Applying niche theories to the evaluation of urban trees:

A tripartite approach on niche breadth, species distribution models, and water use strategy

by

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Declaration

I, the author, confirm that the Thesis is my own work. I am aware of the University's Guidance on the Use of Unfair Means (www.sheffield.ac.uk/ssid/unfair-means). This work has not previously been presented for an award at this, or any other, university.

The work in Chapter 3 of the thesis has appeared in the following published article:

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Chapter 4 has been submitted but is not yet accepted. Major methods and research framework remain unchanged, but much of introduction, data formats/presentation and discussion are subject to change according to reviewers' feedback.

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To my lovely nephews
Juwon and Jumin Kim

사랑하는 주원, 주민이에게

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Abstract

The escalating uncertainty associated with climate change, coupled with increased demands in multi-functional ecosystem services, presents a bi-fold challenge in today's urban tree management. To address these challenges, integrating an interdisciplinary and science-based approach into conventional landscape practice is essential. In line with this effort, the thesis explores three perspectives rooted in the ecological theory focusing on the concept of niche, central to explaining biogeographic distributions of species. Each perspective introduces distinct ecological niche aspects: (1) bioclimatic niche breadths, (2) biogeographic distributions that integrate both climate and terrestrial components, and (3) biological interactions within the given geo-ecological and climatic conditions. The first two approaches employ macro environmental factors based on species native distributions while the third approach specifically compares species water use with sap flow measurements. The assessed values based on niche breadths and species distribution models were then juxtaposed with the actual mortality rates of selected *Acer* and *Quercus* species across the three major botanic gardens of the UK, areas predominantly beyond their native range. Considering that the UK has experienced more frequent droughts and heatwave stress in recent decades, analysing the mortality rates specifically during the period of 2000-2021 offered a significant opportunity to test species-specific tolerance. As a result, most ex-situ *Acer* species demonstrated relatively high mortality rates according to their respective niche positions below their lower limits while *Quercus* species in general showed relatively greater resilience regardless of their niche positions. However, there are some species that showed high adaptability counterintuitively beyond their native range. Interestingly, some species that are phylogenetically closer consistently exhibited more similar mortality rates than those species that are environmentally more similar. The finding indicates the presence of inherited phenotypes or genotypes that confer resilience to specific stress. This speculation is further supported by the last analysis, demonstrating how distinct physiological traits respond and interact differently under the identical environmental stress.

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Acronyms and abbreviations

ANN	Artificial Neural Network
AUC	Receiver operating characteristic curve
BG	Botanic garden
BT	Boreal temperate
CART	Classification And Regression Tree
CEM	Climate envelope model
CHELSA	Climatologies at High resolution for the Earth's Land Surface Areas
CMI	Climate moisture index
CT	Cool temperate
ENM	Ecological niche model
ENFA	Ecological-Niche Factor Analysis
ES	Ecosystem service
EVI	Enhanced vegetation index
GAM	Generalised additive model
GARP	Genetic Algorithm for Rule-set Predictions
GBIF	Global Biodiversity Information Facility
GLM	Generalised linear model
FN	Fundamental niche
HS	Habitat suitability
HW	Heatwave
IPNI	International Plant Names Index
KEW	Royal Botanic Gardens, Kew
LES	Leaf economic spectrum
MAP	Mean annual precipitation
MARS	Multivariate adaptive regression splines
MaxEnt	Maximum Entropy model
MODIS	Moderate Resolution Imaging Spectroradiometer
NB	Niche breadth
NC	Niche conservatism
PET	Potential evapotranspiration
PDF	Probability density function
POWO	Plants of the World Online
PWQ	Mean precipitation of the warmest quarter
RBGE	Royal Botanic Garden Edinburgh
RF	Random Forest
Rh	Relative humidity
RM	Regularisation multiplier
RN	Realised niche
rsds	Surface downwelling shortwave radiation
SDM	Species distribution model
SPAC	Soil-plant-atmosphere continuum
SPEI	Standardised Precipitation and Evapotranspiration Index
SR	Survival rates
SRE	Surface-Range Envelope
SWC	Soil water content
TSS	True Skill Statistics
UHI	Urban heat island
VPD	Vapour pressure deficit
WT	Warm temperate
WESB	Westonbirt, the National Arboretum

CHAPTER 1

Introduction

1.1. Reassessing urban trees for the future

The paradigm regarding our interactions with nature has undergone a significant transformation, moving away from the conventional view of natural resources as mere inputs for economic production. The shift has been catalysed by the increasing awareness of the environmental degradation caused by such a utilitarian perspective. Today, there is a growing recognition of the intrinsic value of nature as an essential component of the life support systems, vital not only for their biodiversity but also for the wellbeing of human societies (Gómez-Baggethun et al. 2010; Chenoweth et al. 2018). The advent of nature-based solutions and green infrastructure concepts has underscored the pivotal role of the natural system as effective measures of climate change mitigation and adaptation (Demuzere et al. 2014; Kabisch et al. 2016). This shift in changing perspectives in roles of nature has further driven the development of new urban forests and green space in densely populated cities, converting previously degraded brownfields into revitalised greenfield. Recent tree-planting initiatives ranging from city-wide to national scale, along with numerous global programmes on afforestation, are vivid examples of these changes (Brancalion and Holl 2020; DEFRA 2021; Eisenman et al. 2021).

Introducing new trees into urban landscapes, however, is not a straightforward task as it may appear to be. Particularly during this paradigm shift phase, the decision-making process, from selecting species to placement and management, becomes increasingly complex, necessitating the depth of knowledge and insights beyond conventions and heuristic experience. This complexity primarily arises from the compounded effect of bi-fold challenges: the increasing uncertainty associated with climate change and the heightened expectations placed on urban trees to provision ecosystem services (ES). With the accelerating pace of climate change, the ecological conditions and the level of environmental stresses faced by urban trees are becoming more extreme and unpredictable, posing higher risks of mortality for those trees that are already-vulnerable (IPCC 2012; Zscheischler et al. 2018; Esperon-Rodriguez et al. 2022). Climate-induced tree declines are observed in many cities including but not limited to London (Tubby and Webber 2010), Helsinki (Helama et al. 2009), Copenhagen (Sjöman et al. 2012), and Melbourne (Nitschke et al. 2017). The observation of urban tree declines in these major cities suggest that trees previously considered 'tolerant' may not be suitable for changing climate in the future. Increased tree mortality has already begun to cause a shift in species composition and distributions in natural forests (Engelbrecht et al. 2007; Esquivel-Muelbert et al. 2019). However, unlike natural forest, species compositions in urban areas are mostly determined by human decisions. Therefore, to ensure the long-term survival and health of these urban trees, it is crucial to consider their adaptability to changing climates over an extended temporal scale in the decision-making process (Pataki et al. 2021).

