



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

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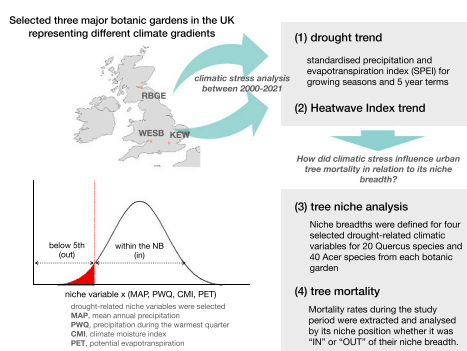
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HIGHLIGHTS

- 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.

GRAPHICAL ABSTRACT

Applying the Concept of Niche Breadth to Understand Urban Tree Mortality in the UK



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ABSTRACT

Accelerated climate change has raised concerns about heightened vulnerability of urban trees, spurring the need to reevaluate their suitability. The urgency has also driven the widespread application of climatic niche-based models. In particular, the concept of niche breadth (NB), the range of environmental conditions that species can tolerate, is commonly estimated based on species occurrence 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* species spanning a 21-year period (2000–2021) from tree inventories of three major UK botanic gardens - the Royal Botanic Gardens, Kew (KEW), Westonbirt, the National Arboretum (WESB), and the Royal Botanic Garden Edinburgh (RBGE) - were analyzed in relation to their NB under long-term drought stress. As a result, *Acer* species were more responsive to drought and heat stress. For *Acer*, positioning below the lower limits of the precipitation of warmest quarter led to an

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increase in the probability of annual mortality by 1.2 and 1.3 % at KEW and RBGE respectively. In addition, the mean cumulative mortality rate increased corresponding to an increase in the number of niche positions below the lower limits of the selected bioclimatic variables. On the other hand, *Quercus* species in general exhibited comparable resilience regardless of their niche positions. Moreover, Mediterranean oaks were most tolerant, with cumulative mortality rates that were lower than those of native oaks in the UK. These findings further highlight the importance of incorporating ecological performance and recognizing species-specific adaptive strategies in climatic niche modeling.

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, increasing frequency of extreme climate events, leading to urban challenges such as flooding, water-scarcity, and the heatwaves 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 change mitigation solutions, their vulnerability has also increased by exposure to heightened climate stress. Increased tree mortality and shifts in species distributions due to climate change has been extensively studied and observed across all forest biomes (Allen et al., 2010; Allen et al., 2015; Engelbrecht et al., 2007; Esquivel-Muelbert et al., 2019; Hartmann et al., 2022; IPCC, 2012), but less is studied about the mortality 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, climatic niche-based approaches are widely applied (Esperon-Rodriguez et al., 2022; Hanley et al., 2021; Marchin et al., 2022; McPherson et al., 2018). 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; Khan and Conway, 2020). The quantification of niche can be achieved using two very different approaches. The first, correlative model, employs statistical relationships to relate environmental conditions with observed species occurrence and to predict species distributions based on its correlative patterns (Morin and Lechowicz, 2008). On the other hand, a mechanistic model attempts to quantify the interactions between the environmental variables and dynamic fitness responses such as growth rates or reproduction rates (Lowry and Lester, 2006; Way and Oren, 2010). This latter model incorporates the biological processes and physiological responses of species in response to changing environmental conditions (Kearney and Porter, 2009). Between these two models, the former approach is more frequently used as species occurrence data has become openly accessible with the advent of biodiversity databases, e.g., the Global Biodiversity Information Facility (GBIF; <https://www.gbif.org/>) (Curry and Humphries, 2007; Edwards et al., 2000). Moreover, advanced modeling algorithms have facilitated more complex predictions (Franklin, 2010).

However, the predictive performance of the correlative model relies on the accurate representation of the species distributions and the inclusion of true/pseudo absence data, which should reflect the realized niche, or the actual area occupied within the theoretical space of the fundamental niche (Lee-Yaw et al., 2022; Sillero, 2011). Nevertheless, in the real-world application, sampling bias is unavoidable, thereby always creating a certain gap between the modeled species distributions and the

theoretical niche (Guillera-Aroita et al., 2015). Moreover, as the natural distributions of species are often limited by non-climatic factors such as biotic interactions or dispersal limitations, climatically suitable habitats might not always be occupied, leading to the reduced realized niche (Peterson and Soberón, 2012). Species could also occupy in unsuitable habitats, namely sink habitats, where local reproduction rate exceeds mortality (Pulliam, 2000). Consequently, the boundaries of the estimated NB are viewed as 'soft' limits (Bocsi et al., 2016; Catullo et al., 2015; Early and Sax, 2014; Warren et al., 2014). In other words, these 'soft' limits do not necessarily reflect the genuine 'physiological limits', as Catullo et al. (2015) defined it: "an absolute constraint on survival within a single generation." In addition, when applying the climatic niche models in assessing vulnerability of urban species, it becomes even more complex. In urban environments, profound anthropogenic interventions have allowed various introduced species to coexist in heterogeneous settings outside their natural habitats (Ossola et al., 2020). These urban species are not 'naturally established' individuals; thus, their occurrences in urban environments have generally not been considered as part of the realized niche. Typically, the occurrence of species in urban environments is excluded during the data preprocessing stage of niche modeling (Booth, 2017). However, how we classify urban occurrence – either as sink habitats (unsuitable habitat that was randomly occupied by species) or as potential niche (suitable habitat that was previously unoccupied due to constraints such as biotic interactions and accessibility) – can greatly impact the interpretation of the NB (Sillero, 2011). One recent study finds that 53 % of species across 164 cities are already subject to unsafe baseline below the lower limits of their climate tolerance (Esperon-Rodriguez et al., 2022). Another global survey of urban tree species conducted by Kendal et al. (2018) revealed that the NB of urban trees is 38 % to 90 % wider than that of the natural distributions. These findings prompt the following intriguing questions: Does the presence of introduced species x in a city y , beyond their NB of natural distributions or being positioned below their lower limits, signify an increased exposure to mortality risk? Alternatively, could it indicate that the species NB was not truly understood in its previously known natural habitats, and may actually possess greater physiological tolerance than we thought? In order to answer this question, additional empirical evidence beyond occurrence data is necessary. These include growth or mortality responses, which Violle et al. (2007) distinguished as 'ecological performance traits' from other plant functional traits. These traits represent the whole-organism performance of sampled individuals within a particular ecological habitat. By integrating these ecological performance traits, we can address some of the limitations inherent in the correlative model (Holt, 2009; Peterson and Soberón, 2012). In particular, mortality data in urban environments can serve as a valuable input in reassessing the NB, thereby further strengthening climatic niche-based approaches. However, 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; Anderegg et al., 2020; Mu et al., 2022; Ogle et al., 2015). In practice, obtaining long-term species-specific ecological performance data on a continental scale is not feasible. Instead, our research focused on the three urban botanic gardens (BGs) in the UK, with the aim of comparing mortality rates of a diverse range of species in relation to their NB. In detail, the mortality rates of the selected *Acer* and *Quercus* species from 2000 to 2021 were investigated whether their mortality rates

corresponded with their niche position, simply when it is positioned within the NB or below the lower limits of the NB. We also incorporated the drought index and heatwave trends over the study period to examine the influence of climate change on the mortality trend. 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; Nitschke et al., 2017; Settele et al., 2014), We hypothesized that the combining effect of warmer temperature and long-term drought would increase the mortality risk for those species position below the lower limits of their NB.

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

- (1) Over the course of the study period, to what extent did the heat and drought stress accumulate? Does the accumulated climatic stress show any correlative pattern with the annual mortality of *Quercus* and *Acer* species?
- (2) Is vulnerability to mortality higher for those species below the lower limits of their NB than those within their NB under accumulated heat and drought stress?
- (3) Which climatic niche variable better explains species vulnerability to mortality?
- (4) Are the outcomes (1) to (3) consistent across the selected BGs?

