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Applying the concept of niche breadth to understand urban tree mortality in the UK

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Highlights

- **Cumulative water stress during growing seasons and heatwaves have continually exacerbated between 2000 and 2021 in the UK**
- **Acer species showed higher vulnerability to accumulated drought and heat stress than Quercus species**
- **Precipitation during warmest quarter (PWQ) was most influential in the mortality response of Acer**
- **Quercus species showed resilience beyond their known lower thresholds of climatic range**
- **Mediterranean oaks outperformed native oaks in the UK**

Abstract

Accelerated climate change has raised concerns about heightened vulnerability of urban trees to failure. Amidst uncertainties, the concept of niche breadth (NB), the range of environmental conditions that species can tolerate, is widely used and estimated based on species presence data over the selected geographic range to predict species response to changing conditions. However, in urban environments where many species are cultivated out of the NB of their natural distributions, additional empirical evidence beyond presence and absence is needed not only to test the true tolerance limits but also to evaluate species' adaptive capacity to future climate. In this research, mortality trends of *Acer* and *Quercus* spanning a 21-year period (2000-2021) from tree inventories of three major UK botanic gardens - Royal Botanic Gardens, Kew (KEW), Westonbirt, the National Arboretum (WESB), and Royal Botanic Garden Edinburgh (RBGE) - were analyzed in relation to their NB under long-term drought stress. Overall, *Acer* was more responsive to drought stress and its mean mortality rate corresponded to their respective niche positions whereas *Quercus* exhibited relatively

indifferent response. The highest mean mortality rate per species (0.59) was found in *Acer* species that were positioned below the marginal NB for mean annual precipitation (MAP), precipitation of the warmest quarter (PWQ), and climatic moisture index (CMI) but within the NB for potential evapotranspiration (PET). Species at the lower end of the mean mortality rates (0.21) during the study period exhibited the exact opposite positions in their respective NBs. On the other hand, we also found many exceptional cases in which species exhibited high tolerance even far below their lower limits of NBs. These findings further highlight the importance of using mortality rates, or ecological performance, as a response trait in niche modeling to strengthen the credibility of suitability assessments in the context of a changing climate.

1. Introduction

Urban trees are important components of green infrastructure that provide ecosystem services such as social, health, economic, and environmental benefits, and are increasingly recognized as valued assets (Chenoweth et al. 2018). In addition, climate-induced urban challenges such as flooding, water-scarcity, and the urban heat island effects have sponsored the growing demand for nature-based solutions to tackle these issues (Kabisch et al. 2016). However, while urban trees are considered as climate mitigation solutions, their vulnerability has also increased by exposure to heightened climate stress. Increased tree mortality due to climate change has been extensively studied and observed across all forest biomes (Allen et al. 2010; IPCC 2012; Allen et al. 2015), but less is studied about mortalities of urban trees. In urban areas where the composition of species is determined by human decisions rather than natural selection, assessing vulnerability is key in the planting of the appropriate species and ensuring consistent delivery of ecosystem services for the future.

To assess urban tree vulnerability and stress tolerance, niche-based approaches are widely applied (McPherson et al. 2018; Hanley et al. 2021; Esperon-Rodriguez et al. 2022; Marchin et al. 2022). The concept of the fundamental niche (Hutchinson 1957) aims to describe n-dimensional environmental conditions under which species can thrive and support positive population growth. The concept is particularly relevant in the context of climate change, as it provides a theoretical framework

for understanding and predicting how species may respond to altering environmental conditions. More specifically, the niche breadth (NB), which represents the extent of the environmental conditions that species can tolerate, serves as a useful metric for evaluating the species' tolerance limits or its position along the niche axis (Carscadden et al. 2020). The NB can be estimated by correlating environmental conditions with various dynamic fitness responses such as growth rates or reproduction rates (Lowry and Lester 2006; Way and Oren 2010). However, it is more frequently extracted using static variables such as presence and absence data within the studied biogeographical region, an approach that gained popularity with the advent of an openly accessible database (Edwards et al. 2000) and modeling algorithms (Franklin 2010).

However, a niche modeling approach based solely on presence and absence data cannot resolve the complexity in urban environments where various introduced species coexist outside their natural habitats. A global survey of urban tree species by Kendal et al. (2019) found that the NB of urban trees are 38% to 90% wider than that of the natural habitats, which raises questions about whether the presence of introduced species in the urban areas is a valid consideration. In a strict sense, introduced species present in the urban environments are not 'naturally established' individuals which is typically excluded in the preprocessing stage of species distribution modeling. However, the possibility of adaptation in urban habitat, facilitated by reduced competition and assisted migration cannot be overlooked (Booth 2017). In other words, empirical evidence beyond presence and absence data, such as growth or mortality response, is needed to determine whether the presence of introduced species in urban habitats can be classified as a realized niche. This would provide a solid foundation for establishing more accurate niche boundaries and further strengthening niche-based approaches by not only identifying the tolerance limits but also by evaluating adaptive capacity through reassessing the NB. Lastly, while the niche is composed of n-dimensions, such empirical evidence can support to identify the more significant dimensions or combination of dimensions among the many that better explain a species adaptation capacities against specific climatic stress.

Here, we examine the mortality response of urban trees from 2000 to 2021 to test whether mortality corresponds to the niche position, specifically when it is within the NB or below the minimum threshold of the NB. The mortality data was collected from the three major botanic gardens-arboreta in the UK, which hold invaluable records of long-term growth for many species in environments

analogous to urban greenspace. We limited climate anomalies to drought index and heatwave events to assess the impacts of climate change as the combination of severe drought and unusually warm temperature, so-called "hotter drought," is the key driver for tree decline and mortality whether it is urban or rural (Allen et al. 2015; Settele et al. 2014).

In summary, the research aims to answer the following questions.

(1) To what extent is climate change impacting upon the mortality of urban trees? Is there any evidence of a threshold that triggers a noticeable change in the mortality trend?

(2) Are those species outside of their climatic NB more vulnerable to climate stress?

(3) Which niche variables better explain species vulnerability to climatic stress?

(4) Are the outcomes (1) to (3) consistent within botanic gardens in different geographical locations in the UK?

2. Material and methods

2.1. Study area and botanic gardens

While the overall climate in the UK is classified as Oceanic climate (Cfb), featuring mild summers and cool winters, by Köppen-Geiger (Peele et al. 2007), there is considerable variability in climate across the UK. The southeast of England is warmer and drier, whereas the southwest is warm and wetter, which contrasts with the cooler and sometimes wetter North. Three major botanic gardens for each represented region, namely the Royal Botanic Gardens, Kew (KEW), Westonbirt, the National Arboretum (WESB), and Royal Botanical Garden Edinburgh (RBGE), were selected (Table 1).

