

Climate change increases global risk to urban forests

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A worldwide climate-change risk analysis for urban forests

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Abstract

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2 Urban forests provide benefits to more than half of the global population, but climate change threatens the delivery of these benefits. We assess climate-change risk of 3,129 tree and shrub species found in 164 cities across 78 countries, using three metrics: exposure; safety 5 margin; and risk. Exposure expresses changes in climate in each city, safety margin measures species' sensitivity to climate change, and risk is the difference between exposure and safety margin. We found 1,759 (56%) and 2,045 (65%) species currently experiencing 8 climate conditions that exceed their safety margin for mean annual temperature (MAT) and 9 annual precipitation (AP), respectively. By 2050, 2,387 (76%) and 2,112 (68%) species will be at high risk from projected changes in MAT and AP, respectively, with greater risk in cities at low latitudes. Our results aid the evaluation of the impacts of climate change on urban forests to secure long-term benefits provided by these forests.

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Introduction

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Urban areas span ~3% of the Earth's land surface area¹, and accommodate more than 4.2 billion people (55% of the global population)². Within cities, urban forests (i.e. all trees and shrubs in a city, present in streets, parks, woodlands, abandoned sites and residential areas^{3,4}) provide environmental services and socio-economic benefits⁵. By 2050, cities are expected to expand in size around the globe, with predictions of 6.6 billion people living in cities by this time (~70% of the predicted global population)². As the human population grows, so too will the societal demands on urban forests.

Planting and preserving climate-resilient urban forests can play an essential role in people's connection to nature⁵ and have the potential to mitigate the adverse effects of global climate change by: (i) shading buildings and paved surfaces as well as reducing energy usage for cooling⁶; (ii) dissipating urban heat through evapotranspiration; and (iii) capturing greenhouse gases and storing carbon through photosynthesis⁷. However, the pace at which climate is changing8 poses a serious threat to the continued persistence of urban forests globally.

Natural and urban ecosystems are already impacted by climate change resulting in sub-optimal tree growth and increased mortality^{9,10}. Climate change is predicted to increase the frequency and severity of extreme events – such as heatwaves, fire and drought8,11,12 – which contribute to extensive tree dieback and mortality globally^{9,13}. Additionally, features of urban environments, including impervious surfaces and the urban heat island (UHI) effect, can locally exacerbate climatic extremes8.

Urban tree mortality has environmental and socio-economic consequences for governments and urban residents^{13,14}. Therefore, urban greening policies target the strategic delivery of ecosystem services and benefits¹⁵. However, for these services to be delivered effectively over the coming decades, it is crucial to quantify exposure to climate change in cities and identify the most vulnerable tree species by quantifying their risk of poor growth and mortality under current and future climates¹⁶. Unfortunately, studies of tree mortality driven by climate change in cities are rare and limited in scope and broad applicability¹⁶. This limits the capacity to assess climate risk for species that are currently experiencing conditions that exceed their climatic tolerance¹⁷. Given the slow growth rates of trees and the importance of promoting tree longevity, successful urban greening must be strategically planned with future climatic conditions in mind to secure the persistence of urban forests into the future.

Here, we present a worldwide climate-risk analysis for urban forests. We assessed the potential impacts of future climate change on 3,129 tree and shrub species present in 164 cities across 78 countries. We calculated three climate-impact metrics: (1) exposure — the extrinsic degree to which a city is exposed to changes in climate; (2) safety margin —the intrinsic sensitivity of each species to climate change in each city according to its climatic tolerance; and (3) risk, calculated as the difference between exposure and safety margin^{17,18}. We calculated species' realised climatic tolerances from their current geographical distributions, while climate risk was determined by the projected future climate in cities where the species are currently present. Because of the mismatch and asynchrony between the speed of contemporary climate change and the time required for long-lived trees and shrub species to respond to climate change^{19,20}, aka the macroclimatic debt²¹, we expect that significant proportions of species in cities are already at risk or partially decoupled from macroclimatic conditions as a result of costly management practices (e.g. water supply). Hence, contemporary urban planning and tree species selection are required to ensure a successful climate mitigation strategy for the future.