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 (Peel 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 the Royal Botanic Garden Edinburgh (RBGE), were selected (Table 1).

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 throughout the temperate climates. Additionally, they are species-rich genera with distinguished niche characteristics, which are advantageous for comparative analysis, as *Acer* species are often sub-canopy species in *Quercus* dominated woodland (Fujiwara and Harada, 2015; Lorimer, 1984; Matheny et al., 2017). 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>). The POWO is an international collaborative open database launched by the Royal Botanic Gardens, Kew in 2017, which provides world plant information such as taxonomy, distributions, traits, and

threat status. The names backbone of the POWO uses the International Plant Names Index (IPNI) Life Sciences Identifier.

We selected four bioclimatic niche variables as potential indicators for mortality response to heat and drought stress (Box 1); the mean annual precipitation (MAP), the mean precipitation of the warmest quarter (PWQ), the mean monthly climate moisture index (CMI) and the mean monthly 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 bioclimatic variables were also excluded as most species in the studied sites fall within the safe range of their NB. 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 arc sec (~1 km at the equator) (Brun et al., 2022; Karger et al., 2021). For selected bioclimatic niche variables, the lower limits of the NB for each species were extracted using the 5th percentiles based on their biogeographical distributions of native range (Esperon-Rodriguez et al., 2022). To do this, we obtained the occurrences of each species from the Global Biodiversity Information Facility (GBIF; Supplementary data S1) and filtered them to include only those from their known native ranges using the POWO. Any invalid georeferenced coordinates (e.g., duplicated or non-terrestrial ones) were removed using the CoordinateCleaner package v2.0-18 (Zizka 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, corresponding values of bioclimatic niche variables for the three BGs were extracted and compared against the lower threshold, the 5th percentile of the NB for each species to determine its position of ‘in’, above the threshold, or ‘out’, below the threshold. In addition to niche positions, selected species were also classified according to Holdridge’s Life Zone (Leemans, 1992), a land classification scheme based on the mapping of vegetation and bioclimatic conditions, using MAT, MAP, and PET ratio (i.e., annual PET to MAP). As a result, the biogeographical ranges of our species were categorized into boreal temperate (BT), cool temperate (CT), and warm temperate (WT) habitat zones. Each of these groups is further subdivided based on precipitation levels: dry, moist, and wet. A complete list of classified species can be found in Supplementary data S1.

2.3. Mortality data

We obtained mortality records of all *Acer* and *Quercus* species for the period between 2000 and 2021, along with all living records as of the 2021 year-end. We filtered the mortality records, excluding all deaths that were unrelated to climate. This entailed removing records of trees intentionally removed for landscaping or development, early removals of poor specimens, and entries with unknown death years. We also excluded deaths identified as physical damage such as storm damage, over-competition, or deaths in a nursery. Lastly, 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 for each species as a

Table 1

Overview of the selected botanic gardens: the Royal Botanic Gardens, Kew (KEW), Westonbirt, the National Arboretum (WESB), and the Royal Botanic Garden Edinburgh (RBGE).

BG	Latitude	Longitude	City	MAT °C	MAP mm	Soil texture
KEW	51.4813	-0.29276	London	10.7	661	Sandy loam
WESB	51.6065	-2.21947	Westonbirt	10.0	931	Silt clay loam
RBGE	55.9666	-3.21092	Edinburgh	9.5	818	Sandy loam

Box 1

A list of abbreviations used.

Features		Definition
SPEI	SPEI _{growing}	The sum of monthly SPEI during the growing season (April to October) of the year
	SPEI _{5yr}	The sum of SPEI _{growing} from the current year <i>j</i> to <i>j</i> -4
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

response to climate stress in a specified time interval following as in (1),

$$\mu_0 = D_t/R_t \tag{1}$$

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. The overall tree mortality data is summarized in Table 2.

2.4. Selections of climate anomalies

Drought and heatwaves 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 monthly climatic water balance information (Vicente-Serrano et al., 2010) as in the Eq. (2).

$$D_i = P_i - PET_i \tag{2}$$

The difference (D) between precipitation, P at month *i* and potential evapotranspiration, PET_i is accumulated over a specified time scale and standardized to represent deviations from the mean values. In this research, we used the sum of monthly SPEI during the growing season (April to October), $SPEI_{growing}$ and the sum of SPEI for the previous 5 years including 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 °C (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 °C, 27 °C for the WESB, and 25 °C for the RBGE.

All daily meteorological data, including minimum, maximum, mean air temperature, and precipitation, was acquired from the CEDA Archive (Met Office, 2019) 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.

2.5. Statistical analysis

We conducted the mortality analysis at both genus and species-level. To associate climate anomalies with annual mortality rates, we considered all individuals within a genus as a base sample size. In this manner, the pure effects of niche positions were calculated by negating the influence of species. For genus-level analysis, 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). In discrete time, it is noted that the hazard function represents the probability of experiencing the event (mortality) in a given interval rather than a rate. The general representation of this hazard function is expressed in (3), (4), and (5),

$$\eta = C^{-1}(\mu) = \alpha + \beta X_{is} \tag{3}$$

$$C(\mu) = \log(-\log(1 - \mu)) \tag{4}$$

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

where the linear predictor η of the covariate *X* of the individual *i* at a

Table 2

Summary of tree mortality data by botanic gardens: the Royal Botanic Gardens, Kew (KEW), Westonbirt, the National Arboretum (WESB), and the Royal Botanic Garden Edinburgh (RBGE).

Genus	Status	KEW	WESB	RBGE
All <i>Acer</i>	Number of live trees (end of 2021, <i>n</i>)	537	1034	1024
	Number of total species (<i>n</i>)	80	94	70
	Number of selected species for NB (<i>n</i>)	22	32	34
	Cumulative dead trees (end of 2021, <i>n</i>)	240	269	414
	Cumulative mortality rate (%)	30.8	20.7	28.8
	Mean annualized mortality rate (%)	2.0	1.3	2.2
All <i>Quercus</i>	Number of live trees (end of 2021, <i>n</i>)	1425	328	385
	Number of total species (<i>n</i>)	104	131	66
	Number of selected species for NB (<i>n</i>)	19	7	13
	Cumulative dead trees (end of 2021, <i>n</i>)	156	100	103
	Cumulative mortality rate (%)	9.9	23.4	21.1
	Mean annualized mortality rate (%)	0.4	1.1	1.4

time period of s , consisting of coefficient β and the intercept α , is the inverse log-log function, also known as complementary log-log (cloglog), of the probability of mortality μ . Here, the exponential of the model coefficients provides an estimate of the hazard ratio where a hazard ratio > 1 indicates an increased risk of the mortality. In this research, the term ‘mortality risk’ will be used interchangeably with ‘hazard ratio’ for clarity within the context. The dataset was converted into a format of ‘person-period data’ table as depicted in Suresh et al. (2022). To answer the research questions, the NB locations of individual

species for the four selected bioclimatic niche variables were used as dichotomous covariates. Additional model selection process is described in the supplementary data (Table S1).

In addition to the annual mortality rates, cumulative mortality rates at species-level during the entire study period were calculated as described in the Eq. (1). We used Kruskal-Wallis test to assess the difference in mean cumulative mortality rates between groups categorized as ‘in’ and ‘out’ of the selected NB, given that the mortality rates represented non-parametric data.

