{Y} * H^{Z} * DWD \tag{1}$$

Equation 1. The general structure of the allometric equation used to calculate aboveground volume of each tree (m^3), where X, Y and Z are species-specific parameters, D is diameter at breast height, H is tree height, and DWD is a species-specific Dry Wood Density factor. See Table S5 for species-specific parameters and DWD values.

The DWD for each species (Table S5) was obtained from the DRYAD dry wood density database, using estimates obtained from European trees where possible (Chave et al., 2009). To find urban-specific parameters for use in the allometric equations, a literature search was carried out on Google Scholar using the search terms "urban" and "tree" and "allometric" and "equation". Few urban specific allometries were available compared to those in natural forests, therefore a compilation of urban allometric equations (McPherson et al., 2016) was used as a starting point to find parameters. When possible, species-specific parameters were used as these are more accurate (McHale et al., 2009). When these were not available, parameters from a closely related species were used (for example the urban specific parameters for *Quercus ilex* were used for *Quercus pubescens*). When this was not possible, and due to limited species-specific parameters in the literature, generalised urban tree parameters were used. These were split into two categories, urban conifer and urban broadleaf species, and were created using a combination of conifer and broadleaf species-specific urban parameters by McPherson et al., (2016). The inventories from three cities (Bristol, Girona and Hamburg) did not include tree height, which equation 1 requires; in these cases, urban-specific allometric equations which only required DBH were used (Table S5).

2.5. Calculating baseline and future climates

Climatic variables were extracted at baseline (1979–2013), '2050' (average conditions during 2041–2060) and '2070' (average conditions during 2061–2080) for each city from the CHELSA database which