Results

66 Exposure

Exposure (*E*) is the degree to which a city is exposed to projected climatic change^{22,23} and measures the magnitude of change in climate in a given city between baseline (average during 1979-2013) and future (2050 or 2070) climatic conditions. Under the Representative Concentration Pathway (RCP) 6.0 (for RCP 4.5 see **Table S1**) and according to an ensemble of 10 Global Circulation Models (GCMs), all 164 studied cities are predicted to

undergo increases in all temperature variables (mean annual temperature, MAT; maximum temperature of the warmest month, MTWM; and minimum temperature of the coldest month, MTCM) (Tables 1, S1). The increase in MAT and MTWM is predicted to exceed 2°C for 54 cities in 2050 and increase to 119 cities in 2070. Regarding changes in precipitation, cities are predicted to become drier in 2050 in terms of annual precipitation (AP, n = 138) and precipitation of the driest quarter (PDQ, n = 96). Cities towards the Equator will be exposed to larger decreases in AP, whereas cities at high latitudes will be subject to larger increases in MAT, MTWM and MTCM (Table S2; Figs. 1, S1-S2).

Safety margin

The safety margin (*S*) describes intrinsic species sensitivity to climate change and indicates potential tolerance to changing climate conditions ^{18,24} within a given city. The safety margin is calculated as the difference between baseline climate conditions (e.g. MAT or AP) for the city and the species' tolerance limit in relation to the direction of change for the climate variable being examined (e.g. the upper limit in case of warmer MAT or the lower limit in case of drier AP) (**Fig. S3**). For each climate variable, we found species that are currently exceeding their safety margins in all cities in which they are currently planted: (1) MAT, 532 species (17% of all study species); (2) MTWM, 465 (15%); (3) MTCM, 430 (14%); (4) AP, 789 (25%); and (5) PDQ, 665 (21%) (**Appendix 1**). We also identified cities that currently have all their species exceeding their safety margins; across all 164 cities, the mean proportion of species subject to unsafe current climate conditions was 53% (**Table 1**; **Figs. 2**, **S4**).

Notably, although we found high numbers of species exceeding their safety margins in at least one city, for most of the species, safety margins were narrow. A narrow safety margin indicates that baseline climate conditions are close to the species' upper or lower tolerance limit in relation to the direction of change (e.g. baseline MAT is too close to the species' warm limit under the expectation of a warmer climate). Median values of safety margins were 0.2°C for MAT, 0.32°C for MTWM, -6.1°C for MTCM, 56.5 mm for AP and 7.78 mm for PDQ. For MAT, 1,277 species (41%) are exceeding their *S* by <1°C, while 149 species (5%) exceed their *S* by >10°C. Similarly, for MTWM and MTCM, 1,189 (38%) and 153 (5%) species, respectively, are exceeding their *S* by <50 mm for AP and by <10 mm for PDQ (Fig. 2; Fig S4).

Risk

Risk (R) refers to the potential for adverse consequences on biological systems^{25,26}, and is defined here as the difference between cities' exposure and species' safety margins (R = E - S). By 2050, under RCP 6.0 (for RCP 4.5, see **Table S3**), projected changes in climate will result in an increase in numbers of species at risk (i.e. city's future climate will exceed the species' safety margin; R > 0) in at least one city where they are planted in terms of changes in MAT, MTWM and AP. However, warmer and wetter projections of MTCM and PDQ in some cities will benefit species by decreasing their future risk (**Table 1**; **Fig. 3**).

By 2050, several species are projected to be at risk in all cities where they are currently planted and this is true for all climate variables we considered: (1) MAT, 1,200 (38%); (2) MTWM, 862 (29%); (3) MTCM, 688 (22%); (4) AP, 1,006 (32%); and (5) PDQ, 661 (21%). For all climate variables, the plant families with the largest number of species at risk were Myrtaceae, Fabaceae and Rosaceae, while 62 families had 100% of their species at risk (e.g. Dipterocarpaceae, Cunoniaceae and Taxaceae). Conversely, we found 742 (24%; MAT), 989 (32%; MTWM), 1,241 (40%, MTCM), 929 (30%; AP) and 1,280 (41%; PDQ) species at no risk in all cities where they are currently planted (**Appendix 1**).

We found a tendency for the mean climate-change risk to increase towards the Equator (**Fig. 3**, **Table S4**). For all climate variables, except MTCM, the proportion of species at risk in each city is predicted to increase in 2050 and 2070 (**Tables 1**, **S3**), with 65% being the mean proportion of species at risk across all 164 cities in 2050 under RCP6.0 (**Figs. 3**, **S5-S6**). Comparing risk profiles across climate variables by 2050, 287 (9%) species were identified to be at risk for all five climatic variables simultaneously and 1,832 (59%) species were predicted to be at risk because of changes in at least three climatic variables. No risk was observed for 772 species (25%) in any city where they are currently planted (**Fig. S7**).

By 2050 and RCP6.0, the magnitude of risk for most of the species reached median values of 1.8°C (MAT), 1.4°C (MTWM), 7.3°C (MTCM), 102.9 mm (AP) and -9 mm (PDQ). We found 1,006 (32%) and 1,060 (34%) species at risk by <1°C increase of MAT and MTWM, respectively. While 716 (23%) and 811 (26%) species are predicted to be at risk by <50 mm for AP and by <10 mm for PDQ (**Fig. S6**).

