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A worldwide climate-change risk analysis for urban forests

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1 **Abstract**

2 Urban forests provide benefits to more than half of the global population, but climate change
3 threatens the delivery of these benefits. We assess climate-change risk of 3,129 tree and
4 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
6 measures species' sensitivity to climate change, and risk is the difference between exposure
7 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
10 be at high risk from projected changes in MAT and AP, respectively, with greater risk in
11 cities at low latitudes. Our results aid the evaluation of the impacts of climate change on
12 urban forests to secure long-term benefits provided by these forests.

13

14 **Introduction**

15

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

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

30 Natural and urban ecosystems are already impacted by climate change resulting in
31 sub-optimal tree growth and increased mortality^{9,10}. Climate change is predicted to increase
32 the frequency and severity of extreme events – such as heatwaves, fire and drought^{8,11,12} –
33 which contribute to extensive tree dieback and mortality globally^{9,13}. Additionally, features of
34 urban environments, including impervious surfaces and the urban heat island (UHI) effect,
35 can locally exacerbate climatic extremes⁸.

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

48 Here, we present a worldwide climate-risk analysis for urban forests. We assessed
49 the potential impacts of future climate change on 3,129 tree and shrub species present in
50 164 cities across 78 countries. We calculated three climate-impact metrics: (1) exposure —
51 the extrinsic degree to which a city is exposed to changes in climate; (2) safety margin —the
52 intrinsic sensitivity of each species to climate change in each city according to its climatic
53 tolerance; and (3) risk, calculated as the difference between exposure and safety margin^{17,18}.
54 We calculated species' realised climatic tolerances from their current geographical
55 distributions, while climate risk was determined by the projected future climate in cities
56 where the species are currently present. Because of the mismatch and asynchrony between
57 the speed of contemporary climate change and the time required for long-lived trees and
58 shrub species to respond to climate change^{19,20}, aka the macroclimatic debt²¹, we expect
59 that significant proportions of species in cities are already at risk or partially decoupled from
60 macroclimatic conditions as a result of costly management practices (e.g. water supply).
61 Hence, contemporary urban planning and tree species selection are required to ensure a
62 successful climate mitigation strategy for the future.

63

64 **Results**

65

66 ***Exposure***

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

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

80 ***Safety margin***

81 The safety margin (S) describes intrinsic species sensitivity to climate change and indicates
82 potential tolerance to changing climate conditions^{18,24} within a given city. The safety margin
83 is calculated as the difference between baseline climate conditions (e.g. MAT or AP) for the
84 city and the species' tolerance limit in relation to the direction of change for the climate
85 variable being examined (e.g. the upper limit in case of warmer MAT or the lower limit in
86 case of drier AP) (**Fig. S3**). For each climate variable, we found species that are currently
87 exceeding their safety margins in all cities in which they are currently planted: (1) MAT, 532
88 species (17% of all study species); (2) MTWM, 465 (15%); (3) MTCM, 430 (14%); (4) AP,
89 789 (25%); and (5) PDQ, 665 (21%) (**Appendix 1**). We also identified cities that currently
90 have all their species exceeding their safety margins; across all 164 cities, the mean
91 proportion of species subject to unsafe current climate conditions was 53% (**Table 1; Figs.**
92 **2, S4**).

93 Notably, although we found high numbers of species exceeding their safety margins
94 in at least one city, for most of the species, safety margins were narrow. A narrow safety
95 margin indicates that baseline climate conditions are close to the species' upper or lower
96 tolerance limit in relation to the direction of change (e.g. baseline MAT is too close to the
97 species' warm limit under the expectation of a warmer climate). Median values of safety
98 margins were 0.2°C for MAT, 0.32°C for MTWM, -6.1°C for MTCM, 56.5 mm for AP and
99 7.78 mm for PDQ. For MAT, 1,277 species (41%) are exceeding their S by <1°C, while 149
100 species (5%) exceed their S by >10°C. Similarly, for MTWM and MTCM, 1,189 (38%) and
101 153 (5%) species, respectively, are exceeding their S by <1°C. For AP and PDQ, 692 (22%)
102 and 838 (27%) species, respectively, are exceeding their S by <50 mm for AP and by <10
103 mm for PDQ (**Fig. 2; Fig S4**).