Table 1. Overview of the selected botanic gardens

Botanic garden	Latitude	Longitude	City	MAT ℃	MAP mm
KEW	51.4813	-0.29276	London	10.7	661
WESB	51.6065	-2.21947	Westonbirt	10.0	931
RBGE	55.9666	-3.21092	Edinburgh	9.5	818

2.2. Species selections, NB, and habitats

Two genera, *Quercus* and *Acer*, were selected for the analysis. Both genera are important not only in the native UK landscape but also in designed landscapes and urban forests. Additionally, they are species-rich genera with distinguished niche traits, which are advantageous for comparative analysis, as Acer species are often sub-canopy species in *Quercus* dominated woodland. Among the identified *Acer* (*n*=113) and *Quercus* species (*n*=159), we selected 40 *Acer* and 20 *Quercus* species based on their sample size (S1). Species with a minimum of six specimens in at least one botanic garden were selected. Taxonomy of all species was standardized and verified according to the Plant List (TPL; https://www.theplantlist.org) and the Plants of the World Online (POWO; https://powo.science.kew.org).

Five of the drought-related niche variables were selected (Box 1); the mean annual precipitation (MAP), the mean annual temperature (MAT), the mean precipitation of the warmest quarter (PWQ), the climate moisture index (CMI) and the mean annual potential evapotranspiration (PET). Precipitation during the driest quarter or driest month was excluded because the winter dry season for temperate species from East Asia could lead to misleading interpretation on drought response during the growing seasons. Other temperature related variables were also excluded as most species in the studied sites fall within the range of their temperature-based NB of origins. For the same reason, MAT was excluded for *Acer* and PET for *Quercus*. All climate data for NB were obtained from CHELSA v2.1 climatologies at high resolution for the Earth's land surface areas at a spatial resolution of 30 arcsec (~ 1km at the equator) (Brun et al. 2022). For selected niche variables, the lower limits of the NB for each species was extracted using the 5th percentiles based on their biogeographical distributions of origins (Esperon-Rodriguez et al. 2022). To do this, we obtained the occurrences of each species from the Global Biodiversity Information Facility (https://www.gbif.org/), and filtered them to include only those from their known origins using the POWO. Any invalid georeferenced coordinates (e.g., duplicated or non-terrestrial ones) were removed using the CoordinateCleaner package v2.0-18 (Zizska et al. 2019). In addition, to reduce overrepresentation, we applied spatial thinning using the spThin package v0.2.0 (Aiello-Lammens et al. 2015) to remove potentially redundant occurrences that were within a minimum distance of 1 km each other. Finally, climatic values of corresponding niche variables for the three botanical gardens were extracted (S2-Fig.3, 4) and compared against the marginal threshold of each species to determine its position of 'in' or 'out' of the NB range (S1, S2-Fig.1). All analyses were performed using the R statistical language

(version 4.1.0; R Core Team 2021). In addition to NB, selected species were also classified according to Holdridge's Life zone (Leemans 1992) using MAT, MAP, and PET ratio (i.e., annual PET to MAP).

2.3. Mortality data

We meticulously filtered the tree inventory data of the three institutions to include only those trees whose mortality seemed due to climatic stress. We removed records of intentional removals for landscaping or development purposes, early removals of poor specimens, unknown death years, and deaths caused by unrelated environmental factors such as storm damage, overcompetition, or death in a nursery. Additionally, we excluded trees with unknown accession years or those with accession years before 1900, except for those from KEW, which had records starting from 1960 and onwards.

In general, the mortality rate was calculated per species as a response to climate stress in a discrete time interval following as in (1),

$$(1) \quad \mu_0 = D_t / R_t$$

where mortality μ_0 over a period of a specified time interval t (e.g., a year or the entire period), D_t and R_t represent the number of death events and the total number of trees at risk respectively.

Table 2. Summary of tree mortality data by botanic gardens.

Genus	Status	KEW	WESB	RBGE
All *Acer*	Number of live trees (end of 2021, *n*)	537	1,034	1,024
	Number of total species (*n*)	80	94	70
	Number of selected species for NB (*n*)	22	32	34
	Cumulative dead trees (end of 2021, *n*)	240	269	414
	Cumulative mortality rate (%)	30.8	20.7	28.8
	Mean annualized mortality rate (%)	0.020	0.013	0.022
All *Quercus*	Number of live trees (end of 2021, *n*)	1,425	328	385
	Number of total species (*n*)	104	131	66
	Number of selected species for NB (*n*)	19	7	13
	Cumulative dead trees (end of 2021, *n*)	156	100	103
	Cumulative mortality rate (%)	9.9	23.4	21.1
	Mean annualized mortality rate (%)	0.004	0.011	0.014

2.4. Selections of climate anomalies

Drought and heat waves are known to be the most influential stressors that contribute to tree mortality in the context of climate change (Allen et al. 2015; Bradford et al. 2020). To represent the different gradients of drought intensity, we used the standardized precipitation and evapotranspiration index (SPEI). SPEI is a widely used meteorological drought index that utilizes a monthly climatic water balance information (Vicente-Serrano et al. 2010) as in the equation (2).

(2) $\text{SPEI}_i = \text{P}_i - \text{PET}_i$

The difference between precipitation, P at month i and potential evapotranspiration, PET_i is accumulated and converted to standard deviations with respect to the mean values. In this research, we used the sum of monthly SPEI during the growing season (April to October), $\text{SPEI}_{growing}$ and the sum of SPEI for the previous 5 years from the current year, SPEI_{5yr}, to account cumulative effects. All monthly SPEI values were calculated using SPEI package v.1.8.1 (Vicente-Serrano et al. 2010).

For heatwave, we calculated the total number of heatwave days for each year, HW_{days}. A UK heatwave is defined as a period of at least three consecutive days with maximum temperatures meeting or exceeding a heatwave temperature threshold. The threshold varies by UK county in the range of 25-28℃ (McCarthy et al. 2019). According to the Met Office (2022), the threshold of the heatwave for the KEW at Greater London is set at 28℃, 27℃ for the WESB, and 25℃ for the RBGE.