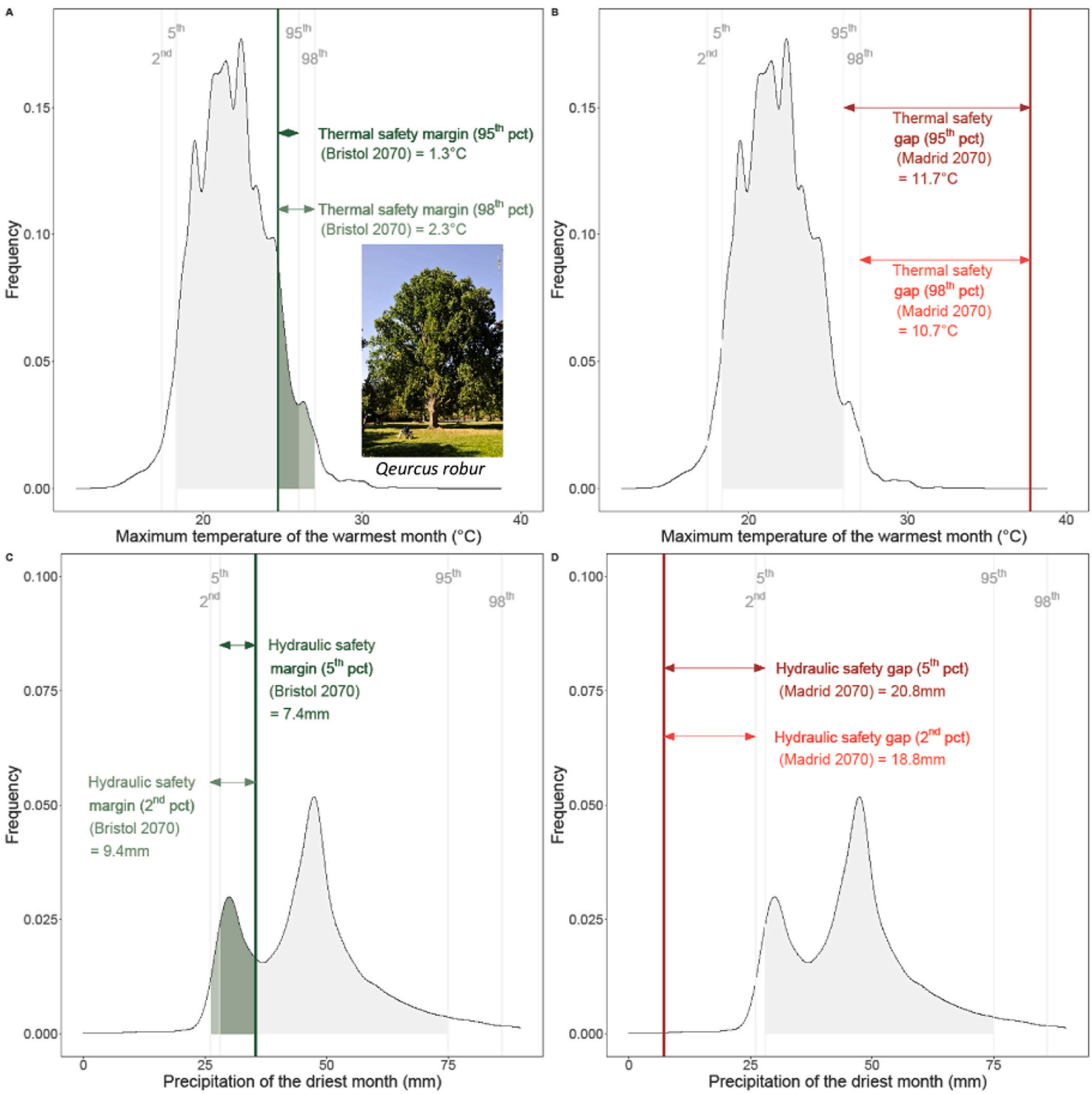

Fig. 2. Schematic explaining the calculation of a) thermal safety margin, b) thermal safety gap, c) hydraulic safety margin, and d) hydraulic safety gap using the Common Oak *Quercus robur* and climatic niches defined using both the 5th - 95th percentiles and 2nd - 98th percentiles. Downward lines show climatic conditions of the focal city in 2070 and horizontal arrows indicate safety margins (when inside the niche) and gaps (when outside the niche). In 2070 *Quercus robur* is thus predicted, when using the 5th - 95th percentile definition, to have thermal and hydraulic safety margins respectively of 1.3°C and 7.4 mm in Bristol (UK, located within the temperate oceanic climate zone), but have significant thermal (11.7°C) and hydraulic (20.8 mm) safety gaps in Madrid (Spain, located within the cold semi-arid climatic zone). Inlaid graphic accessed via Wikimedia Commons, Homoarborea, CC BY-SA 4.0.

provides climatic data at 30 arc sec, ~1 km spatial resolution (Karger et al., 2017). We used the RCP 8.5 emission scenario on which our modelling is based as it currently provides the best match for emissions to at least 2050 under current and stated policies (Schwalm et al. 2020a, b). It also provides highly plausible emission scenarios up to 2100 (Schwalm et al. 2020a, b), but we use a closer time point (average conditions during 2061–2080, referred to as 2070) to ensure greater relevance for urban planners and policy makers. Future climate projections are the average of five different climatic models from CMIP5, which are far apart on the model "family tree" and therefore represent a diversity of models and help to reduce uncertainty in future climate projections (Sanderson et al., 2015). We used Bio5 (mean daily maximum air temperature of the warmest month) and Bio14 (total precipitation of driest month) from the CHELSA database as they provide a good representation of the impacts of other correlated climatic variables on plant growth (Ossola and Lin, 2021). Climatic conditions in highly urbanised sections of our focal cities may be worse for tree growth than implied by these climate projections, as they do not incorporate urban heat islands, and large quantities of impervious surface can reduce soil moisture by reducing infiltration. Consequently, our estimates of thermal and hydraulic risk are likely to be conservative.

2.6. Calculating climate niches

Global occurrence records for all 188 species were downloaded from GBIF (during April 2021) using the RGBIF package in R (Chamberlain et al., 2021). In order to reduce miscalculations of climate niches, spatial data cleaning was carried out using the *CoordinateCleaner* package (Zizka et al., 2019) in R version 4.0.3. Data cleaning followed protocols of Zizka et al. (2019) and removed records which were spatially invalid (e.g. located in the sea), collected before 1950, within 10 km of capital cities (these are likely to be from herbarium records, and may not reflect a species realised niche), duplicate records, and those > 300 km from other records of the same species - as these have too high a likelihood of being erroneous identifications. Baseline climate data from CHELSA were then extracted for each species' spatial distribution and climatic niches were calculated based on the distribution of each species within climatic space (Fig. 2). We calculated climatic niches using the 5th - 95th percentiles, and 2nd - 98th percentiles (based on Kendal et al., 2018; Esperon-Rodriguez et al., 2019). These represent highly plausible representations of the species niche and we do not use minimum and maximum values (0–100th percentiles) as these typically include outliers caused by anomalous occurrences records (Castro-Insua et al., 2018). Climatic niches for each of our focal tree species are presented in a dataset found on our figshare site (see supplementary materials).

2.7. Calculating species thermal and hydraulic safety margins and safety gaps

For each tree species-city combination, we compared climatic conditions at baseline, and projected conditions in 2050 and 2070 for that city with our estimates of species' thermal and hydraulic niches. Safety gaps (i.e., deficits) apply to species which are outside either their thermal or hydraulic niche, and measure the size of the gap between climatic conditions and the boundary of the species' climatic niche. Safety margins measure the maximal change in climate that could occur before a species is outside its climatic niche. Thermal safety margins/gaps were thus calculated by subtracting the city's maximum temperature of the warmest month from the uppermost percentile of the species thermal niche (Fig. 2). Hydraulic safety margins/gaps were calculated by subtracting the city's precipitation of the driest month from the lowest percentile of the species hydraulic niche (Fig. 2).