104 ***Risk***

105 Risk (R) refers to the potential for adverse consequences on biological systems^{25,26}, and is
106 defined here as the difference between cities' exposure and species' safety margins ($R = E$
107 $- S$). By 2050, under RCP 6.0 (for RCP 4.5, see **Table S3**), projected changes in climate will
108 result in an increase in numbers of species at risk (i.e. city's future climate will exceed the
109 species' safety margin; $R > 0$) in at least one city where they are planted in terms of changes
110 in MAT, MTWM and AP. However, warmer and wetter projections of MTCM and PDQ in
111 some cities will benefit species by decreasing their future risk (**Table 1; Fig. 3**).

112 By 2050, several species are projected to be at risk in all cities where they are
113 currently planted and this is true for all climate variables we considered: (1) MAT, 1,200
114 (38%); (2) MTWM, 862 (29%); (3) MTCM, 688 (22%); (4) AP, 1,006 (32%); and (5) PDQ,
115 661 (21%). For all climate variables, the plant families with the largest number of species at
116 risk were Myrtaceae, Fabaceae and Rosaceae, while 62 families had 100% of their species
117 at risk (e.g. Dipterocarpaceae, Cunoniaceae and Taxaceae). Conversely, we found 742
118 (24%; MAT), 989 (32%; MTWM), 1,241 (40%, MTCM), 929 (30%; AP) and 1,280 (41%;
119 PDQ) species at no risk in all cities where they are currently planted (**Appendix 1**).

120 We found a tendency for the mean climate-change risk to increase towards the
121 Equator (**Fig. 3, Table S4**). For all climate variables, except MTCM, the proportion of
122 species at risk in each city is predicted to increase in 2050 and 2070 (**Tables 1, S3**), with
123 65% being the mean proportion of species at risk across all 164 cities in 2050 under RCP6.0
124 (**Figs. 3, S5-S6**). Comparing risk profiles across climate variables by 2050, 287 (9%)
125 species were identified to be at risk for all five climatic variables simultaneously and 1,832
126 (59%) species were predicted to be at risk because of changes in at least three climatic
127 variables. No risk was observed for 772 species (25%) in any city where they are currently
128 planted (**Fig. S7**).

129 By 2050 and RCP6.0, the magnitude of risk for most of the species reached median
130 values of 1.8°C (MAT), 1.4°C (MTWM), 7.3°C (MTCM), 102.9 mm (AP) and -9 mm (PDQ).
131 We found 1,006 (32%) and 1,060 (34%) species at risk by <1°C increase of MAT and
132 MTWM, respectively. While 716 (23%) and 811 (26%) species are predicted to be at risk by
133 <50 mm for AP and by <10 mm for PDQ (**Fig. S6**).

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

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

141

142 **Discussion**

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

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

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

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

179 Global warming impacts urban vegetation by increasing dieback and mortality and
180 altering species phenology^{13,38,39}. Future risk is higher in cities located closer to the equator
181 where economic resources to mitigate climate change are generally more limited⁴⁰.
182 Management options for altering or mitigating rising temperatures, particularly the extremes
183 (maxima and minima), are limited⁴¹. As such, vulnerable species will require more intensive
184 and costly management actions and replacement if they cannot cope with climate change.
185 We found cities with high proportions of species at risk located in countries identified as
186 vulnerable by the ND-GAIN index (e.g. India, Niger, Nigeria and Togo). Noteworthy, for
187 those low-latitude cities at high risk, climate warming (MAT exposure) is lower at low
188 latitudes compared to cities at higher latitudes, particularly in the Northern Hemisphere;
189 therefore, species' comparatively narrow safety margins at low latitudes might be driving the
190 more elevated risk there. This highlights a potential mismatch between species selected and
191 planted in those cities and the changing climatic conditions that have occurred over the last
192 few decades. Furthermore, differences in risk among cities, particularly those that are close
193 geographically, might be driven by the species composition of each city (**Fig. S8**). Presently,
194 species selection during urban planning has been based on past and current climate,
195 without accounting for future climate change¹⁶, and also on human management, prioritizing
196 particular characteristics, such as canopy size or aesthetics⁴², leading to poor considerations
197 of potentially narrow safety margins. Therefore, considering future climate change in species
198 selection as a prospective strategy should become a priority in cities worldwide, but
199 particularly so in low-latitude cities near the equator.