All daily meteorological data, including minimum, maximum, mean air temperature, and precipitation, was acquired from the Met Office Library & Archive for the following three weather stations with source id of 723 (KEW), 692 (WESB), and 253 (RBGE). When there was missing data during the specific period, we used the data from the nearest station data instead. For example, we replaced missing data for monthly precipitation during the months of June and July, 2007 for KEW with data from the Heathrow weather station (source id 708). The climate variables used in this study were summarized in the following Box 1.

Box 1. A list of abbreviations used

features		definition
SPEI	$\text{SPEI}_{growing}$	The sum of monthly SPEI during the growing season (April to October) of the year
	SPEI_{5yr}	The sum of $\text{SPEI}_{growing}$ from the current year j to j-5
HW	HW_{days}	Sum of all heatwave days of the year

NB	MAP	Mean annual precipitation
	PWQ	Mean sum of precipitation during the warmest quarter
	CMI	Mean climate moisture (precipitation - potential evapotranspiration) index over 1 year
	PET	Mean monthly potential evapotranspiration over 1 year
	MAT	Mean annual temperature

2.5. Statistical analysis

To assess the mortality trend over a period, the probability of mortality was estimated based on a discrete-time hazard approach using Gompertz link function (Salas-Eljatib and Weiskittel 2020; Suresh et al. 2022). The general representation of this hazard function is expressed in (3), (4) and (5),

(3) $\eta = C(\mu) = \alpha + \beta X_{is}$

(4) $C(\mu) = log(-log(1 - \mu)$

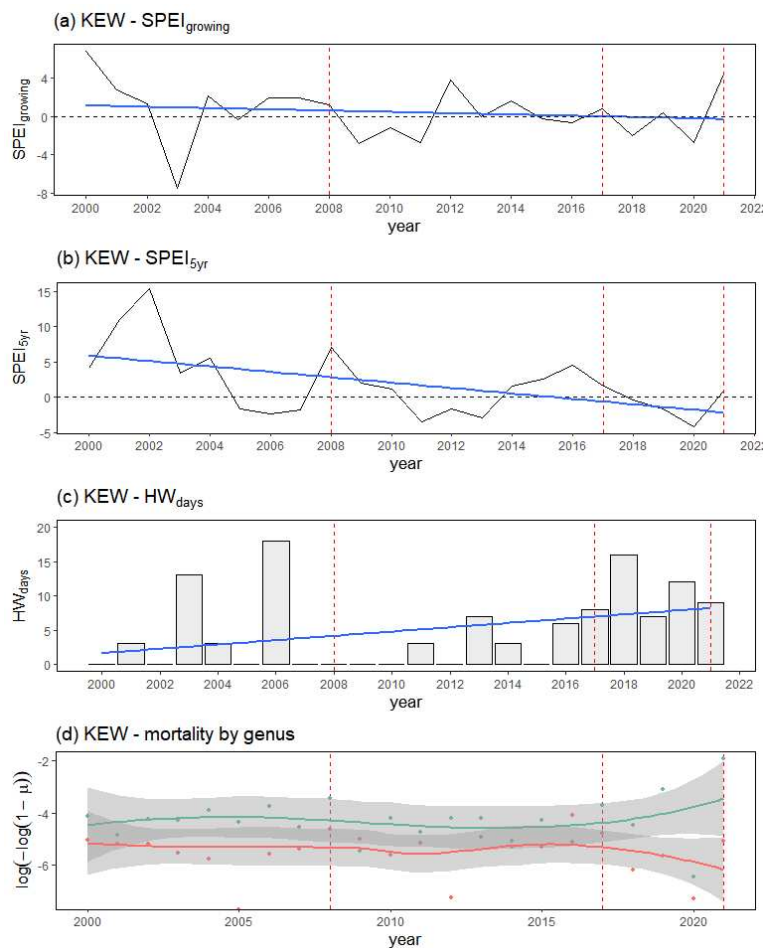(5) $\mu = C^{-1}(\eta) = 1 - exp(-exp(\eta))$

where the linear predictor η of the covariate X of the individual i at a time period of s, consisting of coefficient □ and the intercept □, is the inverse log-log function, also known as complementary log-log (cloglog), of the probability of mortality μ. To answer the research questions, the location of individual species in the four selected NB was used as dichotomous covariates. Additional model selection process is described in S2 (Table 1). In addition, the difference in the mean value of mortality rates by its location group of the NB over the entire period was tested using Mann-Whitney U test, as the mortality rate data followed beta distributions.

3. Results

Over the period of 2000-2021, the UK experienced a steady and gradual increase in moisture stress. This is particularly evident in the annual trend of $SPEI_{5yr}$, cumulative water balance preceding 60-months, which shows a noticeable downward slope ranging from -0.29 to -0.38 (Fig.1-b, f, j). A marked sharp decline in $SPEI_{growing}$ is noted in the year 2003 across all sites and 2018 for WESB and RBGE (Fig.1-a, e, i). The year 2006 also exhibited a severe drought accompanied by the highest

number of HW$_{days}$ across all sites, except for KEW where its intense water deficit was balanced out by the precipitation in the following months. Although overall patterns in the SPEI trend are similar across the sites, the occurrence of HW$_{days}$ is most prominent in KEW with an increasing intensity in terms of frequency and duration after 2011 (Fig.1-c, g, k).