2.8. Calculating 'at risk' carbon

'At-risk' carbon is defined as the amount of carbon stored by a species at a location where it has a thermal or hydraulic safety gap in the focal time period. At these locations and time-points a species is unlikely to survive unless additional horticultural care is provided (Ossola and Lin, 2021). Species-specific estimates of at-risk carbon are summed to calculate the percentage of carbon stored in a city's trees that are at-risk in 2050 and 2070. This process is conducted using climatic niches calculated with the 5th - 95th percentile definitions and repeated using the 2nd - 98th percentile definitions.

2.9. Statistical analysis

We used a generalised linear mixed model (implemented using *glmer* in R version 4.0.3) to model the percentage of each city's currently stored carbon that is at risk as a function of time point (3 level factor: current, 2050 and 2070), climate zone (5 level factor) and city (as a random factor). We used a binomial logistic model structure with logit link and conducted analyses using at risk carbon defined using both the 5th - 95th and 2nd - 98th percentile definitions.

3. Results

Across all cities urban trees stored large amounts of carbon, albeit with substantial variation in typical values per tree which ranged from 60 kg C in Madrid to 1050 kg C in Belfast (Table S1, which also provides data for each urban area's inventory on species diversity, number of trees and the total carbon stored).

3.1. Climate projections

Regardless of the Köppen zone, all cities are projected to experience strong increases in the temperature of the warmest month; average increases per climatic zones are within the range of 4.5 °C to 5.4 °C from baseline to 2070 (Fig. S1). Cities in most climatic zones are also projected to experience substantial reductions in precipitation during the driest month, although some locations within the humid continental zone are projected to experience moderate increases in rainfall during the driest month (Fig. S1).

3.2. Temporal change in at risk carbon

Using climatic niches calculated using 5th - 95th percentile definitions reveals a significant increase in at risk carbon from baseline to 2050 and 2070 (Table 1). Risks are significantly elevated in the cold semi-arid zone (Table 1; Fig. 3; median 0.02 % of carbon is estimated to

Table 1
Results from binomial logistic models of the percentage of carbon stored in urban trees at baseline that will be threatened in the future due to thermal or hydraulic safety gaps arising from climate change across 22 European cities. Parameter estimates (± one standard error) are reported for time point (reference set to baseline) and climatic zone (reference set to the temperate oceanic climate). Analyses are conducted using both climatic niche definitions (percentiles of occupied climatic niches).

	Climatic niche definition	
	5 – 95 %	**2–98 %**
Time point	2050: 2.986 ± 0.117, $P < 2e^{-16}$ 2070: 4.248 ± 0.130, $P < 2e^{-16}$	2050: 2.566 ± 0.126, $P < 2 \times 10^{-16}$ 2070: 4.275 ± 0.140, $P < 2 \times 10^{-16}$
Climatic zone	Cold semi-arid 5.132 ± 1.889, $P = 0.007$ Humid continental 1.276 ± 1.433, $P = 0.373$ Humid subtropical 4.170 ± 1.598, $P = 0.009$ Warm Mediterranean 2.580 ± 2.566, $P = 0.315$	Cold semi-arid 5.616 ± 1.757, $P = 0.001$ Humid continental 1.224 ± 1.339, $P = 0.361$ Humid subtropical 4.349 ± 1.487, $P = 0.003$ Warm Mediterranean 2.195 ± 2.389, $P = 0.358$