For each country, we obtained their 2019 Readiness score quantified by the Notre Dame Global Adaptation Initiative (ND-GAIN)²⁷. ND-GAIN is an index of a country's vulnerability to climate change and its capacity for investment in adaptation actions²⁷. We found climate risk for urban forests was higher in cities projected to undergo decreases in precipitation, increases in temperature and in countries with low ND-GAIN scores (**Table**

S5). This finding implies that these cities may have limited capacity to cope with the impacts of future climate change on their urban forests.

Discussion

Climate-driven changes to urban forests will have adverse consequences for city dwellers and governments globally, although the magnitude of these consequences will vary across cities. The mitigation of climate change impacts ultimately will depend on the available resources in each city and its capacity to respond and cope with climatic changes as they occur.

Urbanization affects the UHI effect and water cycling inputs via alteration in interception, infiltration and runoff, which are likely to shape species' growth and survival, in and around the city^{34,35}. Depending on the location of trees within cities, such changes in UHI and water cycling may affect species safety margins and increase their future risk. However, projections of UHI and urban precipitation changes are still lacking at a global extent, limiting the incorporation of these urban effects. Nevertheless, urban forests that experience declines in precipitation will be more vulnerable than those facing higher rainfall, although significant increases in precipitation might also represent a risk factor, i.e. flooding²⁸. Human management, such as irrigation or stormwater capture, can aid in mitigating the effects of low precipitation by providing supplemental water during periods of severe climate stress²⁹ and promoting evapotranspiration (local cooling effect), which will be crucial to mitigate heatwaves in cities³⁰. However, it may become increasingly difficult to mitigate the adverse effects of climate change through management actions to offset soil water deficits, particularly under limited urban water supply and in places where water is increasingly scarce^{31,32}. These types of costly management actions may explain why so many tree species are currently present in cities with climates that already exceed their current safety margins at the dry margin for precipitation.

Urban forests are often water stressed or closely coupled to regional precipitation and water balance; hence, species growing under hydrologically stressful conditions are more vulnerable to extreme climate events³³, resulting in dieback and higher mortality rates³⁴. However, our results show that cities currently harbour many species living beyond their safety margins suggesting there are additional management actions (e.g. irrigation) and biological factors (e.g. trait plasticity) facilitating species' presence in cities and decoupling them from macroclimatic fluctuations. Being planted in an area, however, does not necessarily mean that a species is performing well in that location. There is also a difference

between being able to tolerate and persist in certain conditions and being able to grow well and maintain ecological functions. That is, species whose safety margins are exceeded may be able to locally survive through local compensation effects, but would not have the capacity to function and remain healthy under those conditions^{35,36}. The long-term stability of urban forests depends on the identification of species that are resilient to long-term climate change and are able to thrive and survive³⁷.

Global warming impacts urban vegetation by increasing dieback and mortality and altering species phenology^{13,38,39}. Future risk is higher in cities located closer to the equator where economic resources to mitigate climate change are generally more limited⁴⁰. Management options for altering or mitigating rising temperatures, particularly the extremes (maxima and minima), are limited⁴¹. As such, vulnerable species will require more intensive and costly management actions and replacement if they cannot cope with climate change. We found cities with high proportions of species at risk located in countries identified as vulnerable by the ND-GAIN index (e.g. India, Niger, Nigeria and Togo). Noteworthy, for those low-latitude cities at high risk, climate warming (MAT exposure) is lower at low latitudes compared to cities at higher latitudes, particularly in the Northern Hemisphere; therefore, species' comparatively narrow safety margins at low latitudes might be driving the more elevated risk there. This highlights a potential mismatch between species selected and planted in those cities and the changing climatic conditions that have occurred over the last few decades. Furthermore, differences in risk among cities, particularly those that are close geographically, might be driven by the species composition of each city (Fig. S8). Presently, species selection during urban planning has been based on past and current climate, without accounting for future climate change 16, and also on human management, prioritizing particular characteristics, such as canopy size or aesthetics⁴², leading to poor considerations of potentially narrow safety margins. Therefore, considering future climate change in species selection as a prospective strategy should become a priority in cities worldwide, but particularly so in low-latitude cities near the equator.