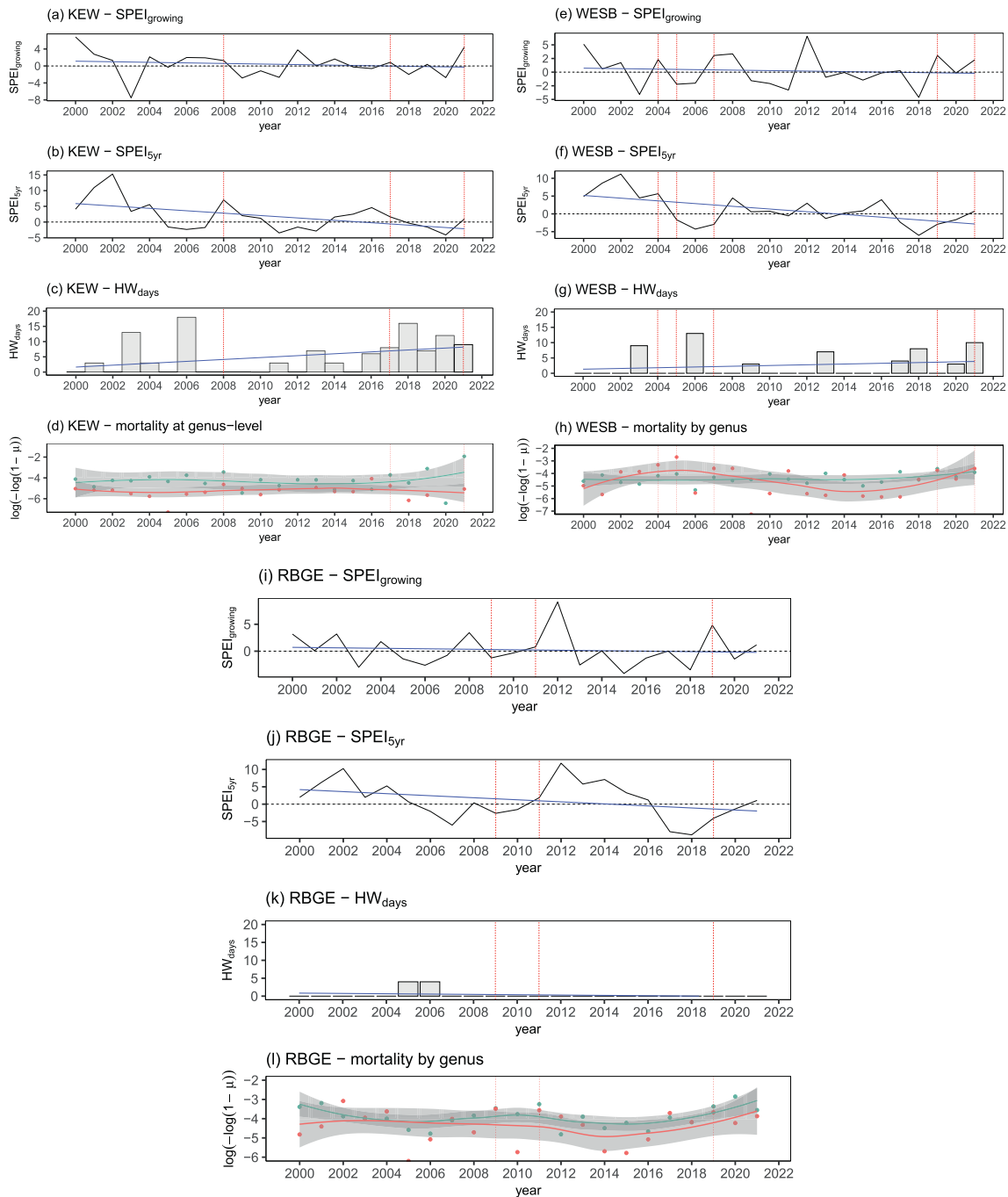


Fig. 1. The climate trend over the period of 2000 to 2021 and regression fit for KEW, (a) $SPEI_{growing}$ (slope=0.07, $p=0.5$) (b) $SPEI_{5yr}$ (slope=-0.38, $p=0.01$) (c) HW_{days} (slope=0.31, $p=0.1$); for WESB © $SPEI_{growing}$ (slope=-0.04, $p=0.66$), (f) $SPEI_{5yr}$ (slope=-0.38, $p=0.004$) (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 at genus-level for *Acer* (green) and *Quercus* (red) over the corresponding period at (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 range of mean over the period.

All analyses were performed using the R statistical language (version 4.1.0; R Core Team, 2021). We used 'jtools' package version 2.2.2 for the summary of hazard model (Long, 2022) and 'effects' package version 4.2-2 for the visualization of models (Fox, 2003).

3. Results

3.1. Mortality in relation to cumulative heat and drought stress

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 mortality of both *Acer* and *Quercus* for all three BGs. The two intervals share common recurring patterns: the co-occurrence of negative SPEI_{growing} and the lowest peak of SPEI_{5yr} in the year preceding a high mortality event. In general, SPEI_{5yr} curve falls to the lowest negative several years after a sharp drop in the SPEI_{growing} curve. For instance, followed by the intense drought in 2003, the SPEI_{5yr} reached the lowest point after three years later in 2006 and 2007 (Fig. 1-b, f, j). When the SPEI_{5yr} reaches its lowest point and coincides with another short-term drought, it creates the period of heightened vulnerability. Nonetheless, the second interval of 2019–2021 shows a slight variation from this pattern. The second interval is particularly notable as all three botanic gardens displayed sharp upward trends in mortality for *Acer*, with KEW exhibiting the most pronounced incline and the least with WESB. The big drop in SPEI_{5yr} in 2018 for RBGE and WESB, and in 2020 for KEW, resulted from a series of repeated droughts from 2013 rather than a single intense drought event. The SPEI_{5yr} for KEW, for instance, 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 contrasts with *Quercus*, for which the increase in mortality was small ($n = 9$) in the same year, 2021.

Nonetheless, this pronounced incline in mortality among *Acer* at KEW compared to the other BGs, can also be attributed to additional heat stress. Notably, KEW experienced heatwaves every year from 2013 for nine consecutive years, with the sole exception of 2015. In contrast, there were no records of heatwaves at RBGE during the same period. However, among the three BGs, RBGE recorded the lowest values for both SPEI_{growing} and SPEI_{5yr} in the preceding year of the second interval. From 2015 to 2018, RBGE experienced repeated intense droughts with the mean SPEI_{growing} of -4.15 , leading to substantial accumulation of drought stress, as indicated by the SPEI_{5yr} of -8.8 in 2018. These values are markedly lower compared to the respective values for WESB (-1.46 and -6.0) and those for KEW (-0.24 and -0.35).

3.2. The effects of niche positions on the mortality risk

Our hypothesis, that postulates higher mortality with species positioned below the lower limits of their respective NB, was more supported from the analysis with *Acer*, and less straightforward for *Quercus*. Among the four selected bioclimatic niche variables, PWQ had the strongest effects on the mortality risk (hazard ratio). Specifically, the risk of mortality for *Acer* species positioned below the lower limits of their respective NB for PWQ, denoted as 'PWQ (out)', is 97 % and 99 % higher compared to those within the NB, at KEW and RBGE, respectively (Table 3). With the best fit model of the reduced number of variables, this risk slightly increases to 105 % and 103 % at KEW and RBGE respectively. This corresponds to a 1.2 % and 1.3 % increase in the predicted probability of annual mortality at any given time interval (Fig. S2 and Fig. S4). Similarly, *Acer* species below the lower limits of CMI, denoted as 'CMI (out)', exhibited increasing mortality risk at WESB. This amounts to a 37 % increase in risk according to the best fit model, which corresponds to a 0.7 % increase in the predicted probability of annual mortality of *Acer* species (Fig. S3). On the other hand, the risk decreases when *Acer* species that are positioned below the lower limits of PET, denoted as 'PET (out)' by 35 % at RBGE (Table 3). This is also translated to a 0.9 % decrease in the predicted annual mortality (Fig. S4). The 'PET (out)' suggests that the species originated from climates with greater evapotranspiration demands, also indicating that the current location, RBGE, is cooler and more humid.