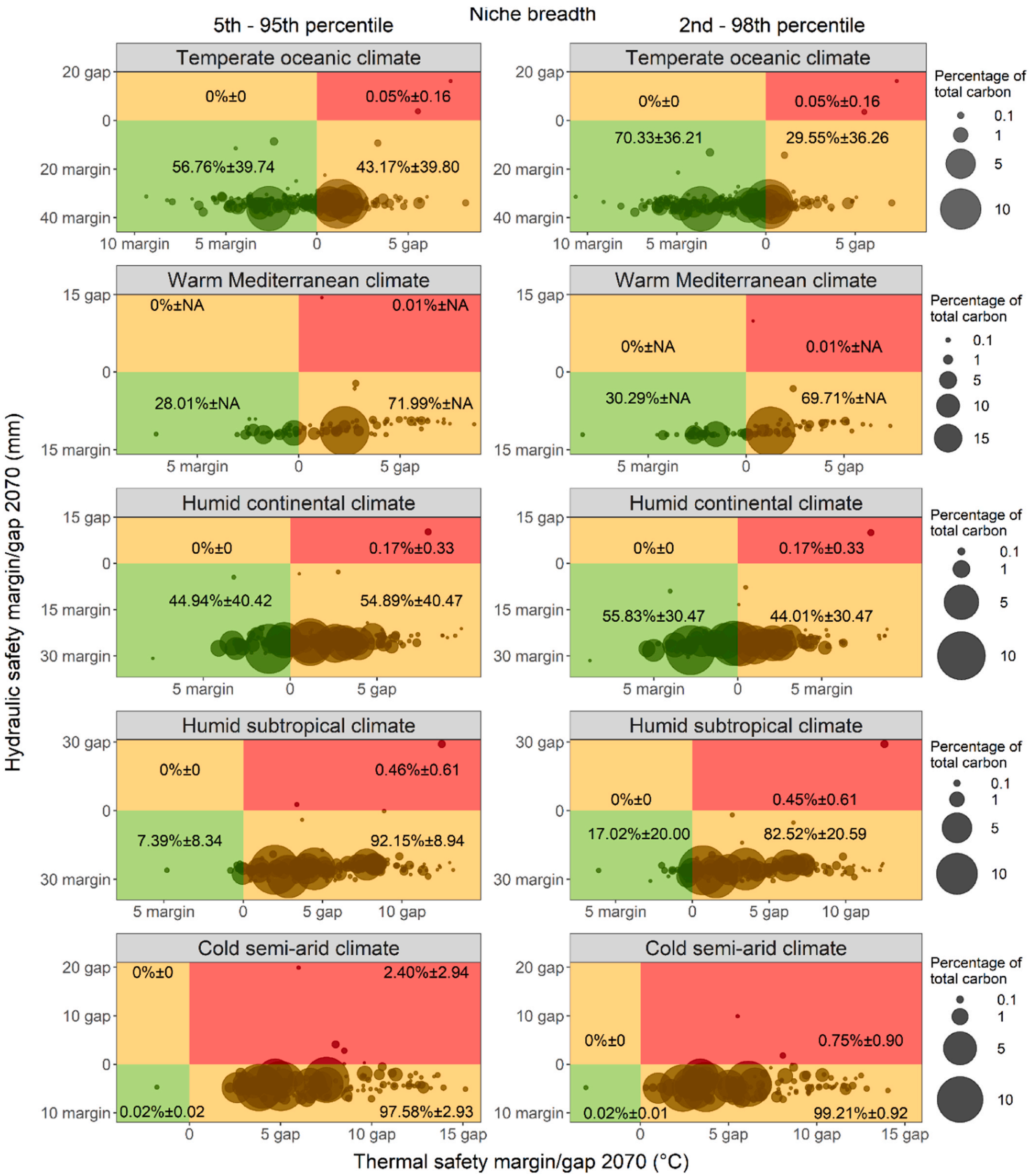

Fig. 3. Mean hydraulic and thermal safety margins/gaps of all species within each climate zone in 2070. Each point represents a species, with its size representing the percentage of the climate zone's current carbon stored in that species. Species in the lower left green quadrant are safest with species having both thermal and hydraulic safety margins. Species in orange areas have only thermal safety gaps (bottom right quadrant) or hydraulic safety gaps (top left quadrant). Species in the red quadrant (top right) have both hydraulic and thermal safety gaps. Percentages in each quadrant show the amount of carbon stored by all species in each quadrant. Note the variation in the Y axis scales across climate zones. Examples of species in each climate zone's quadrant are provided in Table 3 (5th - 95th percentiles) and Table S2 (2nd - 98th percentiles).

be safe in 2070). Within our data this zone is represented by Caceres and Madrid (both 0 % of carbon being safe in 2070). Risks are also significantly elevated in the humid subtropical climate zone (Table 1; Fig. 3; median 5.72 % of carbon being safe in 2070). Within our data this zone is represented by Bologna (0 % of carbon being safe in 2070), Budapest (7.3 % of carbon being safe in 2070) and Girona (16.4 % of carbon being safe in 2070). Similar patterns arise when using climatic niches calculated with the 2nd - 98th percentile definitions with risks again increasing from baseline to 2050 and 2070 across all climatic zones, but being significantly elevated in the cold semi-arid (median 0.02 % of carbon being safe in 2070) and humid subtropical climate zone (median 11.71 % of carbon safe in 2070; Table 1; Fig. 3). See Table 2 for estimates of the % of safe carbon in 2050 and 2070 in each of our 22 cities, under each set of niche definitions. Whilst there is a general pattern of a temporal increase in carbon at risk in all cities, the percentage of carbon that is at risk remains small (< 5 %) in some, but not all, cities in the temperate oceanic climate (Assen, Belfast, Bristol, the London borough of Camden, and Dublin) and humid continental (Helsinki) climate zones (Table 2).

Across all climatic zones the vast majority of this risk is from changes in temperature pushing focal species outside their thermal niche, with between 30 ± 36, median 13 % (temperate oceanic climate, n=12, 2nd - 98th niche definition increasing to 43 ± 40, median 47 % under the 5th - 95th niche definition) and 98 ± 3, median 98 % (cold semi-arid climate, n=2, 5th - 95th niche definition increasing to 99 ± 1, median 99 % under the 2nd – 98th niche definition) of current stored carbon threatened by this mechanism by 2070 (Fig. 3). The magnitude of the thermal safety gap is often greater than 2.5°C, especially in the cold semi-arid, and humid subtropical climate zones under both the 5th - 95th (Fig. S2) and 2nd −98th percentile definitions (Fig. S3). In contrast, reductions in precipitation during the driest month that pushes trees outside their hydraulic niche threatens at most 5 % (cold semi-arid climate, 5th - 95th niche definition) of current stored carbon by 2070 (Fig. 3) and safety gaps are not substantial (Fig. S2, Fig S3).