Risk associated with increases in MTWM highlights that extreme heat represents a significant threat to urban forests. Cities with the highest risk for heatwaves might be those with a current high UHI effect⁴³. However, we found no correlation between current climate variables and current daytime average maximum land surface temperatures (i.e., a proxy for the UHI effect⁴³), probably related to the decoupling between cities' macro and microclimate. Predicted changes in extreme seasonal variables (i.e. MTWM, PDQ), therefore, impose thermal and hydrological stress on plant species. However, warmer temperatures in MTCM indicate that species will be relieved from cold stress as the urban environment may become more favourable in the future. Nonetheless, some species require a winter cold period (i.e.

vernalization) for proper functioning⁴⁴, and future climate change may represent a risk for those species.

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Our climate risk assessment method targets two key goals. First, the metrics are easy to interpret and reproducible in cities with access to tree occurrence data. Second, it provides a useful approach for identifying which species are most at risk of future climate change (Fig. S9). The safety margin and risk metrics can help to guide prioritization and substitution with more resilient species (i.e. lower risk) in the coming decades. For example, planted species far exceeding their safety margin may be prioritized over others for monitoring and potential replacement. In contrast, planted species with positive safety margins and low risk may be monitored without need of replacement as they could potentially tolerate new climate conditions. Species identified as "no risk" across all cities where they are planted represent a valuable resource for creating climate-proof urban forests. These resilient species provide a palette of potential candidates to be planted in cities where they currently occur, and in those with similar climates after assessing the broader risks associated with introductions (e.g., invasiveness)³³. Therefore, our method can provide a path forward to inform local governments, prioritise monitoring, improve species selection, prioritize mitigation actions for urban forests under future climates, and maximise societal benefits in a warmer world.

While we have assessed the global climatic risk of urban forests, there are some limitations to consider when interpreting findings derived from our method. First, species' realised niches (as assessed here) depend, partly, on sampling effort. We used occurrence records that we related to bioclimatic variables to approximate species' realised climatic niches. However, biotic (e.g. competition and facilitation), other abiotic (e.g. soil and nutrients) factors and dispersal limitations are not accounted for, meaning that one may underestimate or overestimate the true species' climatic niches. Second, the safety margin describes a species' potential tolerance to changing climate conditions within a given city. However, species distribution data are often incomplete, potentially leading to the under/overestimation of the actual realised niche, and individuals at the margin of their geographical range may exist there because of peculiar but highly suitable microclimate conditions (i.e. "source" populations) or as climate relicts (i.e. persisting amidst unsuitable conditions and thus being "sink" populations). Furthermore, artificial selection for horticultural production may change the breadth of climatic conditions tolerated by species as has occurred in agricultural crops⁴⁵r, with flow-on effects where different species' cultivars or varieties are used in urban forests. Third, our approach does not fully consider species' adaptive capacity and trait plasticity, which facilitate species' resilience to climate change, and the potential feedback mechanisms between climate and biota (e.g. the role of

vegetation in modulating temperature). Other environmental factors can also mitigate (e.g. presence of water bodies) or exacerbate (e.g. pollution) the effects of climate change. Finally, given that in many cities comparatively few tree species are abundant, weighted climate risk could be employed to correct for any influence of rare species.

Ideally, to improve species selection in relation to climate, one would utilise information on environmental tolerances, as well as ecological functional approaches⁴⁶ and trait-based analysis⁴⁷⁻⁴⁹. However, robust trait data are limited and not readily available for all species worldwide, which increases uncertainty around decision making. To maintain healthy urban forests in a changing climate, it will be necessary to address economic constraints, the provision of adequate time and effort for establishing and maintaining urban plantings and filling the knowledge gaps in appropriate species selection. We highlight the importance of using prospective — rather than retrospective — strategies to preserve urban forests to ensure resilience to climate change. We emphasize the importance of taking immediate actions in terms of the climate emergency⁸ to secure the survival and persistence of urban forests globally and the benefits provided by these socio-ecological systems.

Materials and Methods

Urban forests composition and urban areas

We obtained data of tree and shrub species present in cities from the Global Urban Tree Inventory (GUTI) database⁵⁰. This database compiles presence data for 4,734 tree and shrub species found in 473 urban areas globally and includes data from published and unpublished tree inventories, online data portals and tree species lists contained in studies published in the scientific literature. Details on the compilation of these data are given elsewhere⁵⁰.

Across the 473 cities, the average number of species per city reported in GUTI was 92 species (standard deviation ± 106), with 72 cities having fewer than 10 species. A small number of recorded species for a city likely represents under sampling of the diversity of species and their respective climate niches than is present. To assess possible sampling bias of climate niches for cities with small numbers of species, we randomly sampled the full set of species in the dataset to get a mean climate variable expected for *X* number of species (i.e. simulating cities with varying numbers of species). We then assessed the stabilisation of the mean (and variance around the mean) as we increase the number of species sampled. High instability of the mean at low numbers of species would indicate

potential bias in the range of climate niches represented by the sample. Based on a visual assessment, we removed cities with fewer than 50 species (**Fig. S10**) as well as cities that were identified as municipalities or local areas within major cities. These resulted in 164 cities from 78 countries and 3,129 tree and shrub species (165 families).