The overall mortality trend is relatively stable with a noticeable upward shift as it heads towards the end of the study period (Fig.1- d, h, l). In general, *Acer* consistently experienced higher mortality rates than *Quercus* at all three sites. Nonetheless, there were two intervals within the study period, 2007-2009 and 2019-2021, which exhibited positive anomalies in both *Acer* and *Quercus* for all three sites. The second interval (2019-2021) is notable as all three botanic gardens displayed sharp upward trends for *Acer*, with KEW exhibiting the most pronounced incline and the least with WESB.
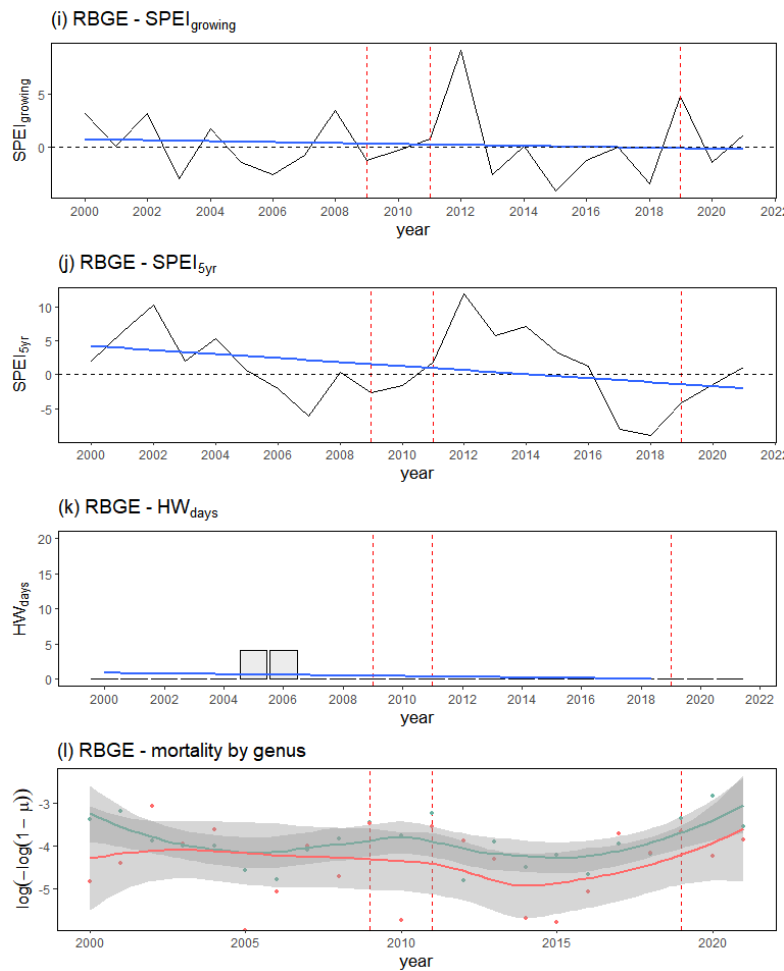
(e) WESB - SPEI$_{growing}$

(f) WESB - SPEI$_{5yr}$

(g) WESB - HW$_{days}$

(h) WESB - mortality by genus

(i) RBGE - SPEI$_{growing}$

(j) RBGE - SPEI$_{5yr}$

(k) RBGE - HW$_{days}$

(l) RBGE - mortality by genus
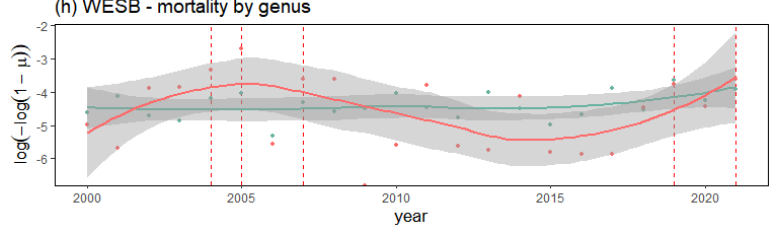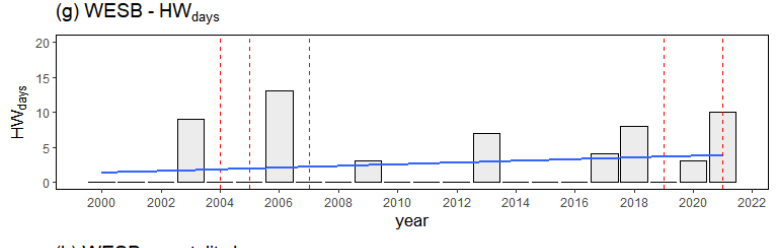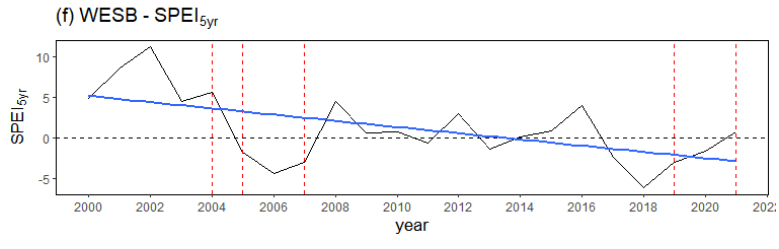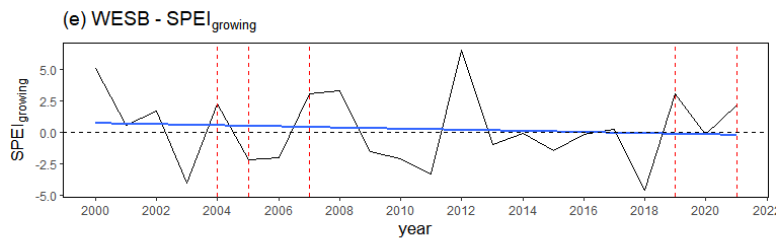
Figure 1. The climate trend over the period of 2000 to 2021 and regression fit for KEW, (a) SPEI$_{growing}$ (slope=0.07, p=0.5) (b) SPEI$_{5yr}$ (slope=-0.38, *p*=0.01) (c) HW$_{days}$ (slope=0.31, *p*=0.1); for WESB (e) SPEI$_{growing}$ (slope=-0.04, *p*=0.66), (f) SPEI$_{5yr}$ (slope=-0.38, p=0.004) (g) HW$_{days}$ (slope=0.12, *p*=0.39), and for RBGE (i) SPEI$_{growing}$ (slope = -0.04, p = 0.68), (j) SPEI$_{5yr}$ (slope=-0.29, p=0.1) and (k) HW$_{days}$ (slope=-0.04, p=0.26). The mortality trend of Acer (green) and Quercus (red) over the corresponding period for (d) KEW (all species *n*=80), (h) WESB (all species *n*=94), and (l) RBGE (all species *n*=70). Vertical dotted lines indicate the years when both *Acer* and *Quercus* exhibited positive mortality anomalies, meaning that they had higher mortality rates than the normal mean range over the period.

The effect of species' position in relation to its NB on mortality risk was relatively evident for *Acer*, but not straightforward for *Quercus*. While each site varied with different model selection, KEW and RBGE exhibited a similar pattern in *Acer* where PWQ and mortality were positively correlated (Table 3). MAP appears to be equivocal and less determining for *Acer* as it generally corresponded to a wide range of mortality rates (Fig.2) and even negatively related for KEW (Table 3). However, its median mortality rate was consistently higher for those positioned below the marginal NB of MAP in all three botanic gardens. Although CMI and PET were not the dominating factors, they were important sub-indicators when they were presented with MAT and PWQ (Table 5). The highest mean

mortality rate (0.59) was observed in a group of species that positioned below the marginal NB of all three variables, MAP, PWQ, and CMI and within the NB of PET, whereas species above the marginal NB and below the NB of PET exhibited a low mean mortality rate (0.21). It is also notable that WESB exhibited a weak or non-existent relationship with all niche variables, which appears to form divergent patterns from KEW and RBGE.