3.3. Relative dominance of sensitive and resilient species

Within each climate zone substantial amounts of carbon are often stored within a single species that will be outside its thermal safety gap by 2070 (Table 3; Table S2). These values range from 50 % in the warm Mediterranean zone under both percentile niche definitions (stored in *Platanus hispanica*) to 5 % (2nd - 98th percentile definition: stored in *Aesculus hippocastanum* in the temperate oceanic zone) and 10 % (5th - 95th percentile definition: stored in *Populus nigra* in the humid continental zone). Within each climatic zone, the species with the highest carbon storage that will remain within its climatic safety margins in 2070 typically stores less, often substantially less, carbon than the species with the highest carbon storage that is outside its climatic safety margins (Table 3). The one exception is the temperate oceanic zone using the 2nd - 98th percentile niche definition (Table S2).

4. Discussion

This study highlights statistically significant temporal increases in the proportion of carbon currently stored in urban trees across much of Europe that is likely to be threatened by climatic conditions moving beyond species' climatic niches by 2070. There is substantial variation across climate zones in the vulnerability of carbon stored in urban trees to future climate change, but increases occur in all zones. Southern latitude cities, particularly those in cold semi-arid and humid subtropical climates, are expected to have the highest proportion of currently stored carbon at risk in the future. Northern latitude cities, especially some of those in temperate oceanic and humid continental climates, are predicted to have a much smaller proportion of carbon at risk. The future vulnerability of carbon stored in urban trees is primarily driven by thermal rather than hydraulic risk. The patterns and order of

Table 2
Percentage of threatened carbon at each time point in each study city using niches calculated with both percentile definitions.

City	Time point	Percentage threatened carbon 2^{nd} - 98^{th} percentiles	Percentage threatened carbon 5^{th} - 95^{th} percentiles	Köppen zone
Assen	current	0.0	0.0	Temperate oceanic
Assen	2050	0.6	0.9	Temperate oceanic
Assen	2070	0.9	1.3	Temperate oceanic
Belfast	current	0.0	0.0	Temperate oceanic
Belfast	2050	0.0	0.0	Temperate oceanic
Belfast	2070	0.0	0.0	Temperate oceanic
Bologna	current	22.6	43.4	Humid subtropical
Bologna	2050	89.0	96.2	Humid subtropical
Bologna	2070	99.8	100	Humid subtropical
Bolzano	current	0.3	7.4	Temperate oceanic
Bolzano	2050	21.5	45.7	Temperate oceanic
Bolzano	2070	65.6	72.4	Temperate oceanic
Bordeaux	current	0.3	3.8	Temperate oceanic
Bordeaux	2050	21.3	30.2	Temperate oceanic
Bordeaux	2070	30.5	81.0	Temperate oceanic
Bristol	current	0.0	0.0	Temperate oceanic
Bristol	2050	1.5	1.6	Temperate oceanic
Bristol	2070	1.7	4.0	Temperate oceanic
Budapest	current	0.3	7.4	Humid continental
Budapest	2050	22.9	68.6	Humid continental
Budapest	2070	71.4	92.7	Humid continental
Caceres	current	19.4	23.8	Cold semi-arid
Caceres	2050	89.7	100	Cold semi-arid
Caceres	2070	99.9	100	Cold semi-arid
Camden (London)	current	0.0	0.0	Temperate oceanic
Camden (London)	2050	0.4	0.6	Temperate oceanic
Camden (London)	2070	0.8	2.7	Temperate oceanic
Geneva	current	2.8	13.4	Temperate oceanic
Geneva	2050	72.1	82.3	Temperate oceanic
Geneva	2070	94.8	96.9	Temperate oceanic
Girona	current	29.8	31.6	Humid subtropical
Girona	2050	45.1	59.0	Humid subtropical
Girona	2070	60.9	83.6	Humid subtropical
Greater Dublin	current	0.0	0.0	Temperate oceanic
Greater Dublin	2050	0.0	0.0	Temperate oceanic
Greater Dublin	2070	0.0	0.0	Temperate oceanic

(continued on next page)

Table 2 (*continued*)