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

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

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

227 While we have assessed the global climatic risk of urban forests, there are some
228 limitations to consider when interpreting findings derived from our method. First, species’
229 realised niches (as assessed here) depend, partly, on sampling effort. We used occurrence
230 records that we related to bioclimatic variables to approximate species’ realised climatic
231 niches. However, biotic (e.g. competition and facilitation), other abiotic (e.g. soil and
232 nutrients) factors and dispersal limitations are not accounted for, meaning that one may
233 underestimate or overestimate the true species’ climatic niches. Second, the safety margin
234 describes a species’ potential tolerance to changing climate conditions within a given city.
235 However, species distribution data are often incomplete, potentially leading to the
236 under/overestimation of the actual realised niche, and individuals at the margin of their
237 geographical range may exist there because of peculiar but highly suitable microclimate
238 conditions (i.e. “source” populations) or as climate relicts (i.e. persisting amidst unsuitable
239 conditions and thus being “sink” populations). Furthermore, artificial selection for horticultural
240 production may change the breadth of climatic conditions tolerated by species as has
241 occurred in agricultural crops⁴⁵, with flow-on effects where different species’ cultivars or
242 varieties are used in urban forests. Third, our approach does not fully consider species’
243 adaptive capacity and trait plasticity, which facilitate species’ resilience to climate change,
244 and the potential feedback mechanisms between climate and biota (e.g. the role of

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

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

260

261 **Materials and Methods**

262 ***Urban forests composition and urban areas***

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

269 Across the 473 cities, the average number of species per city reported in GUTI was
270 92 species (standard deviation \pm 106), with 72 cities having fewer than 10 species. A small
271 number of recorded species for a city likely represents under sampling of the diversity of
272 species and their respective climate niches than is present. To assess possible sampling
273 bias of climate niches for cities with small numbers of species, we randomly sampled the full
274 set of species in the dataset to get a mean climate variable expected for X number of
275 species (i.e. simulating cities with varying numbers of species). We then assessed the
276 stabilisation of the mean (and variance around the mean) as we increase the number of
277 species sampled. High instability of the mean at low numbers of species would indicate

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

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

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

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

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

320 ***Climate data***

321 Baseline and future climate data were obtained from CHELSA Version 1.2 climatologies at
322 high resolution for the earth’s land surface areas⁵⁹, at a spatial resolution of 30 arc-seconds
323 (~1 km at the equator). A detailed description of the generation of these data is given in
324 Karger, et al.⁵⁹. We selected five climate variables; two of them describing mean conditions:
325 (1) mean annual temperature (MAT) and (2) annual precipitation (AP); and three variables
326 describing extremes of climate: (3) maximum temperature of the warmest month (MTWM);
327 (4) minimum temperature of the coldest month (MTCM); and (5) precipitation of the driest
328 quarter (PDQ) (**Table S6**). These variables are known for their biological relevance and
329 influence on species distributions, ecological interactions and species survival^{60,61}. All
330 climate data were projected to the Mollweide projection system (ESRI:54009) at a 1-km
331 resolution using bilinear interpolation. Throughout the text, we refer to “baseline climate” as
332 the average climate conditions during the baseline period 1979-2013.

333 For future climate data, we downloaded projections for 10 General Circulation
334 Models (GCMs): (1) bcc-csm1-1; (2) CCSM4; (3) CESM1-CAM5; (4) CSIRO-Mk3-6-0; (5)
335 GFDL-CM3; (6) HadGEM2-AO; (7) IPSL-CM5A-MR; (8) MIROC-ESM-CHEM; (9) MIROC5;
336 and (10) NorESM1-M (**Table S7**). We extracted values of the five climate variables from all
337 10 GCMs and estimated the median for all our analyses. By selecting multiple GCMs, we
338 aimed to capture the uncertainty and variability around future climate scenarios. We selected
339 two time periods: 2050 (average for 2041–2060) and 2070 (average for 2061–2080) and the
340 two Representative Concentration Pathways (RCP) 4.5 and 6.0, which project a peak in
341 emissions around 2040 and 2080, respectively, followed by a decline⁶². Of all GCMs,
342 CSIRO-Mk3-6-0 showed the greatest variability for AP and PDQ (**Fig. S11**). Climate in urban
343 areas is complex and its future projections can be uncertain. However, recent research has
344 enhanced model projections^{43,63-65}; therefore, we downloaded global multi-model projections
345 of local urban climates at a resolution of 0.9° latitude × 1.25° longitude⁶³ for the time period
346 2040-2060 and RCP8.5 and estimated the maximum temperature of the warmest month
347 using the same set of GCMs.