Contrary to *Acer*, the mortality risk of *Quercus* was not significantly affected by species positions of their respective NB. While species NB position of 'PWQ (out)' at KEW showed a strong increase in mortality risk by 368 % (Table 3), this increased risk corresponds to only a 0.6 % increase in the predicted annual mortality (Fig. S5). This is also comparable to the 0.5 % and 0.7 % decrease in the predicted annual mortality with the effect of 'MAP (out)' and 'PET (out)' respectively. Furthermore, it should be noted that the mean annual mortality rate of *Quercus* at KEW is not only five times lower than that of *Acer*, but also the

Table 3

Model estimates of exponentials of coefficients at the genus-level mortality and 95 % confidence interval (CI) of all variables. BGs are abbreviated as follows: the Royal Botanic Gardens, Kew (KEW), Westonbirt, the National Arboretum (WESB), and the Royal Botanic Garden Edinburgh (RBGE). The log scale estimates are exponentiated to yield hazard ratio. Sample sizes (n) are 7471 (*Acer*) and 17,625 (*Quercus*) for KEW; 16,171 (*Acer*) and 4317 (*Quercus*) for RBGE; 8964 (*Acer*) and 4363 (*Quercus*) for WESB. Significance level: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, $p < 0.1$.

		KEW		RBGE		WESB	
		exp(est.)	CI	exp(est.)	CI	exp(est.)	CI
<i>Acer</i>	Intercept	0.02	0.01–0.03	0.02	0.01–0.02	0.02	0.01–0.02
	Year	1.53***	1.30–1.81	1.07	0.97–1.19	1.24**	1.06–1.45
	MAP (out)	0.70	0.44–1.09	1.20	0.83–1.72	0.60	0.22–1.62
	PWQ (out)	1.97**	1.14–3.39	1.99***	1.42–2.77	0.86	0.58–1.27
	CMI (out)	1.14	0.72–1.89	0.90	0.64–1.28	2.23	0.79–6.27
	PET (out)	0.82	0.57–1.18	0.65**	0.45–0.95	1.23	0.87–1.74
<i>Quercus</i>	Intercept	0.01	0.00–0.02	0.01	0.00–0.02	0.02	0.00–0.09
	Year	0.91	0.72–1.13	0.94	0.73–1.22	0.81	0.61–1.06
	MAP (out)	0.18***	0.08–0.41	0.73	0.32–1.65	0.36	0.07–1.89
	PWQ (out)	4.68***	2.29–9.57	1.06	0.52–2.14	0.53	0.13–2.18
	CMI (out)	1.45	0.48–4.37	–	–	–	–
	PET (out)	0.15***	0.07–0.33	2.03*	0.98–4.20	0.76	0.19–3.02

Table 4

Within-species variability in cumulative mortality rates across the BGs for selected *Acer* species. D_t denotes a sum of mortality events during the entire study period out of the R_t , the total individuals at risk. Native range refers to the biogeographical range of species occurrence based on the POWO, Plants of the World Online. Abbreviated BGs are KEW (the Royal Botanic Gardens, Kew), WESB (Westonbirt, the National Arboretum), RBGE (the Royal Botanic Garden Edinburgh). Selected niche variables are MAP (mean annual precipitation), PWQ (precipitation during warmest quarter), CMI (mean monthly climate moisture index), and PET (mean monthly potential evapotranspiration).

Native range	Species	BG	MAP	PWQ	CMI	PET	Mort.	D_t/R_t	
Europe	<i>A. campestre</i>	WESB	In	In	In	In	0.00	0/14	
		RBGE	In	In	In	In	0.00	0/23	
		KEW	In	Out	In	In	0.16	5/30	
	<i>A. platanoides</i>	WESB	In	In	In	In	0.15	3/20	
		RBGE	In	In	In	In	0.14	7/49	
		KEW	In	Out	In	In	0.25	5/20	
	<i>A. pseudoplatanus</i>	WESB	In	In	In	In	0.23	7/31	
		RBGE	In	In	In	In	0.22	10/45	
		KEW	Out	Out	In	In	0.20	2/10	
	North America	<i>A. pensylvanicum</i>	WESB	In	Out	In	In	0.41	5/12
			RBGE	Out	Out	In	Out	0.52	12/23
			KEW	Out	Out	Out	Out	0.71	5/7
<i>A. negundo</i>		WESB	In	In	In	In	0.06	1/18	
		RBGE	In	In	In	In	0.86	6/7	
		KEW	In	In	In	In	0.58	7/12	
<i>A. rubrum</i>		WESB	In	Out	In	In	0.12	3/25	
		RBGE	Out	Out	In	Out	0.22	2/9	
		KEW	Out	Out	In	Out	0.44	7/16	
<i>A. saccharum</i>		WESB	In	Out	In	In	0.25	5/20	
		RBGE	Out	Out	In	Out	0.27	3/11	
<i>A. sacharinum</i>		KEW	Out	Out	In	Out	0.36	5/14	
<i>A. spicatum</i>		WESB	In	Out	In	In	0.78	7/9	
		RBGE	In	Out	In	Out	0.21	3/14	
Asia		<i>A. buergerianum</i>	WESB	In	Out	In	Out	0.16	2/12
			KEW	Out	Out	In	Out	0.00	0/7
			WESB	In	In	In	Out	0.14	7/50
		<i>A. cappadocicum</i>	RBGE	In	In	In	Out	0.16	5/31
	KEW		In	In	In	Out	0.09	2/23	
	WESB		Out	Out	Out	Out	0.60	6/10	
	<i>A. crataegifolium</i>	RBGE	Out	Out	Out	Out	0.75	18/24	
		KEW	Out	Out	Out	Out	0.57	5/7	
		WESB	In	Out	In	Out	0.41	16/39	
	<i>A. davidii</i>	RBGE	In	Out	In	Out	0.45	25/56	
		KEW	In	Out	In	Out	0.54	43/79	
		RBGE	In	In	In	Out	0.00	0/17	
	<i>A. heldreichii</i>	KEW	Out	In	In	Out	0.00	0/8	
		WESB	Out	Out	Out	In	0.27	2/16	
		RBGE	Out	Out	Out	Out	0.13	6/22	
	<i>A. japonicum</i>	KEW	Out	Out	Out	Out	0.00	0/13	
		WESB	In	Out	In	In	0.05	1/22	
		RBGE	In	Out	In	Out	0.24	12/51	
	<i>A. pictum</i>	KEW	Out	Out	Out	Out	0.27	6/22	
		WESB	Out	Out	Out	Out	0.39	37/95	
		RBGE	Out	Out	Out	Out	0.30	33/110	
	<i>A. palmatum</i>	KEW	Out	Out	Out	Out	0.13	22/173	
		WESB	In	Out	In	Out	0.00	0/16	
		RBGE	In	Out	In	Out	0.26	6/23	
	<i>A. stachyophyllum</i>	KEW	Out	Out	In	Out	0.30	3/10	
		WESB	In	In	In	In	0.13	2/15	
		RBGE	In	In	In	In	0.29	13/45	
<i>A. tataricum</i>	KEW	In	Out	In	In	0.66	19/29		

lowest when compared to the rates at the other two botanic gardens (Table 2). Overall, *Quercus* exhibited a slight but non-significant decrease in annual mortality risk, denoted as ‘year’, of <1 across all three sites, indicating more resilience in response to accumulated climatic stress. This is in contrast to *Acer*, which showed an increasing ratio of >1 in the order of KEW (53 %, $p < 0.001$) > WESB (24 %, $p < 0.01$) > RBGE (7 %, $p = 0.18$) (Table 3).