City	Time point	Percentage threatened carbon 2nd - 98th percentiles	Percentage threatened carbon 5th - 95th percentiles	Köppen zone
Hamburg	current	0.0	1.6	Temperate oceanic
Hamburg	2050	1.8	2.5	Temperate oceanic
Hamburg	2070	2.8	70.5	Temperate oceanic
Helsinki	current	0.0	0.0	Humid continental
Helsinki	2050	0.0	1.5	Humid continental
Helsinki	2070	1.5	2.5	Humid continental
Madrid	current	32.9	47.4	Cold semi-arid
Madrid	2050	97.3	100	Cold semi-arid
Madrid	2070	100.0	100	Cold semi-arid
Montpellier	current	0.1	2.1	Warm Mediterranean
Montpellier	2050	5.8	66.5	Warm Mediterranean
Montpellier	2070	69.7	72.0	Warm Mediterranean
Namur	current	0.0	0.0	Temperate oceanic
Namur	2050	0.2	16.5	Temperate oceanic
Namur	2070	22.4	47.3	Temperate oceanic
Paris	current	0.0	0.1	Temperate oceanic
Paris	2050	7.6	41.0	Temperate oceanic
Paris	2070	45.3	46.7	Temperate oceanic
Turin	current	25.4	26.7	Humid subtropical
Turin	2050	47.1	73.4	Humid subtropical
Turin	2070	88.3	94.3	Humid subtropical
Vienna	current	0.4	3.1	Humid continental
Vienna	2050	43.4	58.0	Humid continental
Vienna	2070	59.1	80.0	Humid continental
Warsaw	current	1.0	1.1	Humid continental
Warsaw	2050	3.8	38.2	Humid continental
Warsaw	2070	44.6	45.0	Humid continental
Zagreb	current	25.4	41.6	Temperate oceanic
Zagreb	2050	64.9	88.2	Temperate oceanic
Zagreb	2070	90.4	95.8	Temperate oceanic

magnitude of the threats in our data are robust to variation in the percentiles of occupied climatic space used to define climatic niches. Whilst our analysis focuses on loss of stored carbon, this will be associated with the loss of numerous other ecosystem services derived from urban trees which scale with their biomass and size, including water uptake which can alleviate flood risk, temperature regulation, and removal of particulate matter and other pollutants. Impacts on these ecosystem services vary with species' traits and planting configurations (e.g. Chen et al. 2017; Wang et al. 2023) and require explicit modelling to generate robust estimates, but we anticipate that these will be large.

Table 3
The highest carbon storing species in each Köppen climate zone within each category of thermal and hydraulic safety gaps and margins in 2070 (each quadrant of Fig. 3) using the 5th - 95th percentile niche definition (see supporting material Table S2 for equivalent results using 2nd - 98th percentile niche definition). This highlights individual species, currently present in cities, that are notably at risk from (safety gaps) and resilient (safety margins) to future European climates. Numbers in brackets show the percentage of total carbon stored by the species in that Köppen zone. NA means no species are within that category by 2070.

Köppen zone	Thermal and hydraulic safety gap	Thermal safety gap only	Hydraulic safety gap only	Thermal and hydraulic safety margin
Warm Mediterranean	*Pterocarya fraxinifolia* (0.0004 %)	*Platanus hispanica* (52.01 %)	NA	*Celtis australis* (11.97 %)
Humid subtropical	*Prunus pissardii* (0.14 %)	*Celtis australis* (14.68 %)	NA	*Platanus occidentalis* (2.35 %)
Humid continental	*Salix salamonii (0.07 %)*	*Populus nigra* (9.74 %)	NA	*Tilia europaea* (3.95 %)
Temperate oceanic	*Salix salamonii* (0.03 %)	*Quercus robur (14.01 %)*	*NA*	*Platanus hispanica* (9.44 %)
Cold semi-arid	*Acer campestre (0.79 %)*	*Celtis australis* (11.66 %)	NA	*Lagerstroemia indica* (0.02 %)

4.1. Limitations

There are numerous approaches to assessing plant species' tolerances to future climatic conditions. Our approach of estimating climatic niche breadths and safety gaps/margins is suitable and regularly used for assessing species' climatic tolerances and responses to climate change, especially for long-lived species (such as trees) in which the capacity for rapid evolutionary change is limited (Esperon-Rodriguez et al. 2024; Murakami et al. 2023; Perez-Navarro 2022). Indeed, European tree species at the edge of their climatic ranges might have reduced growth and survival rates (Kunstler et al. 2020). Whilst methodological details, such as spatial scales used for climatic niche modelling, the quality and density of occurrence records, and uncertainties related to climate change projections and emission scenarios, among others, can alter precise estimates of climatic niches, our approach provides a robust broad-brush indicator of sensitivity (Carrell et al. 2023). Because of the partial coverage of the tree inventories used and their geographic spread across European cities, our estimates should not be treated as precise predictions of the future, rather they should be viewed as indicators of spatial and temporal variation in the threat of climate change to current urban tree stocks across Europe, as well as the direction of these changes over the time scenario used in this study.