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

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

367 ***Species' realized climate niche and cities' climate***

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

375 Then, for all species, we estimated their niche breadths (**Appendix 2**) and the upper
376 and lower limits of the temperature and precipitation variables, respectively, based on the
377 global geographic range for each species, whereas cities' climate values were estimated
378 using all grid cells of each city. Spatial autocorrelation of climate variables associated with
379 the species occurrences was assessed using the *raster* package⁶⁷ based on Moran's *I*. We
380 used kernel density functions to estimate the upper and lower bounds of the distribution of
381 values across the species range to determine whether cities are likely to exceed species'
382 limits. For this, we selected the threshold of the 95th percentile of MAT and MTWM and the

383 5th percentile of MTCM, AP and PDQ. We used these thresholds to assess the extremes of
 384 these variables as indicative of species safety margin (i.e. species' thermal and drought
 385 stress tolerance for survival and growth)¹⁷ and towards the main direction of change for the
 386 variable being examined (e.g. the warm limit in case of warmer MAT or the dry limit in case
 387 of drier AP). Throughout the text, when referring to these climate variables, we imply the use
 388 of the 95th (MAT, MTWM) and 5th (MTCM, AP, PDQ) percentiles, accordingly (**Fig. S3**).

389 ***Climate change impact metrics***

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

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

$$397 \quad E = City_{FutureClimate} - City_{BaselineClimate}$$

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

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

$$410 \quad S = \begin{cases} Species_{ClimateVariable[i]} - City_{BaselineClimate} & (MAT, MTWM, MTCM) \\ City_{BaselineClimate} - Species_{ClimateVariable[i]} & (AP, PDQ) \end{cases}$$

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

414 between $\text{Species}_{\text{ClimateVariable}[j]}$ and the long-term average climatic conditions experienced in
415 the focal city (i.e. $\text{City}_{\text{BaselineClimate}}$) is calculated as the ‘safety margin’ (S) for each focal
416 species-by-city combination¹⁷. That is, a positive safety margin ($S > 0$) indicates that the
417 species has a climatic tolerance limit which exceeds current baseline climatic conditions in
418 the focal city (e.g. cooler or wetter and thus safer under warmer and drier future conditions);
419 whereas a negative value ($S < 0$) indicates that the species is already now experiencing
420 “unsafe” climatic conditions under the baseline (e.g. warmer than the warm limit or drier than
421 the dry limit) that the species can actually withstand according to its known limits for
422 temperature or precipitation) (**Fig. S3**).

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

$$430 \quad R = \begin{cases} E - S_{(MAT,MTWM,MTCM)} \\ S - E_{(AP,PDQ)} \end{cases}$$

431 Linear regressions were fitted to evaluate the relationship between: (1) climate
432 exposure and cities’ latitude; (2) species’ risk and cities’ latitude (assessing Northern and
433 Southern hemispheres independently); and (3) species’ risk and UHI, using independent
434 linear models (i.e. the *lm* function in R). The relationship between species’ risk with ND-
435 GAIN score and climate exposure was analysed using linear mixed-effects models (i.e. the
436 *lmer* function from the lme4 package⁶⁸) followed by ANOVA analysis, using country and
437 species as random intercept terms. Models were developed for each climatic variable as a
438 response variable and model performance was evaluated through the calculation of the F -
439 statistic at a significance level of $P < 0.05$. All analyses were conducted using the statistical
440 software R version 4.0.5⁵³.

441

442 **Competing Interests**

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

444

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453 authors.

454

455 **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.