While adaptability to changing climate is primary consideration in selecting species, there is a growing demand to maximise the multiple benefits of urban trees, encompassing myriads of ES including health benefits, climate change mitigation and adaptation and conservation of biodiversity. The burgeoning body of research on this topic underscores growing recognition of the need to quantify and evaluate how urban trees contribute to these services (Zaman-ul-Haq et al. 2022). Ideally, such empirical evaluations should guide the selections and inform management practice, tailored to unique requirements and the characteristics of specific environments. However, despite substantial scientific literature with empirical evidence and the development of tree assessment tools such as i-Tree (www.itreetools.org), significant challenges remain in effectively translating and applying this knowledge to practice (Sjöman and Nielson 2015; Raum et al. 2019). The barriers to informed decision making and implementation are multifaceted and complex; they include, but are not limited to, the predominance of studies in controlled environments, fragmentation and dispersion of information, along with conflicting empirical findings, the necessity to balance trade-offs among various ES in maximising its benefits, and challenges related to upscaling to a broader ecosystem dynamics due to complex urban heterogeneity (Andersson et al. 2015; Pataki et al. 2021). These factors collectively underscore the gap between theoretical research and its practical application in urban forest and landscape management.

Confronted with these mounting challenges, a pressing need emerges regarding fundamental re-evaluation of the criteria and processes involved in urban tree selection. Recognising that the adaptability to changing climate is a prerequisite for unlocking all other benefits derived from the healthy ecosystem functions, it is crucial to prioritise species based on re-assessed suitability.

1.2. Previous research and knowledge gaps

1.2.1. Selecting trees within the legacy landscape practice

Urban landscapes today are substantially concentrated on limited selections of species and are becoming increasingly homogeneous across global cities, despite the continual introduction of species from abroad (Morgenroth et al. 2016, Ossola et al. 2020). This is partially due to the stressful urban environment that leads to the selection of ‘safe’ species that are known to survive in similar conditions (Sieghardt et al. 2005). Often these selections are limited to few species recognised as being universally ‘tough’ across broad regions, even on a global scale (Farrell et al., 2022). On the other hand, cultural preferences in aesthetics and availability in nurseries further influence the choices of species. It is interesting to note that the market dynamics play a role in the distribution of species. The availability of species can be primarily driven by demands of those buyers’ preference, which, in turn, drives nurseries to narrow down their offerings to those high-demand species to maximise economies of scale. The economic efficiency achieved through large-scale production enables nurseries to offer popular species at more accessible prices, thereby, be more attractive to buyers (Conway and Vecht, 2015). This dynamic establishes the positive feedback loop between demand and supply. Those species that are proven to be tolerant and fulfil aesthetic needs are more likely to be commercially viable through systematic efficiency. Prioritising systematic efficiency has led to the overlooking of not only species diversity but also genetic diversity within species (Polakowski et al., 2011). Moreover, it makes it challenging to diversify once established. The composition of vegetation in urban areas is largely shaped by a chain of decision-making processes based on the 'risk-averse' strategy grounded in the past experiences of stakeholders, including those landscape architects, municipal planners, and nurseries, rather than the research-based knowledge (Sjöman and Nielson 2015). Growing interest in ecological functions within landscapes in light of climate change has driven a strong motivation to make changes in landscape practice. However, landscape practitioners often find it difficult to balance between the scientific principles and conventional approach amidst floods of literature and information (Hooper et al. 2008; Sjöman and Nielson 2015). For instance, urban environments which are highly heterogeneous and distinct from natural habitats, require considerate ecological considerations. To list a few, they include distinct urban forms and features such as impervious surface (Randrup et al., 2001; Sjöman et al., 2010), inorganic soil characteristics (De Kimpe et al., 2000; Jim, 1998) and below-/aboveground infrastructure; restricted biological control elements such as microbiota (Watkins et al., 2020) and the invertebrate community (Kotz et al., 2000); and additive stress such as air pollution (Locosselli et al., 2019), urban heat (Percival, 2023) and drought stress (Franceschi et al., 2023; Sjöman et al., 2015). As these multiple considerations sometimes generate mixed evidence or trade-off, recommended species selections at regional level can change at local scale (Breyer and Mohr, 2023). Furthermore, there are aspects where the current system may not adequately support the up-to-date standards required for biosecurity or climate adaptation. For instance, the biosecurity toolkit for landscape architecture published by Landscape Institute recommends identifying the sources of seed or plant materials (Landscape Institute, 2019). However, the majority of current nursery systems do not maintain information at a detailed provenance level (Sjöman and Watkins, 2020).

Amidst these challenges and widespread confusions, the main theme of this thesis is stemmed from the two most fundamental criteria in selecting urban species, (1) climate suitability and (2) benefits to urban environment. This is because climate is the predominant constraint on species fitness in any given environment (Woodward, 1987). Determining whether a species is within its physiological tolerable climatic range is a prerequisite before conducting all other peripheral assessments. In addition, when a species is in good fit, the interspecies performance is then quantitatively comparable for further ecosystem assessment. Here, urban trees are broadly referred to as trees managed by urban, sub and peri-urban areas as part of regional green infrastructure. This includes trees not only on streets and in urban park/garden, but also those composing urban, sub, or peri-urban forests.

1.2.2. Niche based approach

The growing concern over urban tree declines in light of climate change has spurred the interest in predictive models that can inform species-specific suitability for cities at regional scale in the future climate. Studies such as those conducted by Burley et al. (2019), Khan and Conway (2020), Kim et al. (2020) and Yang (2009) applied species distribution models (SDM) to identify vulnerable or suitable urban species to climate change scenarios. Other studies by Hanley et al. (2021), McPherson et al. (2018), and Roloff et al. (2009) have sought to identify suitable species by integrating climate envelope models with physiological tolerance tests to selected environmental stress. The former approach assesses general habitat suitability of the physical space for the selected species. The latter approach focuses on quantifying the range of environmental conditions that species can tolerate. For instance, the range of maximum temperature during the warmest month can be considered as a surrogate measure for the heat tolerance of the species. Both of these approaches in general begin with delineating a species' ecological niche, which is grounded in the Hutchinsonian niche theory (Hutchinson, 1957). It conceptualises an ecological niche as an abstract *n*-dimensional environmental space, mirroring the same *n*-dimensional environmental attributes of the physical space occupied by species. When species are found in the areas beyond their ecological niche boundaries, they are considered to be exposed to a high likelihood of regional extinction. This framework assumes that the ecological niche would remain stable over time, allowing for reciprocal projections of new distribution ranges or stress tolerance under the future climate scenarios, based on those pre-defined environmental ranges. Nonetheless, given that the foundation of the niche theory is deeply embedded within evolutionary ecology, applying these theories in urban environments is challenging due to distinct discrepancies (Niemelä 1999); urban environments are significantly disrupted by both direct and indirect human interventions over a very short period, unmatched in the spatio-temporal scope of evolutionary ecology. For instance, urban species pools are more sensitive to patch-scale habitat features than city-wide ecological gradients (Casanelles-Abella et al., 2021). Furthermore, while species distribution data is fundamental to the development of niche models, the inclusion of current distributions within urban areas is largely ignored due to its anthropogenic interruptions. Most niche-based approaches rely on public institutional surveys of natural distributions, often deliberately excluding urban distributions when training models (Burley et al., 2019; Khan and Conway, 2020; Kim et al., 2020; Yang, 2009). Given that more than half of urban tree species globally are already out of their native distribution range (Esperon-Rodriguez et al., 2022), some studies have raised the importance of recognising the presence of these species in re-defining their niche breadth (NB) — i.e., extents of environmental tolerance (Bocsi et al., 2016; Booth, 2015; Vetaas, 2002). However, the interpretation of species presence beyond their native distribution range — whether it should be viewed as an expansion of their ecological niche (Kendal et al., 2018) or populations at risk (Esperon-Rodriguez et al.,

2022) — is a matter of debate. And, without empirical evidence available supporting either perspective, this ambiguity will likely persist.