For all 3,129 tree and shrub species, we obtained occurrence records from two sources: (1) the Global Biodiversity Information Facility (GBIF.org; 18 December 2019 GBIF Occurrence Download https://doi.org/10.15468/dl.cpwlwc); and (2) sPlotOpen, an environmentally balanced, open-access, global dataset of vegetation plots (German Centre for Integrative Biodiversity Research (iDiv): https://doi.org/10.25829/idiv.3474-40-3292). Vascular plant species recorded in this dataset represent cover or abundance of naturally co-occurring species within delimited areas⁵¹. For sPlotOpen, we only retained occurrence information (i.e. plot coordinates) and for GBIF, we only retained occurrence records with sufficient information on geographical coordinates. Records were overlaid on a 1×1 km raster grid and reduced to a single point per species within each cell. Additionally, occurrence records were filtered and cleaned by removing spatially invalid or suspect records that could lead to miscalculation of species' climatic niches and duplicate records using the CoordinateCleaner package⁵² in R version 4.0.5⁵³. We retained only species with more than 20 occurrence records. We found 2,555 species (82%) shared between GBIF and sPlotOpen (data from 95,104 vegetation plots). The average number of occurrence records per species (GBIF + sPlotOpen) was 1,041 (± 518), with a maximum of 92,331 occurrences (Quercus robur). Taxonomy was standardized and verified against GBIF and then against The Plant List (TPL; www.theplantlist.org) using *Taxonstand* package⁵⁴ in R⁵³.

Polygons defining the spatial boundaries of 6,018 urban areas (i.e. cities) globally were obtained from Kelso and Patterson⁵⁵ as a shapefile (WGS84; 1:10 million; EPSG:4326). These data were projected to the Mollweide projection, an equal-area pseudocylindrical map projection (ESRI:54009). Additionally, we obtained population size⁵⁶ of all 164 cities, daytime average maximum land surface temperatures (i.e. representative of the urban heat island effect)⁴³ for 122 cites, and for each country the 2019 Readiness score quantified by the Notre Dame Global Adaptation Initiative (ND-GAIN). ND-GAIN is an index of a country's vulnerability to climate change and its capacity for investment in adaptation actions²⁷. This index measures a country's exposure, sensitivity and ability to adapt to the negative impact of climate change based on six life-supporting sectors (food, water, health, ecosystem services, human habitat and infrastructure)²⁷.

Similarities of species composition among cities were evaluated using non-metric multidimensional scaling (NMDS) based on a presence-absence matrix. The NMDS

approach projects multivariate data along latent axes based on distances between assemblages but preserves the underlying dissimilarity structure of the original dataset⁵⁷. The distance between cities in the ordination space reflects the dissimilarity in species composition, such that cities with similar scores are expected to have similar species composition. For this analysis, we used the *vegan* package⁵⁸, and the function *metaMDS*, without auto transformation and Jaccard coefficient as the metric for the presence–absence community by site matrix.

Climate data

Baseline and future climate data were obtained from CHELSA Version 1.2 climatologies at high resolution for the earth's land surface areas⁵⁹, at a spatial resolution of 30 arc-seconds (~1 km at the equator). A detailed description of the generation of these data is given in Karger, et al.⁵⁹. We selected five climate variables; two of them describing mean conditions: (1) mean annual temperature (MAT) and (2) annual precipitation (AP); and three variables describing extremes of climate: (3) maximum temperature of the warmest month (MTWM); (4) minimum temperature of the coldest month (MTCM); and (5) precipitation of the driest quarter (PDQ) (**Table S6**). These variables are known for their biological relevance and influence on species distributions, ecological interactions and species survival^{60,61}. All climate data were projected to the Mollweide projection system (ESRI:54009) at a 1-km resolution using bilinear interpolation. Throughout the text, we refer to "baseline climate" as the average climate conditions during the baseline period 1979-2013.