461

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621

622 **Tables**

623

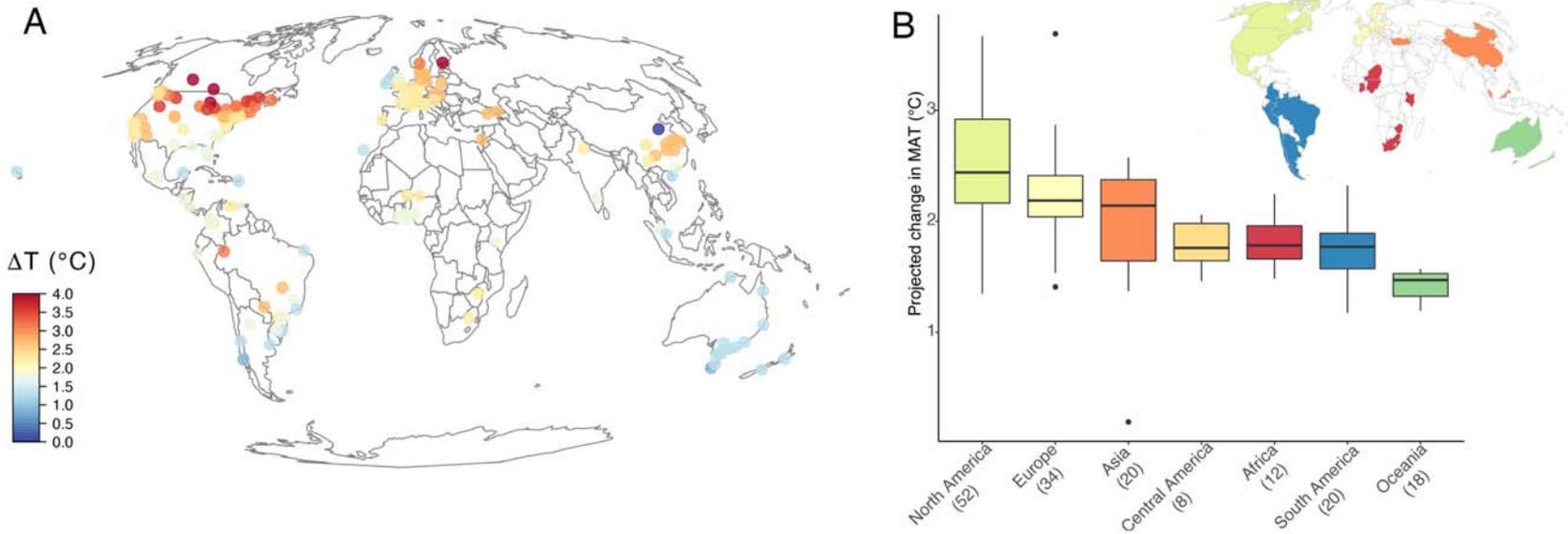
624 **Table 1.** Predicted mean (standard deviation) changes (i.e. exposure) of mean annual temperature (MAT), maximum temperature of
 625 the warmest month (MTWM), minimum temperature of the coldest month (MTCM), annual precipitation (AP), and precipitation of the
 626 driest quarter (PDQ) across 164 cities in 2050 and 2070; number of species (and proportion in brackets) currently exceeding their
 627 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
 628 100% 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	Exposure		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

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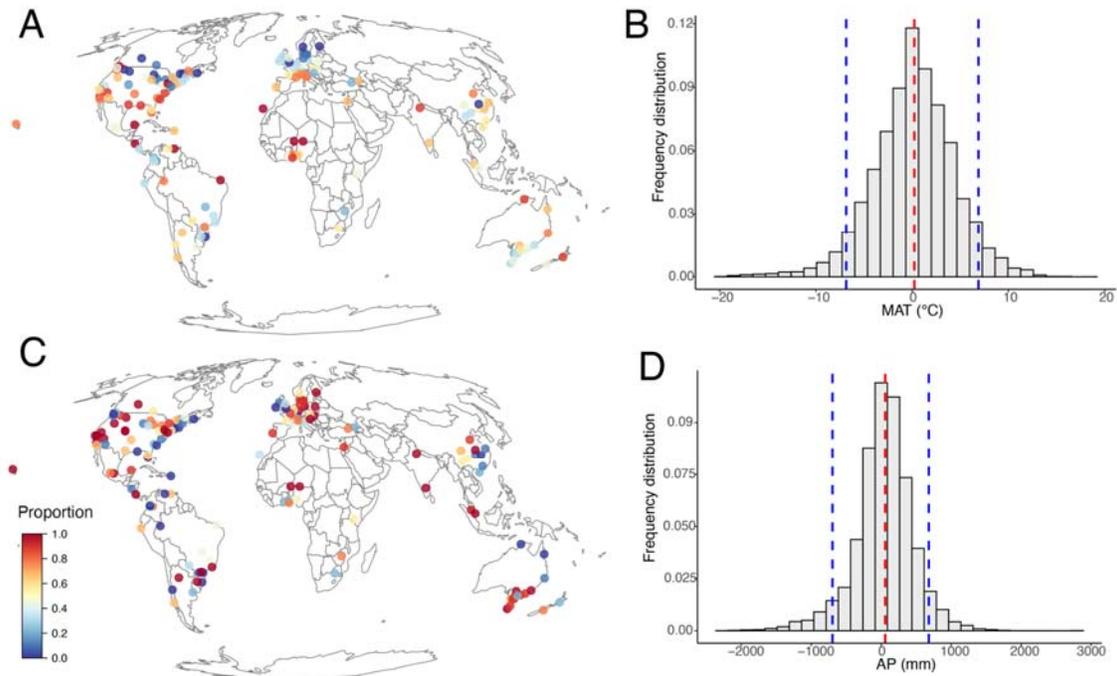
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Figures



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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.