1.2.3. Ecosystem service-based approach

Another perspective in assessing urban trees relates to the need to quantify ES which is often translated into either monetary value — e.g., hedonic pricing, avoided cost, or insurance value — or non-monetary values — e.g., mental health, social cohesion and resilience (Dunford et al., 2018; Gómez-Baggethun and Barton, 2013). This is to address the systematic undervaluation of ecological dimensions, of which economic contributions have been largely neglected, by advocating for the integration of these values into economic decision making (Gómez-Baggethun et al., 2010). The types of urban ES that are assessed in the highest demand are related to climate regulations ES; Urban cooling, carbon sequestration and stormwater mitigation are the top three ES that showed the highest number of peer-reviewed papers over the recent decade (Zaman-ul-Haq et al., 2022). Among these services, the contribution of urban trees to carbon offset is notably modest, accounting for only 0-3% annually (Baró et al., 2015; Lindén et al., 2020; Pataki et al., 2009). This limitation is primarily attributed to the imbalance between the vast magnitude of fossil fuel emissions and the relatively limited capacity of urban trees to sequester carbon, due to restricted spatial extents and the scale at which urban forestry can operate (Pataki et al., 2021). Given the limited scale in highly fragmented and heterogeneous environments, urban trees are therefore more effective as climate adaptation measures at a local scale, such as neighbourhood patches and urban parks. At these smaller scales, urban trees can help to improve human thermal comfort from urban heats (Jung et al., 2021; Santamouris et al., 2017; Wang et al., 2018) or to reduce stormwater runoff (Asadian and Weiler, 2009; Zölch et al., 2017). These climate regulations by urban trees are intrinsically connected to tree transpiration and water use, operating within the intricate dynamics of soil-plant-atmosphere continuum (SPAC). Moreover, being responsible for the reintroduction of approximately 40% of the regional precipitation back into the atmosphere, tree transpiration is an integral component of the water cycle within the broader ecosystem (Schlesinger and Jasechko, 2014). Given these critical roles of plant water use in ES provisioning within broader ecosystems, transpiration often becomes the central focus of the study as proxy metrics to assess climate regulations ES (Dimondi and Nikolopoulou, 2003; Hörnschemeyer et al., 2021; McCarthy et al., 2011). However, many of these studies that estimate plant transpirations rely on standardised vegetation properties such as leaf area index, overlooking species-specific characteristics. Widely adopted ES assessment tools such as i-Tree and InVEST models (Natural Capital Project, 2024) also incorporate physical attributes, such as leaf area index, crown diameter or tree height into their models, but do not take species-specific traits into account. Such approaches utilise conventional hydrological models which view vegetation as constant factors embedded in a meteorology-based approximation, for example in the Penman-Monteith equation (Allen et al., 2011; Fatichi et al., 2016). However, Forster et al. (2022) emphasised that species-specific canopy conductance can limit the accuracy of these conventional models. Other studies such as those by Ballinas and Barradas (2016), Gupta et al. (2018), Pataki et al. (2011), Rahman et al. (2017) and Stratópoulos et al. (2018) showed that canopy conductance varied significantly among species and ultimately influenced the effects of urban ES. Szota et al. (2018) and Tan et al. (2020) further advanced the idea and used species-specific transpiration and related traits in evaluation of suitable species that deliver desired benefits to the fullest potential. The significance of studies on transpiration and water use strategy is increasingly acknowledged as plant water use is an essential metrics in evaluating climate regulations ES and understanding plant adaptation under climate change. Yet, it is in a nascent stage facing many challenges (Kannenberg et al., 2022). Specifically, many studies on transpirations often focus on a limited selection of species and are confined to narrow spatio-temporal frames, employing unstandardised unit metrics (Poyatos et al., 2021). This results in fragmented data that are challenging to synthesise, making it even more difficult to draw broader, generalisable conclusions on plant water use, a subject already known as highly variable across different environmental contexts.

1.3. Research aims and questions

The overall aim of the thesis is to evaluate urban trees from the three different perspectives, tolerance, species distribution models, and water use within the general framework of niche theories. Specifically, by examining the interactions of individual species with specific environmental conditions at a localised scale and connecting these findings to the broader contextualised niche models, it seeks to address the knowledge gap between the theoretical niche models and the field evaluation of urban species. In particular, it highlights the relationship between species specificity within local context and the broad environmental pressures that shape their survival and adaptation, aiming to unravel how coexisting species or species of similar environmental range distinctively function under varying local environmental conditions. This approach holds particular significance for those urban species that are present beyond their native range of distributions, especially when their current conditions impose stress under climate change. By examining these interactions, it becomes more feasible to predict plant responses with enhanced accuracy amidst the direct and indirect human interventions which characterise the fragmented and disruptive nature of urban environments. Acknowledging that theoretical framework of niche operate on macro ecological scale, niche analysis based on species biogeographic distributions alone will not reflect the full complexity of urban environment. However, the insights gained in this thesis can be utilised later in developing the preliminary evaluation framework of urban species concerning the ultimate survival or their contributions to ES in urban landscapes. Therefore, the study aims to address the following fundamental questions.

i) Does the presence of species *x* in a city *y*, beyond their native range of distributions, signify an increased exposure to mortality risk or increased tolerance?

ii) To what extent does the predicted habitat suitability based on SDM align with actual survival rates of species? How should it be interpreted?

iii) How do two co-occurring species vary in their water use under moisture stress across varying environmental conditions?

iv) How is species' distinct water use strategy consistent across varying environmental conditions?

v) What implications do these findings from i to iv have on evaluations of trees in urban landscapes?

1.4. Structural overview

This thesis is presented as an alternate format thesis, comprising three published/to-be-published papers in conjunction with more traditional components such as introduction, literature reviews, and discussion chapters. The thesis is divided into three parts as illustrated in Figure 1.1. The structure allows for a comprehensive presentation of research findings within a coherent theoretical framework.