For future climate data, we downloaded projections for 10 General Circulation Models (GCMs): (1) bcc-csm1-1; (2) CCSM4; (3) CESM1-CAM5; (4) CSIRO-Mk3-6-0; (5) GFDL-CM3; (6) HadGEM2-AO; (7) IPSL-CM5A-MR; (8) MIROC-ESM-CHEM; (9) MIROC5; and (10) NorESM1-M (**Table S7**). We extracted values of the five climate variables from all 10 GCMs and estimated the median for all our analyses. By selecting multiple GCMs, we aimed to capture the uncertainty and variability around future climate scenarios. We selected two time periods: 2050 (average for 2041–2060) and 2070 (average for 2061–2080) and the two Representative Concentration Pathways (RCP) 4.5 and 6.0, which project a peak in emissions around 2040 and 2080, respectively, followed by a decline⁶². Of all GCMs, CSIRO-Mk3-6-0 showed the greatest variability for AP and PDQ (**Fig. S11**). Climate in urban areas is complex and its future projections can be uncertain. However, recent research has enhanced model projections^{43,63-65}; therefore, we downloaded global multi-model projections of local urban climates at a resolution of 0.9° latitude × 1.25° longitude⁶³ for the time period 2040-2060 and RCP8.5 and estimated the maximum temperature of the warmest month using the same set of GCMs.

When we compared future climate changes between global circulation models and global multi-model projections of local urban climates, we found the latter were 0.42 °C (median) warmer than future projections from CHELSA (**Fig. S13**). This finding gives confidence in our estimation of the cities' future climate for 2050 and RCP6.0. However, we highlight that the global multi-model projections of local urban climates do not consider the effects of future urban population growth and future urban land use changes. Therefore, additional effects of future changes in human population and urban land use are not included in our analyses and could further amplify the risk, suggesting that our future estimates are very conservative.

Importantly, we acknowledge that climate data based on coarse-grained spatial interpolations from weather stations that are shielded from direct solar radiation, as used here, can fail to identify areas where conditions are more benign or cooler due to the buffering effect of vegetation cover (i.e. microclimatic processes)⁵⁵ or areas where harsh conditions can be exacerbated by the UHI⁵⁶. We found the current daytime average maximum land surface temperatures (UHI; see details below) can be 8.4°C (median) warmer than air temperature based on future climate changes in 2050 as provided by global circulation models (**Fig. S12**). Therefore, the risks we calculated are likely conservative leaving the possibility of greater risks than what we are reporting if urban warming is intensified in the future.

Species' realized climate niche and cities' climate

For all species, we extracted values of the aforementioned climate variables from all global occurrence records to characterise species' realised climate niches under baseline climatic conditions. For each city, we placed a grid (1 km × 1 km) over its area and extracted the values of all four variables at each cell for both baseline and future climates using the function "exact_extract" from the *exactextractr* package⁶⁶. For global multi-model projections, we extracted climate data from the grid cells closest to the cities' polygon, where the median distance was 25.6 km.

Then, for all species, we estimated their niche breadths (**Appendix 2**) and the upper and lower limits of the temperature and precipitation variables, respectively, based on the global geographic range for each species, whereas cities' climate values were estimated using all grid cells of each city. Spatial autocorrelation of climate variables associated with the species occurrences was assessed using the *raster* package ⁶⁷ based on Moran's *I*. We used kernel density functions to estimate the upper and lower bounds of the distribution of values across the species range to determine whether cities are likely to exceed species' limits. For this, we selected the threshold of the 95th percentile of MAT and MTWM and the

5th percentile of MTCM, AP and PDQ. We used these thresholds to assess the extremes of these variables as indicative of species safety margin (i.e. species' thermal and drought stress tolerance for survival and growth)¹⁷ and towards the main direction of change for the variable being examined (e.g. the warm limit in case of warmer MAT or the dry limit in case of drier AP). Throughout the text, when referring to these climate variables, we imply the use of the 95th (MAT, MTWM) and 5th (MTCM, AP, PDQ) percentiles, accordingly (**Fig. S3**).

Climate change impact metrics

 We selected three climate change impact metrics for our analysis: exposure; safety margin; and risk^{18,23}. These metrics were calculated for all five climate variables, time periods (baseline and future [2050 and 2070]) and RCPs (4.5 and 6.0).

Exposure (E) is the degree to which a city is exposed to climatic change²² and is a measure of how much the climate is projected to change (e.g. warmer or drier) between current and future time periods in a given location; thus, it is calculated as the difference between the city's future and baseline climate as follows:

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$$E = City_{\text{FutureClimate}} - City_{\text{BaselineClimate}}$$

A positive exposure (E > 0) indicates that warmer (or wetter) conditions are expected under future climate change scenarios, while negative exposure (E < 0) indicates that colder (or drier) conditions are expected under future climate change. Here we are more specifically interested in the positive exposure for MAT, MTWM and MTCM, as expected under warmer climates, but negative exposure for AP and PDQ as expected under drier climates.