On the other hand, *Quercus* did not conform to the pattern shown in *Acer* and the median mortality rate remained under 0.2 regardless of its niche positions in most cases (Fig.3, Table 5). However, it should be noted that many *Quercus* species are predominantly from warm temperate (WT) regions unlike *Acer* of which 70% species originated from cool temperate moist (CT-moist) and cool temperate wet (CT-wet) forest (S2-Fig.2). In both KEW and WESB, species below their marginal MAT were slightly higher in survival during the study period (Table 4, Fig.3). This is contrary to the MAT weakly associated with increased mortality rate in RBGE.

Table 3. Model estimates of regression coefficients for selected *Acer* species

	KEW		WESB		RBGE	
	coefficient	Std.error	coefficient	Std.error	coefficient	Std.error
Intercept	**-137.763*****	26.26	**-75.779****	27.11	-29.716	18.54
Year	**0.066*****	0.01	**0.035****	0.01	0.013	0.01
NB						
MAP (out)	**-0.348***	0.16				
PWQ (out)	**0.718****	0.28			**0.709*****	0.17
PET (out)					**-0.377***	0.18
CMI (out)			**0.312***	0.16		

** p < 0.01, * p < 0.05, ' p < 1

Table 4. Model estimates of regression coefficients for selected *Quercus* species

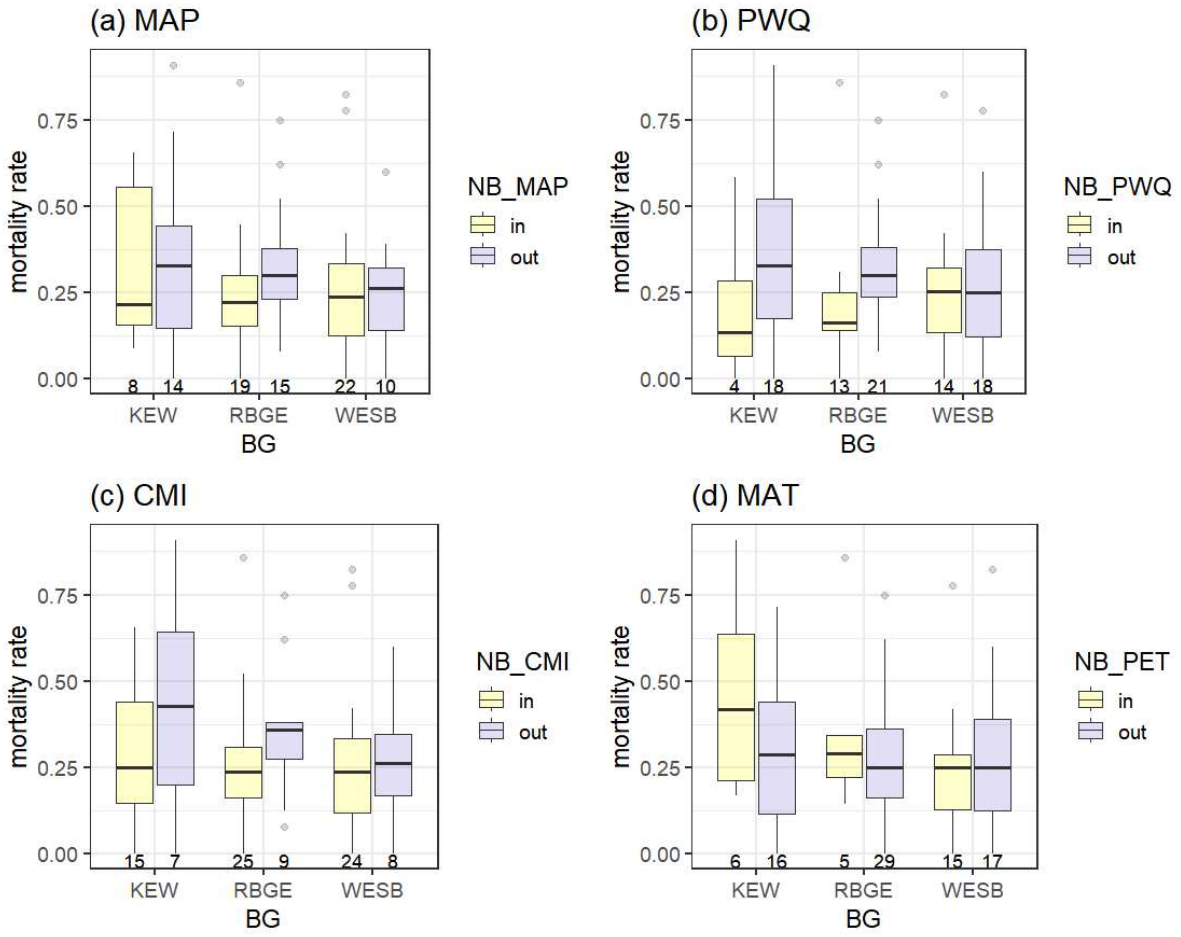|	KEW		WESB		RBGE	
	coefficient	Std.error	coefficient	Std.error	coefficient	Std.error
Intercept	25.642	36.31	58.113	44.30	-1.919	43.68
Year	-0.016	0.02	-0.031	0.02	-0.001	0.02
NB						
MAP (out)	**-1.100****	0.29	-1.166	0.72		
PWQ (out)	-0.696'	0.39				
CMI (out)	**1.611***	0.65				
MAT (out)	**-0.994***	0.42			**0.635***	0.28