The first part of the thesis begins with the background that explains relevance of the topic and theoretical exploration of foundational concepts in ecological theories that underpin three major research chapters. Chapter 1 addresses the gap between legacy landscape practices and growing demands in new knowledge to effectively cope with climate challenges in urban environments. Chapter 2 first introduces the Hutchinsonian niche concept that characterises species in terms of environmental dimensions. This chapter further delves into the biological attributes of species, which are filtered and shaped by environmental conditions yet continually adapt through ongoing interactions. The biological attributes are particularly focused on plant water use strategy and related plant traits as water use plays an essential role in plant survival and productivity, influencing broader ecosystems under changing climate.

Following the introduction and theoretical exploration, the second part of the thesis presents the findings of each research study that answers research questions i to iv, with each set of findings corresponding to its respective chapter. Chapter 3 specifically compares mortality rates between those species within their native climatic NBs and those beyond their climatic NBs. This is to explore the extent to which broad climatic niche variables influence species-specific physiological tolerance in previously unoccupied sites. It should be noted that these trees are not strictly considered those urban trees on the streets which are heavily influenced by microclimate and non-climatic factors. Trees in these botanic gardens are better candidates for bioclimatic niche comparison as other site-specific stress is minimised, allowing the impact of climate can be more pronounced. Specifically, to assess whether species NB location below their threshold significantly influences the mortality rate during a given interval, the commonly used method of discrete time-hazard survival analysis was applied (Tutz and Schmid, 2016). This approach is particularly effective handling time-dependent and discrete event data, which are measured in intervals, e.g., yearly. Moreover, the death of an individual tree, with NB location below a threshold, can occur any time after the observation period but is excluded from the analysis, leading to bias in predictions. This approach differs from traditional models by accommodating these restricted survey data (Suresh et al., 2022). These resulting mortality rates are then converted into survival rates, which are compared with predicted habitat suitability (HS) scores based on species distribution models (SDMs) in Chapter 4. In this chapter, it further investigates the knowledge gap between predictive models derived from the continental scale biogeographic distributions and the underlying biological processes as revealed by observed actual survival rates and phylogenetic proximity. For SDM, MaxEnt was chosen as this algorithm was known to demonstrate strong transferability – capacity to produce more accurate predictions for novel environments that differ from those which the model was trained (Heikkinen et al., 2012). For classification of phylogenetic group, genome analysis by Li et al. (2019) were used as a reference. Chapter 5 narrows down its focus solely on individual biological attributes, specifically plant water use strategy. As plant water use is the key biological attribute that connects physiological tolerance (to drought) and essential benefits (net ecosystem productivity and climate adaptation), this chapter explores the variability of interspecies and intraspecies water use behaviours through sap flux analysis across varying environmental conditions. For this comparative analysis, sap flow measurements were obtained from the SAPFLUXNET database (Poyataos et al., 2021). This global repository provides pre-calibrated sap flow data that has been cleaned and standardised from multiple sources of previously studied experiments, facilitating comparison of sap flow performance across various environmental gradients. Nonetheless, the database does not hold sufficient samples of UK native *Acer* and *Quercus* species. Therefore, samples from North American species, which had the largest number of co-occurring sites for both genera, were selected instead.

The thesis concludes with Chapter 6, in which it synthesises all findings and discusses the implications of these findings for the urban landscapes and the recommendations for future research.

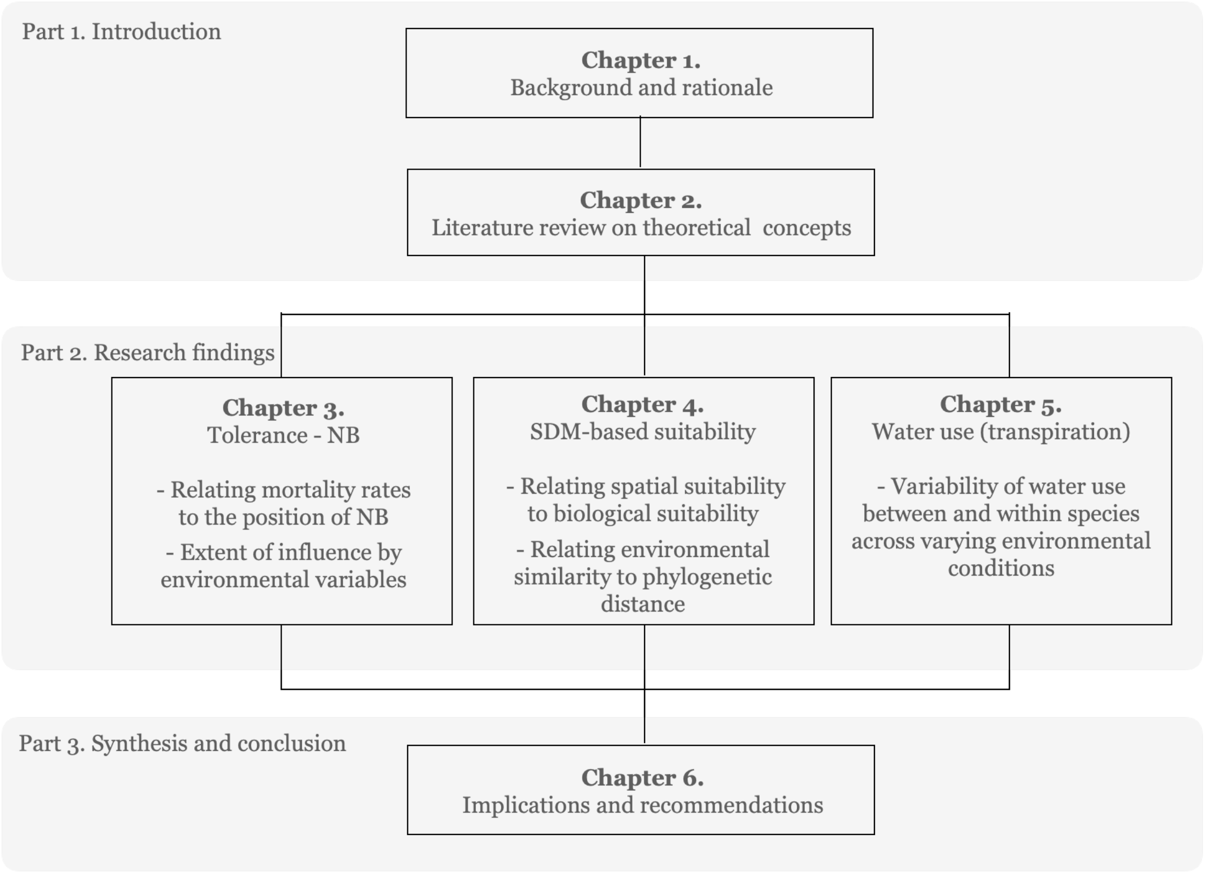

Figure 1.1. Outline of the thesis structure.