The safety margin (*S*) describes a species' sensitivity to climate change (i.e. warmer and drier, on average, here) and indicates its potential tolerance to changing climate conditions that may exceed either of the species' upper or lower climatic limits (i.e., its upper limit for MAT and MTWM and or its lower limit for MTCM, AP and PDQ) within a given city and indicates how much warmer (or drier), a city could become before the upper or lower tolerance limits of its resident species have been exceeded, and was calculated as follows:

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$$S = \begin{cases} Species_{ClimateVariable[i]} - City_{BaselineClimate} & (MAT, MTWM, MTCM) \\ City_{BaselineClimate} - Species_{ClimateVariable[i]} & (AP, PDQ) \end{cases}$$

For S, a species' climatic limit (Species_{ClimateVariable[i]}) was measured as the 95th (MAT, MTWM) and the 5th (MTCM, AP, PDQ) percentiles of the species' climate niche based on its global occurrence records and baseline climatic conditions from CHELSA. The difference

between Species_{ClimateVariable[i]} and the long-term average climatic conditions experienced in the focal city (i.e. $City_{BaselineClimate}$) is calculated as the 'safety margin' (S) for each focal species-by-city combination¹⁷. That is, a positive safety margin (S > 0) indicates that the species has a climatic tolerance limit which exceeds current baseline climatic conditions in the focal city (e.g. cooler or wetter and thus safer under warmer and drier future conditions); whereas a negative value (S < 0) indicates that the species is already now experiencing "unsafe" climatic conditions under the baseline (e.g. warmer than the warm limit or drier than the dry limit) that the species can actually withstand according to its known limits for temperature or precipitation) (**Fig. S3**).

The risk (R) refers to the potential for adverse consequences on biological systems³⁰ and is calculated as the between the city's extrinsic exposure to future climate change and the species' intrinsic safety margin. Thus, if R is positive (R > 0), the exposure to future climate is greater than the current safety margin for the focal species in a focal city (i.e. high risk). Yet, if the difference is negative (R < 0) then exposure (E) to future climate change is still within the range of values allowed by the safety margin (S), thus it is "safe" under future conditions (i.e. low risk) (**Fig. S3**). Risk to climate change (R) was calculated as:

$$R = \begin{cases} E - S_{(MAT,MTWM,MTCM)} \\ S - E_{(AP,PDQ)} \end{cases}$$

Linear regressions were fitted to evaluate the relationship between: (1) climate exposure and cities' latitude; (2) species' risk and cities' latitude (assessing Northern and Southern hemispheres independently); and (3) species' risk and UHI, using independent linear models (i.e. the *Im* function in R). The relationship between species' risk with ND-GAIN score and climate exposure was analysed using linear mixed-effects models (i.e. the *Imer* function from the Ime4 package⁶⁸) followed by ANOVA analysis, using country and species as random intercept terms. Models were developed for each climatic variable as a response variable and model performance was evaluated through the calculation of the F-statistic at a significance level of P < 0.05. All analyses were conducted using the statistical software R version $4.0.5^{53}$.

Competing Interests

The authors declare that they have no conflict of interest to disclose.

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Author contribution

- 456 MER, RVG, PDR, SAP and MGT conceived the article. MER, RVG, LJB, PDR, SAP and
- 457 MGT designed the research. MER, JBB, JL and BR collected and analysed data. MER wrote
- 458 the article. All authors contributed to the discussion of the content and reviewed or edited the
- 459 manuscript before submission. All authors, except for MER, MTG, JL and RVG, are listed
- 460 alphabetically.

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Tables

Table 1. Predicted mean (standard deviation) changes (i.e. exposure) of mean annual temperature (MAT), maximum temperature of the warmest month (MTWM), minimum temperature of the coldest month (MTCM), annual precipitation (AP), and precipitation of the driest quarter (PDQ) across 164 cities in 2050 and 2070; number of species (and proportion in brackets) currently exceeding their safety margins and at high risk of climate change in at least one city where they are planted; and number of cities predicted to have 100% and >50% of their species at risk of climate change in 2050; species (n = 3,129), cities (n = 164). Data for 2050 and RCP6.0.

Variable	Expo	sure	Current safety margin					Climate risk in 2050				
	2050	2070	Species	Species 100%	Cities 100%	Species 50% risk	Cities 50% risk	Species	Species 100%	Cities 100%	Species 50% risk	Cities 50% risk
MAT	2.1°C (0.6)	3°C (0.8)	1,759 (56%)	532 (17%)	2	610 (19%)	78	2,387 (76%)	1200 (38%)	12	854 (27%)	133
MTWM	1.7°C (0.5)	2.6°C (0.7)	1,724 (55%)	465 (15%)	2	684 (22%)	82	2,140 (68%)	862 (28%)	19	941 (30%)	106
MTCM	1.3°C (0.5)	2°C (0.7)	1,124 (36%)	430 (14%)	0	239 (7%)	11	902 (29%)	688 (22%)	0	341 (11%)	6
AP	-57 mm (78.3)	-62 mm (88.7)	2,030 (65%)	789 (25%)	2	897 (29%)	91	2,220 (70%)	1006 (32%)	3	944 (30%)	99
PDQ	-1.3 mm (8.2)	-2 mm (12)	1,880 (60%)	665 (21%)	4	846 (27%)	92	1,849 (59%)	661 (21%)	0	852 (27%)	101