3.3. Variations in cumulative mortality rates at species-level

Cumulative mortality rates at species-level were compared to find if there are any observable patterns of vulnerability to mortality in relation to species-specific niche positions. In line with our hypothesis, cumulative mortality rates, pooled across all BGs, were mostly low (<0.2) for *Acer* species that remained safely within all their respective NBs, with a

few exceptions (Table 4). In addition, as species slipped below the lower limits of two or more NBs, we observed an increase in mean cumulative mortality rates; specifically, *Acer* species below the lower limits of the single NB, PWQ, had a mean rate of 0.27 ($n = 57$, $p < 0.05$), those below the lower limits of both PWQ and MAP had a mean rate of 0.3 ($n = 37$, $p = 0.07$), and those below the lower limits of all PWQ, MAP, and CMI exhibited a mean rate of 0.32 ($n = 24$, $p = 0.1$). The lowest mean cumulative mortality rate for *Acer* is 0.59 ($n = 2$) when species position below the lower limits of all PWQ, MAP, and CMI, but remain within the NB of PET (Table S2). Contrary to *Acer* species, *Quercus* species did not exhibit any significant difference in mean mortality according to their niche positions.

The distribution of mortality rates across species is quite dispersed, indicating substantial species-specific differences (Fig. 2). While mortality rates within each species vary in a similar range, these variations

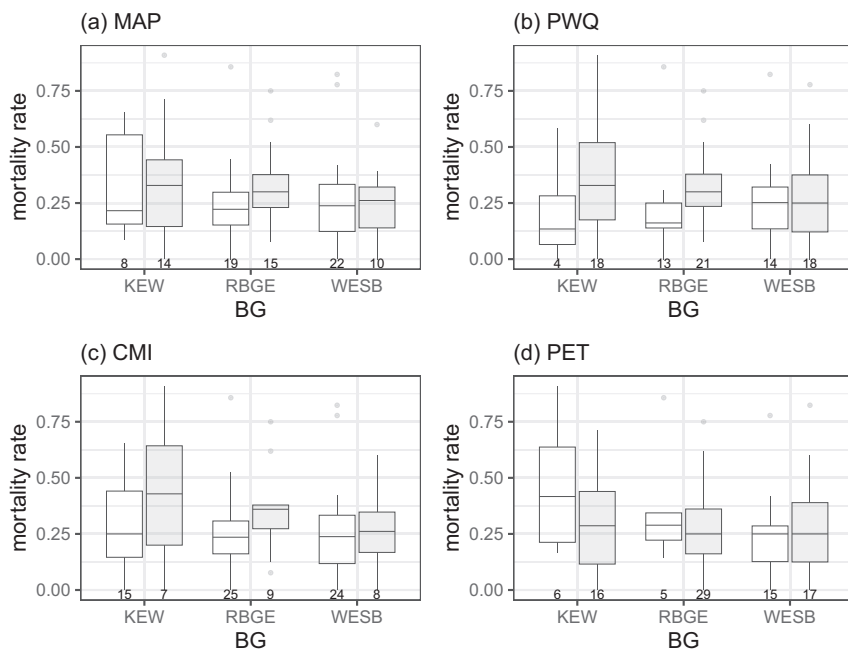


Fig. 2. The distribution of the cumulative mortality rates at species-level for *Acer* by its niche position of their respective NBs. The difference in mean between the “in” (white) and “out” (grey) positions for each bioclimatic niche variable (a) MAP ($p = 0.19$), (b) PWQ ($p < 0.05$), (c) CMI ($p = 1.0$), and (d) PET ($p = 0.65$) was tested using Kruskal-Wallis test (see also Fig. S11). However, when the same test was performed within each BG group, no significant difference was found except for PWQ at RBGE.

often correspond to geographical locations, represented here by BGs. Many *Acer* species exhibit slightly higher mortality rate in the order of KEW > RBGE > WESB (Table 4). This increasing order of mortality rates within species often accompanies a change in niche position from ‘in’ to ‘out’. For instance, cumulative mortality rate of *A. pictum* is 5 % at WESB where its niche position is below the lower limits of the single NB, PWQ.

However, this rate escalates to 27 % at KEW where its niche position shifts to fall below the lower limits of all three variables: PWQ, MAP, and CMI. In contrast to *Acer*, *Quercus* species exhibit the opposite trend: regardless of species niche positions, cumulative mortality rates within species tend to be lowest at KEW (Table 5).

Table 5

Within-species variability in cumulative mortality rates across the BGs of selected *Quercus* species. D_t denotes a sum of mortality events during the entire study period out of the R_t , the total individuals at risk. a, b, and c denote median years since their initial planting (accessioned year): 5 (a), 6 (b), and 11 (c) years, indicating that they were mostly young trees. Native range refers to the biogeographical range of species occurrence based on the POWO, Plants of the World Online. Abbreviated BGs are KEW (the Royal Botanic Gardens, Kew), WESB (Westonbirt, the National Arboretum), RBGE (the Royal Botanic Garden Edinburgh). Selected niche variables are MAP (mean annual precipitation), PWQ (precipitation during warmest quarter), CMI (mean monthly climate moisture index), and PET (mean monthly potential evapotranspiration).

Native range	Species	BG	MAP	PWQ	CMI	PET	Mort.	D_t/R_t
Europe	<i>Q. canariensis</i>	KEW	Out	In	In	Out	0.07	1/15
		RBGE	In	In	In	Out	0.00	0/8
	<i>Q. cerris</i>	KEW	Out	In	In	Out	0.01	1/73
		RBGE	In	In	In	Out	0.00	0/18
	<i>Q. faginea</i>	KEW	In	In	In	Out	0.08	1/13
		WESB	In	In	In	Out	0.08	1/13
	<i>Q. ilex</i>	RBGE	In	In	In	Out	0.07	1/14
		KEW	In	In	In	Out	0.05	8/164
		RBGE	In	In	In	Out	0.21	3/14
	<i>Q. pubescens</i>	KEW	Out	In	In	Out	0.00	0/10
		WESB	In	In	In	In	0.18	30/165
	<i>Q. robur</i>	RBGE	In	In	In	In	0.12	10/81
		KEW	In	Out	In	In	0.07	25/353
		WESB	In	In	In	In	0.31 ^a	4/13
		RBGE	In	In	In	Out	0.19	4/21
<i>Q. petraea</i>	KEW	In	Out	In	In	0.12	3/26	
	KEW	In	In	In	Out	0.05	1/19	
	WESB	In	In	In	Out	0.11	1/9	
North America	<i>Q. agrifolia</i>	KEW	In	In	In	Out	0.00	0/14
		WESB	In	Out	In	In	0.14	1/7
	<i>Q. rubra</i>	RBGE	Out	Out	In	Out	0.20	4/20
Asia	<i>Q. mongolica</i>	KEW	Out	Out	In	Out	0.07	5/68
		WESB	In	Out	In	In	0.11	1/9
		RBGE	In	Out	In	Out	0.24 ^b	11/45
	<i>Q. glauca</i>	KEW	In	Out	In	Out	0.36 ^c	8/22
		RBGE	Out	Out	In	Out	0.41 ^c	5/12
		KEW	Out	Out	Out	Out	0.17	1/6
	<i>Q. serrata</i>	RBGE	Out	Out	In	Out	0.15	3/20
		KEW	Out	Out	Out	Out	0.08	1/13

4. Discussion

4.1. Cumulative drought as inciting factor, heatwaves as contributing factor to mortality

As a general assumption, mortality of trees is understood as the result of the interplay between a series of sequential and simultaneous factors. This concept is well summarized in Manion's tree decline hypothesis, which classifies these factors into 'predisposing', 'inciting', and 'contributing' categories (Manion, 1981). Under this hypothesis, trees can usually withstand a single stress factor. It is the combination of predisposing factors that drive trees vulnerable, an inciting factor causing significant stress, and contributing factors that exploit its weakened state that results in tree decline and eventually mortality. Our research results also indicate that cumulative drought stress from repeated droughts has served as the inciting factor, with heatwaves acting as the contributing factor. While the extent of these factors' influence varied among species, *Acer*, in general, proved to be more susceptible.