CHAPTER 2

Theoretical overviews

2.1. Environmental attributes

2.1.1. Fundamental, potential and realised niche

The fundamental niche is one of the key underpinning concepts in ecology, providing a framework for understanding how environmental conditions influence the biogeographical distribution, abundance, and interactions of populations and communities (Peterson, 2011; Ricklefs et al. 2000). The fundamental niche (FN), first envisioned by Hutchinson (1957) is an abstract formalisation of the ecological conditions that allow the species to persist, which is described in a set of *n*-dimensional hypervolume occupied by species. This abstract space is 'realised' when a species demonstrates a successful occupancy in the actual physical space. The realised niche (RN) is, therefore, a manifestation of the FN in real-world geography. This physical niche space is then always a subset of the theoretical niche as it is limited by multiple constraints in a real world such as negative biotic factors — e.g., competition and predation — and accessibility — e.g., geographical barriers and dispersal limitation (Soberón and Peterson, 2005). Acknowledging this reduction from the FN is critical in application and interpretation of niche models. As illustrated in Case 1 (Figure 2.1), it indicates that species can be absent in environmentally suitable areas due to accessibility constraints or competitive exclusions. The stricter the constraints, the greater the gap between the FN and the RN. Conversely, some species can persist despite the presence of certain unfavourable conditions (Pulliam, 2000). These constraints on distributions by non-climatic factors or presence in unsuitable environments are the real-world cases that may undermine the equilibrium assumption. Niche theories rest on the premise that species are at equilibrium, i.e., their full presence in all suitable locations, where environmental conditions align with their ecological requirements, and their full absence in unsuitable locations (Araújo and Pearson, 2005). The ecological evidence supporting non-equilibrium states (Pili et al., 2020; Walker and Valentine, 1984) prompts intriguing and fundamental questions regarding the presence of introduced species in urban areas. It invites speculation as to whether urban areas, previously uninhabitable, can be considered as a potential niche, i.e., unrealised parts of the FN. Further, it suggests an interesting hypothesis necessitating further investigations: the presence of introduced species in urban areas is an indication of 'realisation' of their potential niche, enabled with removed restrictions in accessibility by human interventions. Under the condition of unrestricted accessibility, the intersection G_0 can be theoretically extended from FN = A ∩ M ∩ B (Case I) to FN = A = M ∩ B (Case II) in Figure 2.

Seeing urban areas as a potential niche is indeed subject to debate as species can be present in unsuitable environments, known as sink habitats (Pulliam, 2000). For certain species, urban areas can be classified as sink habitat when the population is not self-sustained through natural reproduction, requiring assisted introduction from external suitable environments. Although natural reproduction is not the usual way to sustain urban tree population, evidence in reduced reproductive cases should not be overlooked for long-term ecological sustainability and resilient biodiversity in urban biotopes such as urban forests and wetlands (McCauley et al., 2013; Oliveira et al., 2019).

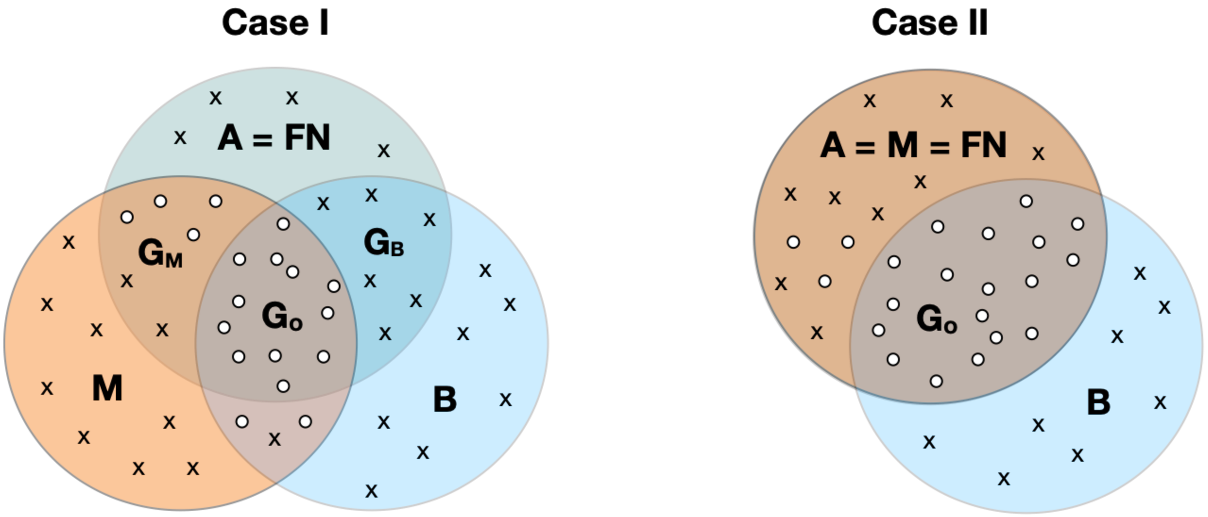

Figure 2.1. A BAM diagram redrawn and modified from Soberón and Peterson (2005) and Peterson and Soberón (2012). A circle **A** represents the geographic regions of a set of suitable abiotic conditions for the species, which is equivalent to the theoretical fundamental niche (FN). A circle **B** represents the region with the right combination of interacting species. A circle **M** represents the regions that are accessible to the species. The intersection of all three circles is the 'realised niche (RN)' physically occupied by the species, $\mathbf{G}_o$; $\mathbf{G}_B$ holds the correct suite of environmental, both abiotic and biotic, conditions but not accessed by species; $\mathbf{G}_M$ is accessible but interrupted by negative biotic interactions. All x represents absences whereas white circles represent presence. Note that presence can occur in unsuitable abiotic conditions.

2.1.2. Niche breadth and niche conservatism

Prior to categorising any habitats as realised or potential niche, it is essential to first define the species-specific niche, decomposed into the breadths of environmental conditions in which species can thrive. In a strict sense, this niche breadth (NB) means to support non-negative population growth (Carscadden et al. 2020). However, direct performance-based measures, such as birth, growth and survival rates, are hard to obtain, and need repeated measures at different life stages over extended periods of time. Instead, readily available species occurrence data is more often used as a surrogate measure to define niche. The presence of species in specific locations serves as an indicator of species capability to adapt and survive at given environmental conditions as we draw upon the classical concept of environmental filtering (Donoghue et al., 2022; Shipley et al., 2006). Thereby, the distribution of a single species can be represented as a suite of multiple niche axes, each corresponding to different environmental gradients, e.g., temperature, precipitation, or humidity, as illustrated in Figure 2.2.