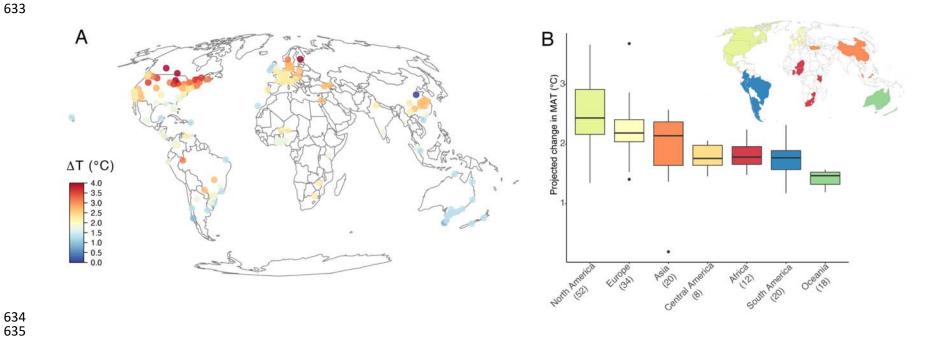


Fig. 1. Exposure to future climate change across the world's cities. Exposure of 164 cities to predicted changes in mean annual temperature (MAT) in 2050 relative to baseline mean annual temperature between 1979 and 2013 (A); boxplot of changes in MAT averaged across cities in seven geographical regions (as colored in insert map); numbers in brackets indicate the number of cities for each region (B). Plots display data for RCP 6.0.

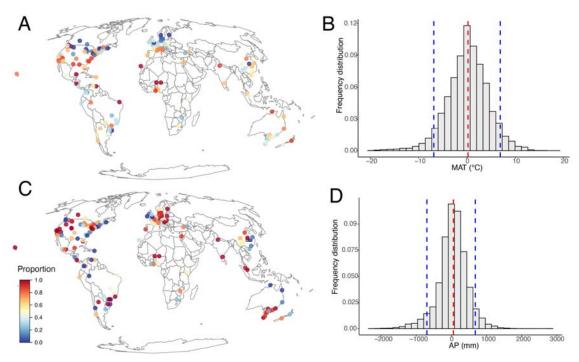


Fig. 2. Contemporary tree and shrub species safety margin across the world's cities. Proportion of species currently exceeding their safety margin for mean annual temperature (MAT; **A**) and annual precipitation (AP; **C**) in 164 cities. Frequency distribution of mean values of MAT (**B**) and AP (**D**) safety margins of each species (n = 3,129) across all cities. Red lines indicate the median and blue lines the 5th/95th percentiles. A positive safety margin (S > 0) indicates species with an upper (MAT) or lower (AP) climatic tolerance limit greater than that of current climatic conditions; a negative value (S < 0) indicates species under "unsafe" climatic conditions.

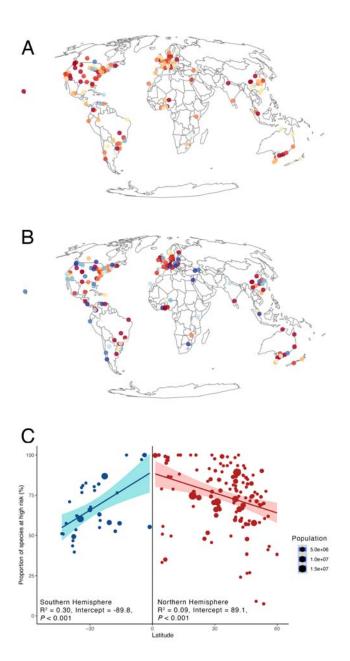


Fig. 3. Species at risk of future climate change impacts across the world's cities. Proportion of species predicted to be at risk from projected changes in mean annual temperature (**A**) and annual precipitation (**B**) by 2050 in 164 cities. Each point represents the proportion of species at risk in a given city. Relationship between the proportion of species at risk and cities' latitude (Northern Hemisphere: n = 129 cities; Southern Hemisphere: n = 35) (**C**). Ribbons indicate the 95% confidence interval for predictions from a linear model. Point size indicates human population size⁵⁶. Data for 2050 and RCP6.0.