While the increase in annual mortality rates among the three BGs was not homogenous, two periods, 2007–2009 and 2019–2021, were identified as common intervals for heightened vulnerability to mortality (Fig. 1). This interval of the increased mortality is attributed to a time lag of one year or more following the co-occurring year of the growing season water deficit and the highest cumulative drought stress. This delayed mortality relative to changes in water balance is also consistent with other studies of long-term drought-induced mortality in forests (Gu et al., 2015), underscoring the significant role drought play in increasing tree mortality in this study. Upon comparing the two intervals, we found the extent of accumulated droughts, represented by SPEI_{5yr}, is more intense in the second interval than in the first, which led to higher mortality towards 2021. Also, Nonetheless, KEW and RBGE exhibit contrasting characteristics in accumulation of drought stress. At KEW, the first interval came in the wake of the intense drought in 2003 while the second interval followed a series of moderate droughts. In addition to drought stress, repeated heatwaves from 2011 onwards have intensified the climatic stress at KEW, contributing to a steep increase in mortality among *Acer* species during the second interval. On the other hand, at RBGE, the second interval succeeded a series of more intense droughts than the one in 2003. Therefore, among the three BGs, RBGE experienced the highest level of cumulative drought stress, leading to increased vulnerability to mortality even in the absence of heatwaves. Interestingly, despite the markedly higher cumulative drought intensity at RBGE, the impact on annual mortality rate of *Acer* is more pronounced at KEW. Specifically, over a 10-year period between 2010 and 2021, and with all the other niche positions fixed at "in", the conditional probability of annual mortality for *Acer* is estimated to increase by 2.0 % ($p < 0.001$) at KEW but only by 0.3 % ($p > 0.05$) at RBGE (Figs. S2 and S3).

When comparing two cases from KEW and RBGE, it is evident that *Acer* species are more vulnerable to heat stress, especially when they are already in a weakened state due to prolonged exposure to moderately dry conditions. While *Acer* species are both early and late successional species, species such as *A. pensylvanicum* or *A. spicatum* from eastern North America and *A. crataegifolium* from East Asia are particularly shade-adapted understory species (Ackerly and Donoghue, 1998; Lei and Lechowicz, 1990). When these species are open-grown, as is typical in BGs, and exposed to full-sun, their leaves - characterized by broader and thinner forms adapted to shades - are more likely to incur damage, leading to a reduced photosynthetic capacity (Teskey et al., 2015). This reduction could reach a critical threshold of carbon starvation, a mechanism that drives mortality for isohydric *Acer* species (McDowell et al., 2008), if the species are already dealing with reduced growth as a response to previous droughts (Leifsson et al., 2023; Morecroft et al., 2008; Mu et al., 2022). The high cumulative mortality rates observed in these species, *A. crataegifolium* (0.57, KEW), *A. pensylvanicum* (0.71, KEW), and *A. spicatum* (0.78, WESB), can be explained in this frame

(Table 4). A recent study also reveals that shade-tolerant species, in particular, are more susceptible to frequent, low-intensity droughts in mesic sites (Sánchez-Pinillos et al., 2022). In addition, even canopy species such as *A. saccharum* are prone to high temperature, exhibiting 40 % of leaf mortality in the upper canopy during spring heatwaves (Filewod and Thomas, 2014).

On the other hand, the increase in mortality of *Quercus* was not as pronounced as that of *Acer* in the second interval. Although certain *Quercus* species, *Q. velutina* and *Q. alba*, have shown higher vulnerability to drought-induced mortality and embolism compared to *Acer* (Benson et al., 2022; Gu et al., 2015), our finding corroborates the prevailing understanding that *Quercus* species are drought tolerant species, attributable in part to their deep root systems and highly efficient hydraulic architecture (Cavender-Bares, 2019; Matheny et al., 2017). They have also been observed to exhibit reduction in growth during the post-drought period (Corcuera et al., 2004; Jenkins and Pallardy, 1995; Scharnweber et al., 2011). However, *Quercus* species demonstrated a faster post-drought growth recovery (Bose et al., 2021) and maintain a higher long-term growth rate in the warmer and drier climate than those in the temperate climate (Perkins et al., 2018). Moreover, species such as *Q. suber*, *Q. canariensis*, and *Q. macrocarpa* exhibited greater tolerance under heat stress, with a critical threshold temperature of >42 °C (Ghouil et al., 2003; Hamerlynck and Knapp, 1994).

4.2. A niche perspective on mortality of *Acer*

Our hazard model reveals that, among the selected bioclimatic niche variables, the niche position of PWQ had significant influence on mortality of *Acer* at KEW and RBGE. This is particularly related to the species compositions, in which many *Acer* species originated from cool temperate forests of Asia (Fig. S6), where seasonal precipitation is primarily influenced by monsoons. The typical PWQ of these species is normally between 400 mm and 800 mm, whereas in the UK, it is only at or below 200 mm (Fig. S7). While PWQ and MAP are positively correlating variables ($r = 0.76$, data not shown), MAP is less discerning than PWQ, as it could potentially misrepresent seasonal humidity and its tolerance limit, specifically during the period of growing season drought.

Nonetheless, the position of a single niche position did not successfully represent the individual species' mortality response. Instead, the combinations of the four niche positions were more informative in elucidating the mortality patterns (Table 4). Given that this study only assessed four selected bioclimatic variables and classified niche position in a simplified binary format, two species of the same niche positions do not necessarily exhibit similar mortality responses. Moreover, some counter-intuitive cases were observed such as in *A. negundo*, which exhibited higher mortality despite its niche positions being within the NBs, or *A. buergerianum*, which exhibited low mortality even when its niche positions are below the lower limits.

Such cases indicate that there may be latent niche variables, which might exert a more significant influence but were not selected in this research. For instance, *A. campestre* and *A. tataricum* are naturally co-occurring in the shrub layer of broadleaved forests in central to eastern Europe, while biogeographical range of *A. tataricum* stretches as far as east Asia (Kabaš et al., 2014). Despite the significant overlap in their distributions and identical niche positions across BGs, *A. tataricum* is notable for its higher cumulative mortality rates (Table 4). One study (Kabaš et al., 2014) finds that the limiting factors for distribution of *A. tataricum* slightly diverge from those of *A. campestre*, with more emphasis on the temperature during the dry season. Additionally, *A. campestre* is observed to exhibit rapid growth and expand canopy coverage quickly in declining oak stands, whereas *A. tataricum* does not demonstrate a significant increase in growth rates (Misik and Kárász, 2020). This is further supported by a field experiment conducted in an urban garden, where *A. campestre* exhibited more stable growth during a summer drought than *A. tartaricum* (Oravec et al., 2023). These

observations hint potential differences in sensitivity towards light exposure, temperature, and water availability between *A. tataricum* and *A. campestre*, which may have contributed to their differential mortality rates.