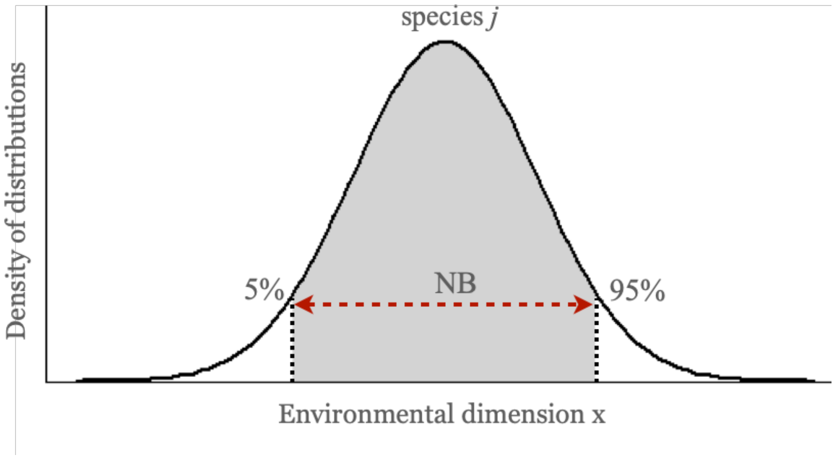

Figure 2.2. The illustration of the niche breadth (NB) of a species *j*.

The NB is a useful concept to describe marginality of a species' niche, reflecting its environmental tolerance and to assess its potential range limits under varying conditions (Carscadden et al. 2020). In general, species with broader NB exhibit adaptability and tolerance to a wide range of environmental conditions, enabling them to inhabit extensive geographic areas. However, their capacity to exploit diverse conditions means they may not excel in any one environment — thereby, named 'generalists' (Sexton et al., 2017). Conversely, species with narrow NB are 'specialists' that are optimised to specific environmental conditions or resources. This specialisation can lead to high efficiency in particular resource use within their preferred habitats, but it also makes these species more vulnerable to environmental changes. Considering that the niche is multi-dimensional, species may specialise in one niche axis but exhibit broader tolerance in other niche axes depending on the correlations in environmental conditions (Carscadden et al. 2020). This multi-dimensionality of the NB and interactions among dimensions — e.g., trade-off — play crucial roles in evolutionary processes, driving species divergence, convergence, and coexistence (Brown 1984; Sexton et al., 2017), as this intricate web of interactions operates across various ecological levels, ranging from genetic and individual levels through populations, extending to community or entire clades (Anderson et al., 2015; Bolnick et al., 2003) (Figure 4).

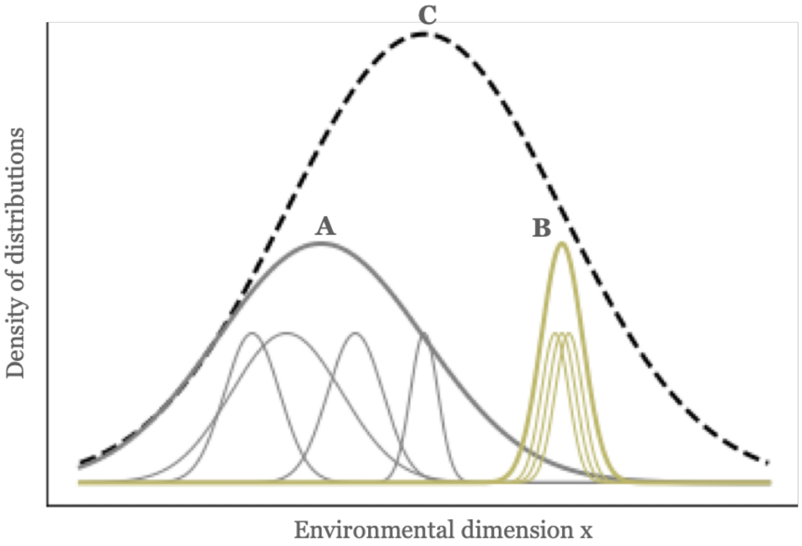

Figure 2.3. The illustration of the niche breadth (NB) in hierarchical levels redrawn from Sexton et al. (2017). Individual-level NBs are encapsulated in the populations or equivalent level NBs represented by curve A ('generalist') and B ('specialist'). The curve C represents the highest phylogenetic hierarchy.

Most importantly, one critical assumption in applying NB concepts in predictive models is that NB is reasonably maintained with consistency, implying that species are likely to occupy similar environmental conditions even in newly introduced habitats. This assumption is supported by the niche conservatism (NC) hypothesis which posits that species' niche, and related ecological traits tend to remain relatively constant over time (Harvey and Pagel 1991; Pearman et al. 2007; Wiens et al., 2010). If a population of a species is forced beyond its known NB, the prevailing hypothesis suggests that it may struggle to persist in the altered conditions, potentially leading to local extinction. The strength and generality of NC is thus critical in predicting how species respond to changing climate (Wiens et al., 2010). To date, the NC hypothesis has received broad confirmation. For example, Wien and Graham (2005) highlighted the extensive impacts of NC across evolutionary biology and biogeographic distributions, while Pearman et al., (2008) emphasised the importance of incorporating both temporal and spatial scale in recognition of these patterns. Qian and Ricklefs (2004) demonstrated a significant NC in disjunct genera between East Asia and North America, evidenced by strong correlation between their geographic distributions and similar climate patterns. This also confirms climatic factors are the major limiting determinants for geographic distributions or RN in abstract term (Thuiller et al., 2004). Indeed, among groups of organisms, plants exhibit the most climatic similarities between their native and introduced ranges (Liu et al., 2020). The hypothesis of NC between sister species can be further tested with methods introduced by Warren et al. (2008). Species that exhibit conserved niches, choose migration over adaptation to changing climate, as evidenced by shifts in species distribution compositions in natural forests (Engelbrecht et al. 2007; Woodall et al. 2009). Yet, contrasting evidence to the NC hypothesis has also sparked debates by recently observed cases in NB expansion or niche shifts due to climate change (Broennimann et al., 2004; Guisan et al., 2014; Liu et al., 2020; Sexton et al., 2017). This is especially evidenced in invasive or naturalised species. For example, Early and Sax (2014) observed majority of naturalised European species in the US occurred outside their native climatic range. In case of urban environments, a global survey of 203 urban tree species found that the NB of urban species was 38% to 90% wider than that of the same species in their native distributions (Kendal et al. 2018). Although it can be argued that the establishment of these species are human-assisted, it is also true that urban environments have been the source of many invasive species (Padayachee et al., 2017). Given that the RN is always a subset of the FN, it can be interpreted as niche expansion by niche filling — that is, expanding to a fuller range within the FN. This can be possible scenario when biotic constraint is removed in the new environment (Mitchell et al., 2006), thereby extending its potentiality of RN. However, it can also be argued as an invasive niche shift as a result of adaptation. An exotic species might undergo evolutionary changes in its new environment, enabling it to occupy new niches. These evolutionary adaptations can result from genetic drift or phenotypic plasticity within the new habitat (Benito Garzón et al., 2019; Sotka et al., 2018; Valladares et al., 2014). However, such evolutionary process occurs in species at varying rate of change (Pearman et al., 2008). This is why majority still remain within the boundaries of conserved niche, while few species exhibit pronounced niche shift (Petitpierre et al., 2012). To gain a more comprehensive understanding and clearly articulate these differing perspectives, further investigation into the interactions of NB dimensions and ecological mechanisms underlying the NC are essential.