Whilst the temporal patterns and magnitude of threat are generally robust to variation in the definitions of species' climatic niches which we use, this is likely not the case for one city (Hamburg), in which the percentage of threatened carbon in 2070 increases dramatically when moving from the 2nd - 98th percentile definition to the more restrictive 5th - 95th percentile definition. However, such changes merely indicate that these urban tree stocks are at the threshold of a tipping point of experiencing climate stress by 2070. This might occur earlier due to some unanticipated weather events and climate extremes not modelled here, like heatwaves and droughts. Moreover, our results may underestimate vulnerability for a variety of reasons. First, climate projections for each city do not include temporal increases in the magnitude of urban heat islands due to urban expansion and densification, which are projected to increase summer temperatures in temperate urban areas by an average of 0.5°C by 2050 (Huang et al., 2019). Second, our climate projections focus on mean future conditions and there will be substantial inter-annual and shorter-term temporal variation, with for example warmer conditions across much of southern Europe in El Niño years. Third, whilst our analyses suggest that changes in precipitation are likely to have negligible impact, our analyses ignore localised enhancement of water stress arising from large amounts of impervious surface cover that prevents infiltration of water into the soil (Gillner et al., 2014) – although in some cases individual trees may benefit from irrigation. Finally, climate models are based on global occurrence records, from native and urban ranges. This is despite the fact that urban tree plantings often use stock from a small number of cultivars that can be reproduced clonally by growers, thus likely restricting the stock's climatic niche (and thus climate tolerance) to just a portion of that which the species as a whole can occupy.

4.2. Drivers of vulnerability

High temperatures can threaten carbon storage by elevating heat stress, potentially leading to reduced photosynthesis and an increased chance of mortality in vulnerable species (Meineke *et al.*, 2016), such as those with larger thermal safety gaps. Indirectly, heat stress can further exacerbate drought-induced mortality (Marchin et al., 2022). European cities at southern latitudes are most threatened due to the high percentages of trees, and thus carbon, with negligible or negative thermal safety gaps. Notably, forests in such regions are experiencing increased damage and mortality linked to climate change (Rebollo et al. 2024). There is significant variation across climate zones (Fig. S3), for example, in some southerly temperate oceanic cities such as Turin, trees are highly threatened by temperature increases (51.68 % of carbon stored in at-risk species in 2070), whilst in northerly temperate oceanic cities such as Belfast trees fare much better (0 % of carbon stored in at-risk species in 2070). On average, the temperate oceanic climate has the lowest risk in the future (although Northerly cities like Helsinki in the humid continental climate also have low risk). Whilst changing precipitation patterns pushing species beyond their hydraulic niche is a minor direct threat, they can amplify the magnitude of a species vulnerability when combined with heat stress (Adams et al., 2009, Marchin et al., 2022). Southern latitude cities (particularly cold semi-arid and humid subtropical climates) are most vulnerable to this as many species have thermal safety gaps and are close to having hydraulic safety gaps; there is less of a risk in cities located in climatic zones with more northern distributions where species have larger hydraulic safety margins (Fig. 3).

4.3. Mitigation of climate change impacts

Our results highlight some locations where urban tree stocks appear likely to be relatively resilient to climate change impacts up to at least 2070, including cities in the north-west section of the temperate oceanic climate zone (including our focal cities in Eire, the UK and the Netherlands), and those in the northern extremes of the humid continental zone (Helsinki). They also highlight regions and cities where urban tree stocks are likely to be severely threatened, typically those in southern and central Europe, particularly those in cold-semi arid and humid continental climate zones – with at least 75 % of the carbon stored in trees estimated to be threatened by climate change by 2070 in ten of our focal cities (Bologna, Boradeaux, Budapest, Caceres, Geneva, Girona, Madrid, Turin, Vienna, and Zagreb).

Our results can also be used to identify good candidate species for urban tree planting programmes designed to ensure the long-term provision of carbon storage, other ecosystem services and biodiversity support functions they provide (Gillner et al., 2014; Meineke *et al.*, 2016; David et al., 2018). Given the time it takes for trees to mature, the design and funding plans for such planting programmes need urgent attention in order to ensure these functions are secured for the future. Species used in these planting programs must have hydraulic and thermal safety margins in the future (green zone in Fig. 3) and ideally already be relatively abundant in the focal city which increases the probability they will be considered culturally acceptable by cities' inhabitants. For example, in temperate oceanic cities, our results show that the London plane (*Platanus hispanica*) stored 9.4 % of total carbon and has both thermal and hydraulic safety margins by 2070, making it a very valuable species which should continue to be planted in this climate zone (Table 3 and Table S2). However, in cold semi-arid and humid subtropical cities *P. hispanica* is predicted to have a thermal safety gap by 2070, and thus less suitable under increasing future temperatures. In southern latitude cities there are fewer high carbon-storing species with both thermal and hydraulic safety margins by 2070. For example, in the cold semi-arid climate, the only species with both thermal and hydraulic safety margins (margins = 1.8°C and 2.9 mm respectively) is the crape myrtle *(Lagerstroemia indica)*, but this does not significantly contribute to carbon storage, being the 54th highest carbon storing species. An exception in southern latitude cities is the stone pine (*Pinus pinea*) in the warm Mediterranean climate, which has both thermal and hydraulic safety margins (margins = 1.7 °C and 11.2 mm respectively) under 2070 conditions and is the 3rd highest carbon storing species at present, making it a suitable candidate species for continued future planting.