Another potential explanation for these discrepancies in mortality rates could relate to the strength of the relationship between NB and range size. According to the NB-range size hypothesis (Brown, 1984), there is a positive correlation between NB and geographical range size. In other words, the more geographically widespread a species is, the more likely it is to be tolerant in a broad array of climatic conditions, consequently exhibiting a wider NB (Slatyer et al., 2013). These species with a wider NB are known to exhibit higher phenotypic plasticity or ecotypic differentiation, which enable them to thrive in contrasting environmental conditions (Ackerly, 2003; Fajardo and Piper, 2021). 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 range size (supplementary data). Although its niche position falls below the thresholds of both NBs of MAP and PWQ, it exhibits the mortality rate (<0.2) considerably lower than those of species with identical niche positions such as *A. rubrum*, *A. sacharinum*, or *A. saccharum* (Table 4 and Fig. S7). Moreover, *A. buergerianum* is observed to focus on leaf-level osmotic control during the drought, adjusting its leaf size and thickness rather than actively reducing transpiration by leaf shedding (Oravec et al., 2023). Such a strategy enables continuous growth and helps to maintain its hydration status under drought. It is further reinforced by specific plant traits, such as glossy leaves with cuticular wax (BGCI, 2023), which helps protect the leaves from water loss under drought and maintain temperature from heat stress (Riederer and Schreiber, 2001). On the other hand, species with narrow NB are often considered less flexible in dynamic conditions but are specialists, adapted to specific geographic environments, exhibiting strong tolerance to selective 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 (data not shown).

Lastly, site characteristics should not be overlooked when examining the relationship between the NB and mortality rates of *Acer* species. Additional latent niche variables beyond bioclimatic variables, possibly related to soil characteristics, could augment the effects of the climatic conditions within the BGs. This could particularly be the case when species with identical niche positions across the three BGs exhibit contrasting response. 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 300 mm more rainfall annually and relatively more fertile soils that exhibit a greater water holding capacity, WESB has provided a more favorable environment, mitigating effects of drought, for species originating from moist regions without additional irrigation. This is evidenced with species such as *A. capillipes* (0.0), *A. carpiniifolium* (0.0), *A. caudatifolium* (0.13), *A. rubrum* (0.12), and *A. negundo* (0.05), the ones from CT-moist to WT-wet, which exhibited very low mortality rates at WESB compared to the mortality rates of the same species at the other two sites, ranging from 0.22 to 0.86. Specifically, *A. negundo* is known to be distributed over a wide range of climatic conditions and is drought tolerant (Overton, 1990). Despite its niche positions falling within the NB across the three BGs, its mortality rates are substantially higher at KEW and RBGE. The contrasting response could be attributed to the highly adaptable root development of *A. negundo* in different soil types. For instance, it is observed to be deep-rooted with abundant fine roots in clay soil, which is contrasted with shallow, lateral root development in alluvial soil (Biswell, 1935). Such rooting behavior, coupled with highly responsive stomatal conductance control (Ranney et al., 1990), might be more advantageous for *A. negundo* in coping with droughts in the clay soil of WESB, compared to sandy soil, where soil water deficit may be

exacerbated due to interactions with high temperatures.

4.3. A niche perspective on mortality of *Quercus*

Unlike *Acer*, *Quercus* did not demonstrate a statistically significant response to its niche positions of any of the selected NBs except at KEW (Table 3). The results largely relied on its species composition which was dominantly selected from warm temperate regions (Fig. S6). Moreover, the number of species represented in *Quercus* was only half of those in *Acer*. In WESB, 67 % of the 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 thus, were 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 European native species, *Q. ilex*, *Q. petraea*, and *Q. robur* exhibited a similar range of mortality rates across the three BGs with 0.06–0.07, 0.12–0.19, and 0.07–0.18 respectively (Table 5). 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 among young trees are not a distinct characteristic of *Quercus* alone. An even higher proportion in young deaths was observed in *Acer* (Fig. S13). However, the high visibility of mortality among young *Quercus* (<15 years) is contrasted with its low mortality rate once they are established with an overall mortality rate of <0.2.

Mediterranean oaks, such as *Q. cerris*, *Q. ilex*, and *Q. suber*, exhibit particularly low mortality of <0.1 (Table 5), which aligns with findings from other studies (Móricz et al., 2013; Thurm et al., 2018). This data further corroborates the predictions by Hanewinkel et al. (2013) that 34 % of Europe would become suitable for Mediterranean oaks by the end of 21st century. Not only do these species safely position within their respective NBs, but their narrow NBs indicate that they are specialists, adapted to warm and dry conditions. For instance, fast growing *Q. cerris* exhibited higher post-drought recovery which enables maintaining higher long-term growth rates compared to coexisting *Q. petraea*, which display relatively suppressed growths after a severe drought (Mészáros et al., 2022).

On the other hand, having niche positions below the lower limits of all three NBs of MAP, PWQ, and CMI did not significantly influence the increase of mortality rates. Such species, which include *Q. acutissima*, *Q. glauca*, *Q. phillyreoides*, and *Q. serrata*, exhibited mortality rates of 0, 0.17, 0.24, and 0.08 respectively. This stands in contrast with those *Acer* species with the same niche position, which exhibited the mean mortality rate of 0.32, and with certain species such as *A. ukurunduense* reaching as high as 0.9. This contrasting response in mortality between the *Acer* and the *Quercus* is particularly intriguing, as these two genera often co-occur in natural habitats, sharing common climatic conditions. Hence, it is evident that these two genera differentiated their niche with their distinctive adaptive strategy in order to co-exist. Essential resources, such as light and water, are effectively partitioned between co-existing *Acer* and *Quercus* species. General observations indicate that *Acer* species have evolved to tolerate shades and develop shallow lateral roots, whereas *Quercus* species have adapted to achieve competitive canopy height accompanied by a deep root system (Abrams, 1990; Ackerly and Donoghue, 1998; Cavender-Bares, 2019; Fallon and Cavender-Bares, 2018). For instance, deep rooting allows *Quercus* species to access the lower soil zone and water table during drought, thereby maintaining stable transpiration or delaying reduction in growth (Bréda et al., 1995; Matheny et al., 2017). In fact, *Quercus* species have displayed the lowest response to climate change in terms of growth compared to other tree species, with some even exhibiting increased growth in central to Northern Europe (Vacek et al., 2023). Further implications can be learned through investigation of the plant functional traits that underpin their adaptive strategy. Nonetheless, this contrasting mortality response may indicate that the minimum threshold of the selected NBs for *Quercus* species could potentially be

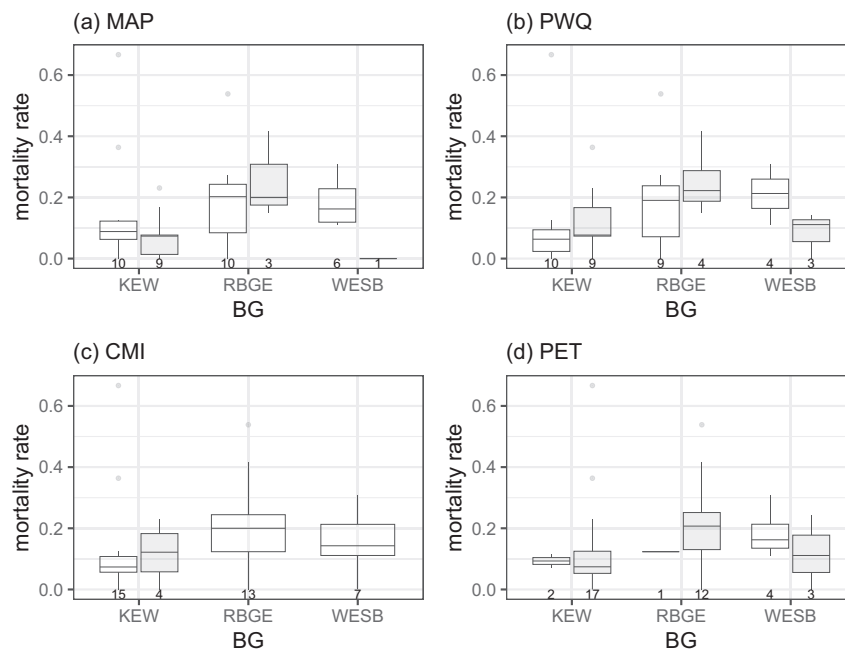


Fig. 3. The distribution of the cumulative mortality rates at species-level for *Quercus* by its niche position of their respective NBs. None of the bioclimatic niche variables exhibited significant difference in the mean between the “in” (white) and “out” (grey) positions with Kruskal-Wallis test (see also Fig. S12).