2.1.3. Species distribution models

Quantitative niche modelling is commonly referred to as ecological niche models (ENMs), climate envelope models (CEMs), bioclimatic models, or species distribution models (SDMs). These terms are used interchangeably with some variations in emphasis by means of purpose (Elith and Leathwick, 2009; Peterson and Soberón, 2012). To be precise, however, it is ENM to estimate the fundamental niche - abstract environmental space, which is then used to outline the actual geographic space, distributional areas predicted by SDM (Peterson and Soberón, 2012). Distinguishing between environmental space and geographical space is crucial in SDM. If SDM relies solely on bioclimatic variables, it may overlook important geographic factors or other interacting aspects related to geographic patterns influencing predictions (Elith and Leathwick, 2009). These include geographic proximity and connectivity, which is also related with topography, movement, dispersal and biotic interactions, or seasonal disruptive events such as glaciation and fire (Dormann et al., 2007; Ferrier et al., 2002; Mayor et al., 2017; Svenning et al., 2010). However, since geographic contexts can also introduce bias in SDM, such as spatial autocorrelation — the tendency for data points closer to each other in space to be more similar than far apart, a careful model configuration strategy is needed to balance between environmental and geographic variables (Araújo et al., 2005).

There are numerous mathematical and machine learning based techniques to fit SDMs. Among them, 12 widely used algorithms were categorised in Figure 2-4. Given that SDMs are projected based on the current species distributions, algorithms are broadly classified by the input species data represented in three formats: presence/absence, presence/pseudo-absence, presence/background and presence-only data. Models calculated with pseudo-absences can differ from those with absences due to the risk that pseudo-absences may not accurately represent true absences (Chefaoui and Lobo, 2008). However, for most regions, systematic biological survey data providing both presence and absences is scarce, and the majority of species records are available in the form of presence-only data within herbarium or museum databases. Consequently, the presence/pseudo-absence or presence/background approach is more frequently used with presence/background approach accounting for more than 50% of cases (Guillera-Arroita et al., 2015).

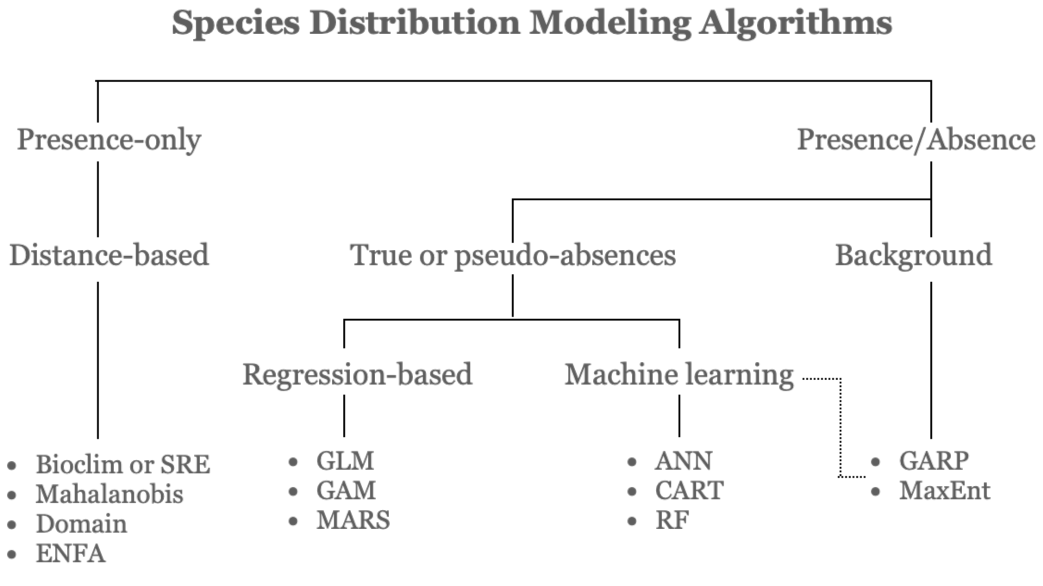

Figure 2.4. A hierarchical classification of SDM algorithms redrawn from Pecchi et al. (2019). SRE (Surface-Range Envelope, Araújo and Peterson, 2012), ENFA (Ecological-Niche Factor Analysis, Hirzel et al., 2002), GLM (Generalised linear model), GAM (Generalised additive model), MARS (Multivariate Adaptive Regression Splines, Elith and Leathwick, 2007), ANN (Artificial Neural Network, Lek and Guégan, 1999), CART (Classification And Regression Tree, Loh, 2011), RF (Random Forest, Breiman, 2001), GARP (Genetic Algorithm

for Rule-set Predictions, Haase et al., 2021), MaxEnt (Maximum Entropy models, Phillips et al., 2006)

These techniques show considerable variations in model performances depending on model configurations and quality of occurrence data (Bahn and McGill, 2013; Elith et al., 2010; Grenouillet et al., 2011; Guisan et al., 2007; Pearson et al., 2006). To improve predictive accuracy of SDMs, there has been mounting literature specifically evaluating preliminary data preparation techniques, configuration and validation methods to fine tune these models. However, despite all these efforts towards technical improvements, there are two very inherent and fundamental limitations to this approach: sampling selection bias and the 'coarseness' of environmental variables, both in terms of scale and relevance.

While we often view the presence or absence of species as a simple yes-or-no situation, the reality of defining these conditions is complex. Especially, presence-only records, lacking associated temporal and spatial scale, can introduce sampling bias (Elith et al., 2011). For example, many herbarium records amassed over extended periods may not reflect current distributions that have been impacted by climate change. Similarly, species observed on a larger scale may not necessarily be observed on a smaller scale although two studied sites share the same environmental range. Additionally, as sampling is often biased towards more accessible locations near cities, the detectability is not constant across sites. This sampling bias can also skew the estimation of environmental relationships, leading SDMs to estimate where species is more likely to be observed rather than where it actually occurs (Guillera-Arroita et al., 2015). Therefore, with presence-only data, it is difficult to yield prevalence of the species — the proportion of the site occupied — regardless of sampling size (Ward et al., 2009).