** p < 0.01, * p < 0.05, ' p < 1

Figure 2. The distribution of the mortality rate per species for *Acer* by its position of each NB.
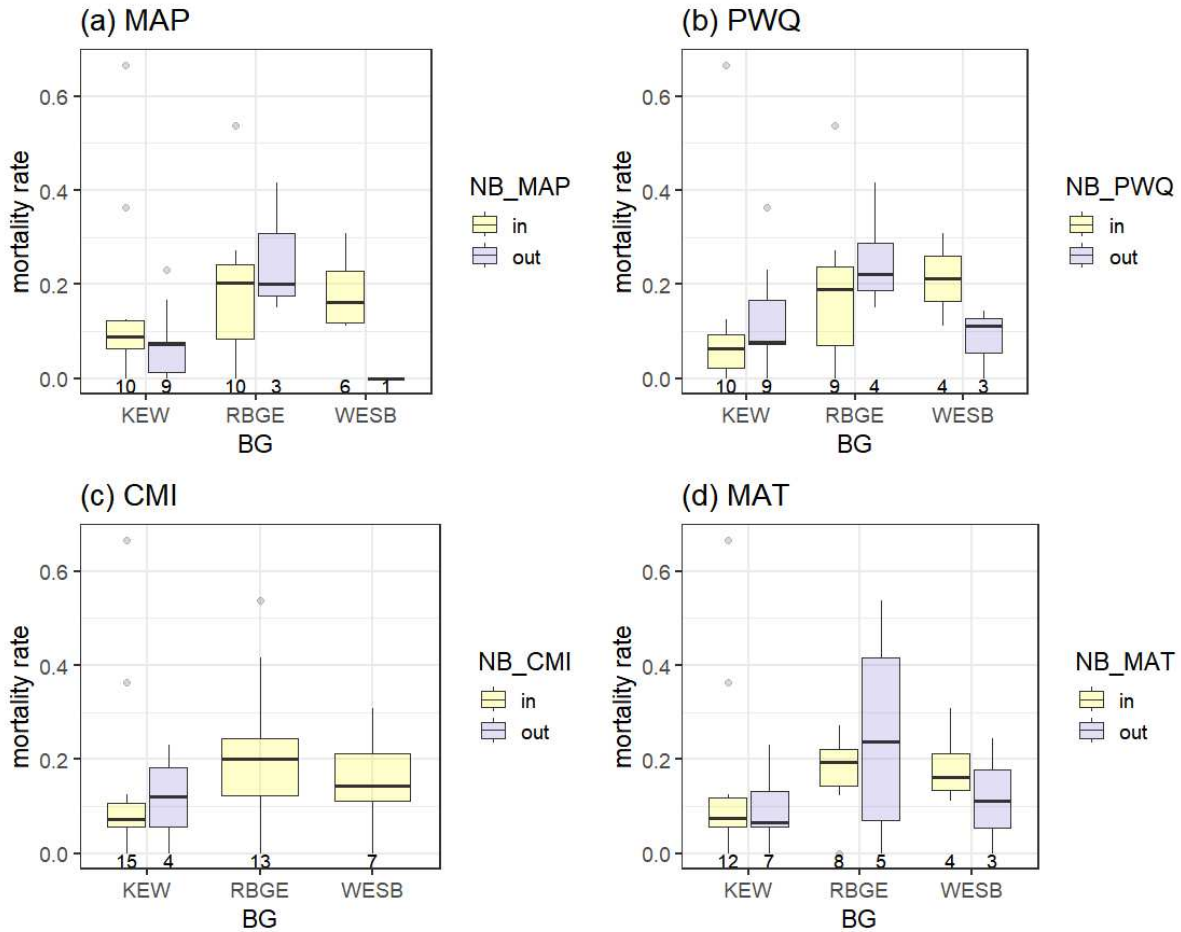
Figure 3. The distribution of the mortality rate per species for *Quercus* by its position of each NB.

Table 5 - The mean mortality rate per species for *Acer* and *Quercus* in combinations of four niche dimensions, *n* = number of represented species where any identical species of different botanic gardens are counted independently. PET was replaced with MAT for *Quercus*

MAP	PWQ	CMI	PET (MAT)	Mean mortality (*Acer*)	n	Mean mortality (*Quercus*)	n
out	in	in	out	0.069	2	0.067	1
out	out	in	in	0.200	1	0.124	4
in	**in**	**in**	**out**	**0.211**	**12**	0.142	10
in	out	in	out	0.273	12	-	-
in	in	in	in	0.274	13	0.216	10
out	in	in	in	0.286	1	0.007	2
out	out	in	out	0.287	11	0.208	1
out	out	out	out	0.315	23	0.199	2
in	out	in	in	0.336	9	0.175	6
out	**out**	**out**	**in**	**0.591**	**2**	0.039	2

aggregated	0.287	88	0.156	39

4. Discussion

4.1. Mortality trends in relation to climate change

Two intervals, 2007-2009 and 2019-2021, that exhibited positive anomalies of mortality rates share common recurring patterns in all three sites. The overlapping occurrence of negative $SPEI_{growing}$ and $SPEI_{5yr}$ in the year preceding the event is associated with high mortality. In general, $SPEI_{5yr}$ curve falls negative several years after a sharp drop in the $SPEI_{growing}$ curve, as seen in the case of 2003 drought which appears as negative $SPEI_{5yr}$ in the following years of 2006 and 2007 (Fig. 1-b, f, j). When the accumulated drought experience reached its highest point, coinciding with a new intense drought of the year, climatic stress was likely exacerbated, leading to increased vulnerability of trees. As trees generally respond to intense drought as reduced growth in subsequent years (Mu et al. 2022; Perkins et al. 2018), it can be presumed that trees with reduced growth from the previous drought face an increased chance of failure when exposed to additional intense drought stress. The second interval of 2019-2021 shows a slight variation from this pattern. The negative $SPEI_{5yr}$ in 2018 for KEW and WESB resulted from a series of prolonged moderate droughts from 2013 rather than a single intense drought event. The $SPEI_{5yr}$ for KEW touched the lowest negative value (-4.1) in 2020, coinciding with $SPEI_{growing}$ of -1.98, and the following year saw the highest number of death events (*n*=84) for *Acer*. This could partially be attributed to the fact that there was delayed record-keeping due to the absence of maintenance during the COVID period. However, even when considering the events occurring over the two-year period, it remains the largest number of deaths during the entire study period. This contrasts with *Quercus*, for which the increase in mortality was small (*n*=9) in the same year, 2021. The distinguishing characteristics of the second interval (2019-2021) for KEW and WESB can also be attributed to a combination of prolonged moderate droughts and heatwaves. In particular, KEW experienced heatwaves every year from 2013 for nine consecutive years with the exception of 2015. On the other hand, there were no records of heatwaves in RBGE during this interval although RBGE also experienced a gradual increase in the growing season temperature (Arnell et al. 2021). However, both $SPEI_{growing}$ and $SPEI_{5yr}$, were lower than those of the other two

sites in the preceding year of the second interval. From 2015 to 2018, the mean $SPEI_{growing}$ was -4.15 and, in 2018, the $SPEI_{5yr}$ was -8.8 for RBGE, which were much lower than the respective values for WESB (-1.46 and -6.0) and those for KEW (-0.24 and -0.35). This indicates that the duration and the intensity of drought experienced in RBGE was greater than in the other two sites. During this second interval, all three botanic gardens saw the unprecedented increase in mortality in *Acer* and slight increase in *Quercus* which align with the global phenomenon of tree declines associated with exposure to intense drought and warming (Allen et al. 2015; Settele et al. 2014).