lower than what appears to be solely based on their natural distribution records. Lastly, it should be noted that the mean mortality rates across all *Quercus* (Fig. 3) and the mortality rate within species (Table 5) are lowest at KEW. This result also contrasts with the finding observed in *Acer* species. Given that Mediterranean oaks are particularly known for deep rooting, and roots generally penetrate sandy soil better than clay soil, KEW may have provided more favorable conditions for those *Quercus* from WT (Canadell et al., 1996). While RBGE is also sandy-loam soil, it sometimes experiences severe winter frosts which could be detrimental to certain species from WT. It is noted that there have been some instances of frost damage exclusively in RBGE. Although these identified cases were excluded from the analysis, it is plausible that a severe winter may have acted as a contributing factor in interactions with other stressors such as drought. Another site-specific event was observed during the severe drought of 2003 and the subsequent two years at the WESB, where an unprecedented number of seventeen mature *Q. robur* (>25 years) succumbed (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 Chronic Oak Decline (COD) symptoms. This symptom is among the most complex diseases involving multiple biotic and abiotic factors but is particularly associated with water stress (Camilo-Alves et al., 2017). It is slowly advancing over decades with progressive deterioration in tree crown conditions preceded by reduced growth rates (Gagen et al., 2019). Although it was not clearly identified as COD from WESB, some of the mortality events could be reasonably associated with COD based on the descriptions of death – continual suppressed growths – and its recent widespread occurrence, particularly in *Q. robur*, in South England over the past decades (Denman and Webber, 2009). Nonetheless, no similar dramatic increase in deaths of *Q. robur* was observed at the WESB following the drought in 2018.

4.4. Limitations and future research directions

The mortality dataset used in this research is unique and exceptional in terms of species diversity, providing insights that are distinct from those typically gathered from street trees or forestry inventories. Despite its unique value, we acknowledge that this dataset, like any, has its own

limitations which present opportunities for further refinement and exploration in future research.

First, an inherent concern with tree inventory data is the potential temporal gap between the actual death event and the record in the survey (Fortin et al., 2008). This gap can arise due to the intricate nature of tree death, which lacks clear definition and is often subjective (Anderegg et al., 2012; Meir et al., 2015), hinging on human observation and interpretation. While the determination of death is based on the observation of leaf defoliation, typically 90 %, during the growing season, it is plausible that some trees might have been preemptively removed by horticultural decision, especially if they are in poor health conditions, to prevent the spread of diseases. We attempted to minimize this discrepancy by excluding those specifically identified as ‘early removal of poor specimen’ at the data filtering stage as described in Section 2.3. On the other hand, we did not remove records of death caused by pathogens, as we interpreted these cases as results of weakened immunity due to stress from increased temperature or drought. Another plausible factor that can influence the gap between the time of actual death and the time it is recorded is the internal survey guidelines and practices within the institution. For instance, while WESB conducts comprehensive annual surveys of all its inventories in July, KEW and RBGE conduct stocktakes on a rolling basis. It means that certain mortality records in KEW and RBGE could reflect a delay of 1 or 2 years from the actual time of death event. In this context, it might be prudent to consider this discrepancy in interpreting the results of annual trend analysis at the genus-level (Fig. 1). However, it should not significantly impact our species-level analysis as we accumulated species-specific mortality data based on the entire 21-year period.

Secondly, the given that trees in botanic gardens are curated for public display, the influence of human intervention should be considered in the interpretation of the analysis. However, the extent of the intervention varies by botanic garden. In WESB, once trees are planted in the arboretum, no additional irrigation support is provided. Similarly, in KEW and RBGE, mature tree collections in the arboretums are not normally irrigated, but trees located in the herbaceous or shrub beds may benefit from irrigation in the event of significant drought conditions. This decision regarding irrigation largely depends on the discretion of horticulturalists. It is also noted that KEW pays particular attention to

saplings in the first five years, which are regularly irrigated to support their establishment. Despite these inconsistencies across the BGs, we noted that within individual species, general patterns and similarities in mortality were still observed. Furthermore, our analysis incorporates mortality data in the post-pandemic year of 2021, which offers a glimpse of the true impact of accumulated drought and heatwaves. The noticeable increase in mortality among *Acer* species could potentially be linked to the reduced maintenance activities during the COVID lockdown in 2020. For instance, 50 % of the total number of death events (5 out of 10) for *A. ukurunduense* at KEW occurred solely in the year of 2021. The species recorded the highest cumulative mortality rate of 0.9 even though these were not saplings, having been established for over 20 years.

Despite certain limitations, our research highlights ongoing needs for future research, aiming to narrow the gap between our theoretical understanding of the modeled niche and the realities of how these niches manifest in urban environment. In doing so, we underscore the critical role of urban botanic gardens and their underutilized inventory data (Hirons et al., 2021). While the conditions of urban botanic gardens may not fully encapsulate the heterogeneity of all urban environments, they provide useful reference for understanding and planning urban forests and public greenspaces. Moreover, their highly diverse living collections can serve as a vital testing ground for assessing suitability of new candidate species for future climate conditions, before their introduction in larger scale urban planting initiative. However, urban botanic gardens are also challenged to enhance their inventory database system to support more complex research programs. Among these enhancements include the systematic collection of data beyond conventional stock-taking and the acquisition and management of more comprehensive biological and ecological information. This expanded resource base would also enable dynamic experiments ranging from tolerance limits to divergent optima of ecological fitness at multiple biological scales, such as genetic-level or population-level NBs, thereby improving the precision of niche-based assessments.

5. Conclusions

The NB is a well-established concept, often used as a proxy for the species' tolerance to certain environmental conditions. However, directly relating NBs with tree mortality, especially in the dual context of climate change and urban settings, can be more complex than it appears, necessitating a multitude of considerations. Tree mortality fundamentally involves an individual organism's physiological responses, encompassing a process influenced by a myriad of external factors and unfolding over various timescales. As such, the NB represented by coarse-scale bioclimatic variables may not accurately capture the impacts on individual trees from extreme episodic events such as drought or heatwaves over shorter periods. Nonetheless, when these individual mortality responses within population accumulate over time and exhibit consistent patterns within similar range of environmental conditions, it lends more confidence to identifying them as an indicator of ecological fitness of certain species at a chosen point or range along the environmental gradient.

As the mild Oceanic climate in the UK experiences climatic shift towards warmer and drier summers with an increased frequency of droughts and heatwaves, urban habitats once suitable for hosting diverse plant collections beyond their natural distributions, such as those from temperate forest of East Asia or Northeast America, have become increasingly subjected to vulnerabilities in recent decades. This change was particularly prominent among *Acer* species, whereas *Quercus* species have displayed comparatively higher resilience. Moreover, Mediterranean oaks are outperforming native oaks such as *Q. robur* and *Q. petraea* in the Southern UK. In comparing *Acer* and *Quercus*, we observed overarching patterns within the genus. However, notable interspecies variations were also evident in relation to selected niche variables. It highlights that species-specific selection of niche variables is

crucial for a more nuanced understanding of their vulnerabilities to mortality, rather than uniformly assessing species against preselected niche variables. This underlies the need to tailor our analysis methods, incorporating ecological performance and the unique niche characteristics of each species, to predict their response to changing environmental conditions more accurately than solely based on occurrence data.

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CRedit authorship contribution statement

Eun Hye Kim: methodology, formal analysis, writing – original draft, visualization

James Hitchmough: conceptualization, supervision, review & editing

Ross Cameron: conceptualization, supervision, critical review

Franziska Schrodt: methodology, review & editing

Kevin Martin: data curation, critical review

Robert Cubey: data curation, critical review

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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