Alongside our analyses, the collection of climate-responsive physiological traits may be useful to provide even more confidence when selecting the most resilient tree species to plant. For example, *Acer monspessulanum* has a hydraulic safety margin in all 9 cities it occurs in by 2070 but also has a high leaf water potential at turgor loss (a physiological trait that suggests a species is resistant to drought (Sjöman et al., 2018)). Recent studies also find that leaf traits such as high thermal tolerance of photosynthesis (T_{crit}) can indicate heat resistant species, for example *Acer rubrum* (Sonti et al., 2021). Our results support this species' heat resistance, with *Acer rubrum* having thermal safety margins in 2070 in 11 of the 13 cities it occurs in.

If climatically suitable species are not currently available, assisted migration of species adapted to the target location may be an important strategy to help both individual species/communities and urban forests/populations adapt to climate change (Fontaine and Larson, 2016). Market availability plays a key role in which tree species get planted by stakeholders, so it is vital to ensure climate-resilient species are readily accessible for planting (Conway and Vander Vecht, 2015). However, assisted migration will require careful management to prevent the concurrent spread of invasive diseases and pests, such as the oak processionary moth. Newly planted trees will also need careful management because young trees can be more susceptible to drought and heat stress (Niinemets and Valladares, 2006). New planting strategies also need to accommodate stakeholders to ensure acceptance. The removal of culturally valued species or the increased allergic reactions to the pollen of novel species can create negative attitudes towards urban trees (Vrinceanu et al., 2021). At the same time, plant traits that generally confer greater climate suitability to warmer and drier conditions (e.g., small, pale and thick leaves) might not be among those preferred by citizens for aesthetic reasons (Zhao et al. 2017), thus limiting the possible uptake of climate-ready species.

Aside from enhancing the resilience of species present and transplanting new species, cities may also employ other strategies to reduce the negative impacts of climate change. Rising urban temperatures associated with the UHIE and climate change may also be mitigated by increasing the quantity of green and reflective roofs and infrastructure (Dandou et al., 2021) and increasing the diversity and canopy cover of urban forests (Wang et al., 2021). Ultimately, the integration of social, nature-based and technical solutions can significantly reduce the risk and costs of tree failures under climate change (Lin et al., 2021). In the short-term, increasing irrigation could enhance survival of drought susceptible species (Nitschke et al., 2017) and reduce urban temperatures (Yang and Wang, 2015). However, this is not always feasible, sustainable or economically viable (Pincetl et al., 2013), especially in places where water is needed most, such as cold semi-arid, humid subtropical and warm Mediterranean climates. In the long term, decreasing impervious surfaces and incorporating permeable structures, such as bioswales, could help improve groundwater recharge and allow better utilisation of rainfall by trees (Xiao et al., 2017). This can often decrease the risk of location-specific drought induced tree mortality (Savi et al., 2015). Higher species and functional trait diversity of urban forests could also improve the overall resilience and carbon storage capacity of urban forests across the continent (Morgenroth et al., 2016; Wood and Dupras, 2021). Therefore, if species composition of an urban forest is altered to increase resilience, diversity should be maintained to decrease the risk of large swathes of common species simultaneously succumbing to disease or pests (Sjöman et al., 2018) and to protect wider urban biodiversity which is dependent on diverse urban tree species (Endreny et al., 2017). Such interim measures are likely to be essential to maintain carbon stocks whilst the species composition of urban tree assemblages is progressively shifted, via climate-ready planting schemes and urban forestry strategies, towards tree species whose niches more closely match future climates.

5. Conclusions

Across most European cities climate change will threaten a substantial amount of the carbon that is currently stored in urban trees. By 2070, cities within each of Europe's five major climate zones will experience climatic threats to at least approximately one third of the carbon their trees contain – with this value projected to reach over 95 % in cities located within the cold semi-arid climate zone. The wide range of benefits other than carbon storage provided by urban trees (such as supporting biodiversity, regulating local climates, improving air quality and reducing flood risk) will also be threatened. To ensure the future safety of urban forests, cities need to alter planting strategies to incorporate more resilient species, and develop mitigation plans to reduce the stress on trees caused by increasing temperatures and water scarcity.

Declaration of Competing Interest

All Authors declare no conflict of interest.

Data Availability

code for the paper 'Climate change threatens carbon storage in Europe's urban trees' (Original data) (Github)

Data for research paper 'Climate change threatens carbon storage in Europe's urban trees' (Original data)(Figshare)

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ufug.2024.128532.

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