4.2. Acer

During the 21-year study period, many *Acer* species that fell below marginal NB tended to exhibit relatively higher mortality rates compared to those within the NB (Fig.2). Among the selected niche variables, PWQ exhibited the highest influence on mortality rates overall. This is particularly related to the species compositions, which mostly originated from cool temperate forests of Asia (S1, S2-Fig.2), where seasonal precipitation is primarily influenced by monsoons. Comparably, MAP is less distinguishing than PWQ as it could potentially misrepresent seasonal humidity and its tolerance limit, specifically during the growing season drought. Nonetheless, the position of a single NB did not successfully represent the individual species' mortality rates. Instead, the combinations of the four NB were more informative in elucidating the mortality patterns (Table 5). The highest mean mortality rate (0.59) was observed when species fell below the marginal NB of all three variables, MAP, PWQ, and CMI and within the NB of PET, whereas the opposite combination exhibited a relatively lower mean mortality rate (0.21). Unlike those three niche variables (MAP, PWQ, and CMI), falling below marginal PET is more advantageous since it indicates that species are adapted to the higher evaporative demand than that of the current condition. CMI and PET were sub-indicators when there was a mismatch between mortality rates and the NB position of MAP and PWQ. For instance, species that showed low mortality rate, even if they fell below the marginal NB of MAP and PWQ, tended to be within the NB of CMI and below the marginal NB of PET.

Such variations in mortality rates can be further explained by inclusion of habitat information and NB width. On a continental scale niche analysis, species native in Europe are generally shown narrower NB compared to those Asian species (S2-Fig.3). Most species with the best combination of

NB positions of MAP (in), PWQ (in), CMI (in) and PET (out) are the ones with narrow NB. In general, species with narrow NB are often considered specialists adapted to specific geographic environments, exhibiting strong tolerance to certain stressors such as drought, frost, or shade (Boulangeat et al. 2012; Pagel et al. 2020). Species such as *A. granatense* and *A. monspessulanum* are specialists narrowly distributed in warm temperate dry forests (WT-dry) adapted to seasonal droughts and, thus,exhibited low mortality rate from 0.0 to 0.18 (S2-Fig.5). On the other hand, species with broader NB tend to display functional traits allowing them to occur in a wider geographic area or to adapt more quickly to changing climate (Pagel et al. 2020; Slatyer et al. 2013). For instance, *A. buergerianum,* a species naturally found in warm temperate wet forest (WT-wet) with its biogeographic distribution spanning from far east Japan to southwestern China, features a relatively broad NB (S1, S2-Fig.3). Although its NB position in MAP and PWQ indicates below marginal threshold, the mortality rate is still very low (< 0.2), with its niche position in CMI (in) and PET (out) (S2-Fig.5), suggesting its adaptation capacity (e.g., high leaf mass per area, waxy leaf) enabling them to adapt in dry conditions (e.g., low CMI and high PET) and to thrive beyond their known natural distributions.

Site characteristics should not be overlooked when examining the relationship between the NB and mortality rates of *Acer* species. It was evident that WESB exhibited no clear distinction between a species' NB position being 'in' and 'out' (Fig.2), although relatively weak positive correlation with CMI was observed (Table 3). In contrast, KEW displayed the more pronounced differences between 'in' and 'out.' These varying responses among the sites can be attributed to its difference in regional climate and soil characteristics. The soils in WESB are sand-stone derived and consist of silty clay and loam, whereas soils of KEW and RBGE are sandy loams (UKRI 2023; Westonbirt 2021). With 100 to 300mm more rainfalls annually and relatively more fertile soils of a greater water holding capacity, WESB might have provided a more advantageous environment for some species from moist regions. *A. capillipes* (0.0), *A. carpinifolium* (0.0), *A. caudatifolium* (0.13), *A. rubrum* (0.12), and *A. negundo* (0.05) are the ones from CT-moist to WT-wet (S1), which exhibited very low mortality rates in WESB compared to the mortality rates of the same species in the other two sites, ranging from 0.22 to 0.86 (data not shown). However, the mortality rates of *A. palmatum* and *A. davidii*, the two most planted *Acer* species in all three sites, exhibited a similar range of mortality across the sites from 0.30 to 0.38 and from 0.42 to 0.44 respectively.

4.3. Quercus

Unlike *Acer*, *Quercus* did not significantly respond to its precipitation related NB, but exhibited modest differences in relation to MAT and CMI (Table 4, Fig.3). The results largely relied on its species composition which was dominantly selected from warm temperate regions (S2-Fig.2). Moreover, the number of species represented in *Quercus* was only half of those in *Acer* (S1). In WESB, 67% of total specimens were concentrated in just 3 species – *Q. robur, Q. ilex* and *Q. petraea* – while 72 out of 84 species had fewer than 5 individuals and were thus excluded from the NB analysis. In KEW, half of total specimens were concentrated in 4 species *Q. robur*, *Q. ilex*, *Q. cerris*, and *Q. rubra*. Among those dominant species, *Q.ilex, Q.petraea,* and *Q.robur* exhibited a similar range of mortality rates across the sites with 0.06~0.07, 0.12~0.19, and 0.07~0.18 respectively. There were some exceptionally high mortality rates shown, but these cases mainly consisted of species within 5 years of planting, suggesting greater influence of potential transplant stress than the climatic stress (Sherman et al. 2016; Struve et al. 2000). High mortality rates in young trees are not a distinct characteristic of *Quercus* alone and equally observed in both *Acer* and *Quercus (S2-Fig. 2, 3)*. However, the high visibility of mortality among young *Quercus* (<15 years)*,* in particular, is contrasted with its low mortality rate once they are established with an overall mortality rate of less than 0.2 (Table 5).