641

642 **Fig. 2. Contemporary tree and shrub species safety margin across the world's cities.**

643 Proportion of species currently exceeding their safety margin for mean annual temperature

644 (MAT; **A**) and annual precipitation (AP; **C**) in 164 cities. Frequency distribution of mean

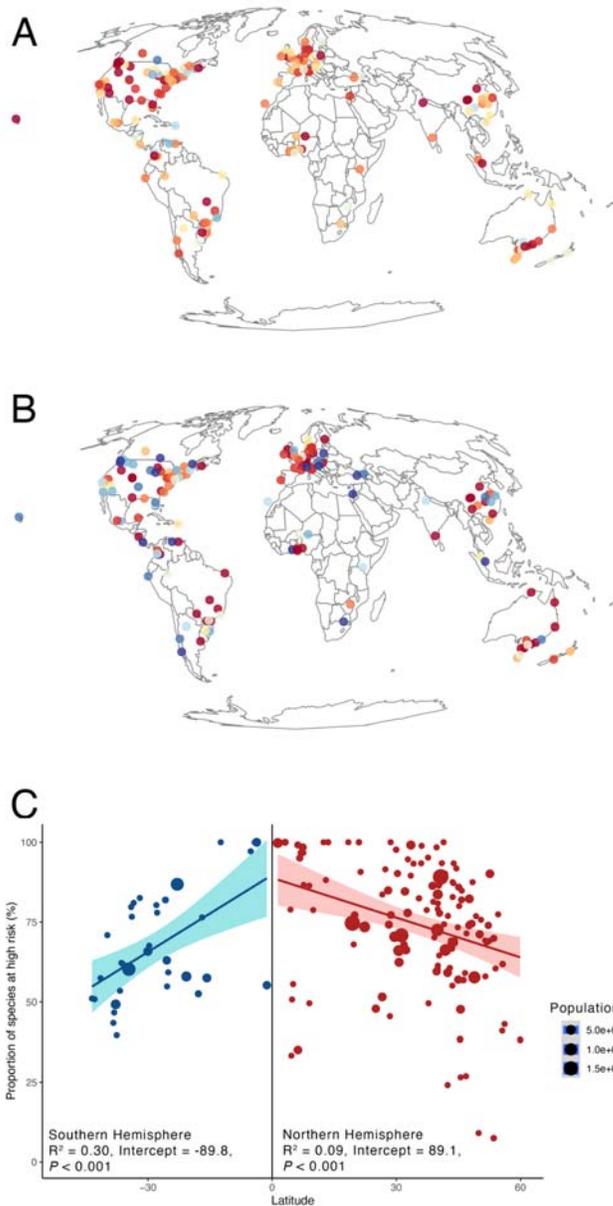
645 values of MAT (**B**) and AP (**D**) safety margins of each species ($n = 3,129$) across all cities.

646 Red lines indicate the median and blue lines the 5th/95th percentiles. A positive safety margin

647 ($S > 0$) indicates species with an upper (MAT) or lower (AP) climatic tolerance limit greater

648 than that of current climatic conditions; a negative value ($S < 0$) indicates species under

649 "unsafe" climatic conditions.



650

651 **Fig. 3. Species at risk of future climate change impacts across the world's cities.**

652 Proportion of species predicted to be at risk from projected changes in mean annual
 653 temperature (A) and annual precipitation (B) by 2050 in 164 cities. Each point represents the
 654 proportion of species at risk in a given city. Relationship between the proportion of species
 655 at risk and cities' latitude (Northern Hemisphere: $n = 129$ cities; Southern Hemisphere: $n =$
 656 35) (C). Ribbons indicate the 95% confidence interval for predictions from a linear model.
 657 Point size indicates human population size⁵⁶. Data for 2050 and RCP6.0.

658