The low mortality rate was consistently observed even in species that fell outside of their NB such as *Q. acutissima, Q.glauca, Q.phillyreoides,* and *Q. serrata.* These species, representing supposedly the worst combination of their NB of MAP (out), PWQ (out), and CMI (out), exhibited no difference in mortality rates (0, 0.16, 0.24, and 0.08 respectively) compared to above dominant species within their NBs. This is also particularly contrasted with *Ace*r because those *Acer* species in the same NB position such as *A.ukurunduense* exhibited the highest mortality rate of 0.9. However, *Acer* species, which are mostly shade-tolerant, sub-canopy species in mesic temperate forests, often co-occur with deep-rooted canopy *Quercus* and have evolved with differentiated adaptation strategy (Abrams 1990: Ackerly and Donoghue 1998; Cavender-Bares 2018; Fallon and Cavender-Bares 2018). Further implications can be learned through investigation of the plant functional traits among co-occurring species under the same climatic conditions, although this is beyond the scope of this research. It is also noted that *A. ukurunduense* co-occur with *Q. mongolica* in CT-moist forests

(Fujiwara and Harada 2015), but its minimum threshold of MAP NB is higher than that of *Q. mongolica* (S1). On the other hand, *Quercus* species in corresponding NB positions are all from warmer regions (WT-wet), exhibiting similar patterns of low mortality rates with wider NB as in *A. buergerianum* (WT-wet). Collectively, the selected *Quercus* species in this research have not shown significant difference in mortality rates according to their NB positions, which suggests that the minimum threshold of the precipitation-related NB could be lower than what appears to be solely based on their natural distribution records.

Site-specific characteristics are less apparent for *Quercus* ($p > 0.05$) (Fig.3). However, an unprecedented number of seventeen mature *Q. robur* (> 25 years) succumbed during the severe drought of 2003 and the subsequent two years at the WESB (Fig.1-I), in contrast to only one or two deaths of the same species during the same period at the other two sites. This could be potentially linked to Acute Oak Decline (AOD) symptoms which have been increasingly problematic affecting approximately one third of England and Wales woodlands (Brown et al. 2017). Several factors associated with the AOD symptoms include warm temperature and brown earth soils rich in clay, both of which are more characteristic of the WESB (Brown et al. 2018). Nonetheless, no similar dramatic increase in deaths of *Q. robur* were observed at the WESB following the drought in 2018.

4.4. Changing species-specific mortality rates due to shifting NB

Although more evidence is needed, it is worth noting that a consistent pattern of increasing mortality rates was observed in a single *Acer* species as a species' niche position shifted from 'in' to 'out' (S2 Fig.11). For instance, *A. campestre* and *A. platanoides*, which exhibited zero to relatively low mortality at WESB and RBGE where they were positioned within all four NBs, showed a slight increase in mortality rate in KEW with its NB position shifted from 'in' to 'out' for PWQ. Similarly, *A. pensylvanicum* exhibited mortality rates in increasing order of 0.41 (WESB), 0.52 (RBGE), and 0.71 (KEW) according to its position below marginality from a single NB (PWQ), two NBs (MAP and PWQ), to all three NBs (MAP, PWQ, and CMI) respectively. In summary, the species-specific mortality rate for *Acer* tends to be lowest at WESB where environmental conditions are relatively moister, therefore mostly above the marginality, than that of KEW.

5. Conclusions

Tree death is contingent on past stresses, which may progress slowly from the accumulated effects of exogenous stress over multiple timescales (Anderegg et al. 2012; Olge et al. 2015). As climate change is expected to accelerate, uncertainties regarding ecosystems responses have raised concerns over biodiversity and the appropriate selection of trees for future generations. While ecological niche modeling is widely used to predict species suitable distribution range in natural habitats (Holt 2009), urban habitats pose a challenge in application of the niche-based approach. In urban environments, which include species beyond their natural habitats and ecological assumptions, it is difficult to estimate the true tolerance limit of species based solely on their presence information.

Despite its limitations, analysis of mortality trends in a diverse collection of species in botanic gardens over a considerable period of time provides unique insights into climate change. As with natural forests, cultivated urban trees in botanical gardens have also been affected by climate change, characterized by frequent droughts and warming temperatures (Fig. 1). Increased mortality trend coincided with the compounded effects of $SPEI_{growing}$ and $SPEI_{5yr}$ at their lowest point, suggesting that some individuals failed to recover from accumulated drought stress and crossed a threshold immediately after the onset of new drought. Correspondingly, the year 2018 appears to be a transition period after which the accumulation of stress was further exacerbated with heat stress, surpassing the tolerance limit of many species including those that survived from the severe drought in 2003.

Furthermore, we found that the mean mortality rates of *Acer* in general increased as their positions shifted from 'in' to 'out' along the precipitation-related NBs while the mortality of *Quercus* appeared to be relatively independent of these NBs, exhibiting stable mortality rates (<0.2) regardless of their positions of the NBs. For *Acer*, PWQ was found to be the most significant indicator of mortality among the four selected niche variables, while combining all four would provide a more comprehensive explanation for variations in mortality rates. However, we also found many cases in which species exhibited low mortality rates even when their positions were far below the minimum threshold of their respective NBs. Such results, contrary to our expectations, and those responses of *Quercus* species raise additional questions: Were their minimum thresholds lower than their NBs of natural distributions? Were there other latent niche variables, such as soil moisture or distance to groundwater, that were more significant and influential? Do we need to consider species-specific

characteristics, such as plant functional traits potentially enabling them to survive beyond their limits? Or was it simply due to microclimatic conditions adjusted by human interventions which could be a likely case in urban botanic gardens? The essence of studying mortality response of urban trees lies in identifying varying patterns in species-specific mortality that do not conform to our expectations. The ultimate goal is to enhance understanding of plant responses in a changing climate based on the assessment of "ecological performance" to niche variables (Violle et al. 2007). Here, ecological performance is not limited to mortality rates and can be extended to growth rates or reproduction rates to determine the optimum of NBs in relation to their tolerance limit. It may also include additional niche dimensions such as soils, light, biotic interactions (e.g., habitat overlapping), and the plant functional traits beyond the climatic variables. Lastly, it is argued that niche-modeling based on species-level occurrence data could underestimate or overestimate the NB (Carscadden et al. 2020). To further enhance analysis, species-level NB can be broken-down to NBs at different scales, such as genetic-level or population-level NB, within a species from various biogeographical regions. In urban environments, where the collection of such empirical evidence in demand is challenging due to limited diversity, it is particularly relevant to utilize data from urban botanic gardens that are already capable of aggregating long-term data across highly diverse species. Their roles in conserving and promoting genetic diversity through their living collections are once again emphasized, calling for future research on how to incorporate their data into urban ecosystem assessment and niche modeling.

Acknowledgements

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