The correlational model which relies on the relationship between environment-observation, is advantageous for quick approximation of predictions at a relatively coarse scale (Morin et al., 2007). This 'coarseness' may arise from sampling selection bias as discussed, but it is also influenced by the choice of environmental variables. Although theoretically, all ecologically relevant variables should be included in the SDMs, the variables actually used in modelling often do not fully align with what is understood about the species' ecological needs (Gardner et al., 2019). In particular, the increased likelihood of extreme weather events underscores the importance of incorporating climate variables that are physiologically significant. For instance, Fay et al. (2003) demonstrates that greater fluctuations in rainfall, without reduction in the total rainfall, can lead to decreased growth, above-ground net primary productivity, in a tall-grass prairie. In fact, most SDMs employ pre-configured, readily available bioclim predictors which effectively summarise mean conditions of regional landscapes but are less effective in capturing the physiological tolerance or underlying mechanisms. It is important to note that environmental variables are particularly sensitive both in temporal and spatial dimensions. For instance, the study by Austin and Niel (2011) highlighted how small- scale landscape features, such as the orientation of slopes, can significantly influence the temperature variations — comparable to shifting 200 km northward. Nonetheless, SDMs that integrate such proximal and biophysically relevant variables are still relatively rare and understudied.

Acknowledging these limitations of SDMs, there have been ongoing attempts to incorporate mechanistic processes into these models, aiming to capture the underlying ecological dynamics more effectively (He et al., 2019; Hülsmann et al., 2018; Morin et al., 2007; Swab et al., 2012). Often these underlying processes are linked to so-called 'functional traits' which also play crucial roles in shaping species distributions (Kearney et al. 2010; Morin and Lechowicz 2008). Understanding these traits in relation to generalised species' adaptive patterns and strategies across species distributions (Lavorel et al. 1997) can aid in refining 'coarseness' of SDMs, thereby contributing to the enhancement of the models' predictive accuracy.

2.2. Biological attributes

2.2.1. Strategy-traits-ecosystem relations

One of the efforts to mitigate the ‘coarseness’ of the SDMs included attempts to integrate mechanistic processes into the models (Kearney et al. 2010; Morin and Lechowicz 2008). The mechanistic approach, however, requires accurate understanding on the interactions between the species’ fitness and its environment, along with estimates of various trait-related parameters (Buckley et al., 2010). Essentially, traits help explain differences in growth and survival across resource gradients and thus help explain the distribution of species. The idea of linking plant traits in generalising species distribution patterns was not new and dated back to the early 1800s, long before the term ‘niche’ had been coined (Von Humboldt and Bonpland 1807). These early studies were later used as evidence supporting Darwin’s theory of evolution (Darwin, 1859, Origin of Species, Chapter XI; Vasconcelos, 2023). In general, plant traits assume two contrasting ecological principles: environmental filtering and niche differentiation. As discussed earlier, environmental filtering suggests that the certain environmental conditions — e.g., precipitation or temperature —can select for species with similar traits conducive to optimal performance and survival under these conditions (Donoghue et al., 2022; Shipley et al., 2006). Conversely, niche differentiation suggests that co-occurring species are likely to exhibit significant trait variations —or trait specialisations —in order to avoid direct competition over the same resource pool (Ricklefs et al., 2000). These trait variations can be grouped into several thematic dimensions that reflect their strategic choices related to the acquisition, utilisation and conservation of resources. For instance, Grime (1979, 1988) introduced his C-S-R strategy scheme to classify plant traits, grouping them into Competitive (C), Stress tolerant (S), and Ruderal (R) dimensions. The core concept revolves around how species respond to disturbances and adapt to opportunities for either fast or slow growth. Another well-known example is the leaf economic spectrum (LES) proposed by Wright et al. (2004). This framework focuses on the leaf functional traits along the fast and slow growth continuum. Leaf traits at the fast-end enable plants to quickly exploit available resources driving increased productivity — high return — at the cost of shorter lifespan. On the other hand, traits at the slow-end allow plants to endure in resource-limited environments at the cost of lower return — e.g., low rates of photosynthesis. The LES extends to other organs such as stems and roots as consistent strategies (Díaz et al., 2004; Reich, 2014).

Therefore, traits tend to correlate with one another and exhibit similar patterns, reflecting their strategic economic choices in response to limited resources. These trait correlations can be global (Díaz et al., 2004) or sometimes conditional within habitats (Reich et al., 2003). Variations in correlative trait patterns among individual species influence the collective community forms and functions of ecosystems and their processes. For example, sites with fertile soil and frequent disturbance may favour annual grasses that adopt a fast growth strategy, facilitating carbon and nitrogen cycle with increased annual productivity and decomposition rates (Jones and Woodmansee, 1979). In contrast, pine dominated forests in nutrient-poor and relatively dry soil exhibit slow growth with low understory vegetation, which leads to slowed-down carbon and nitrogen cycles (Hart et al., 2006).

In essence, two types of pressures, environmental constraints (filtering) and biotic interactions (differentiation), shape plant forms and functions that would optimise their acquisition, utilisation, and conservation of resources, resulting in unique vegetation patterns and communities at global and regional scale (Díaz et al., 1998; Grime, 1979; Reich et al., 2003; Thuiller et al., 2012; Woodward 2008). Consequently, slight shifts in environmental conditions can introduce a change in the plant community, which, in turn, trigger a cascade of changes in related ecosystem functions and processes.

2.2.2. Plant water use strategy

Within plant communities, water is the most critical resource which governs plant growth and survival, given its essential role in the exchange of carbon and water during photosynthesis. In the real world where water resources are not always readily available, plants evolved their distinct adaptive strategies to optimise between carbon assimilation and water use, tailoring their response to constraints on accessing water (Anderegg et al., 2018; Flo et al., 2021). This delicate regulation of water use versus carbon uptake under water-restricted conditions entails strategic choices across a broad range of timescale. Plants sensitively adjust their stomata openings, constantly toggling between open and closed states in response to daily changing vapour pressure deficit (VPD) (Flo et al., 2022). During periods of the seasonal water-restrictions, trees may face strategic decisions over growth whether to shed or to retain leaves (Brodribb and Holbrook, 2003). Further, decisions on longer-term investment over evolutionary periods are ultimately manifested in the morphological traits concerning allocation of biomass between aboveground and belowground organs, as well as the trade-off between leaf area and thickness or the density and width of hydraulic architecture (Reich et al., 2003). The more restricted the conditions, the more specialised plant traits become, thereby, leading to a particular strategic choice.

Understanding plant water use strategy is increasingly important as drought-induced tree mortality has been extensively observed and expected to increase regardless of biomes under changing climate (Allen et al., 2010; McDowell et al., 2008). Moreover, it not only governs plant survival under drought but also significantly influences broader ecosystem carbon and water fluxes through the soil-plant-atmosphere continuum (SPAC) (Anderson et al., 2003; Faitichi et al., 2016; Stoy et al., 2019). Trees are responsible for returning up to 40% of local precipitation by releasing water back to the atmosphere (Schlesinger et al., 2014). Particularly in urban environments, trees play a crucial role in urban cooling and stormwater runoff mitigation through transpiration and water absorption (Rahman et al., 2020; Pataki et al., 2011; Szota et al., 2018; Thom et al., 2022). Given the significance of these processes, generalising plant water use strategy in relation to their ecological niche and changing environmental conditions is critical in evaluation of urban trees. For instance, co-occurring species which share a similar ecological niche may exhibit contrasting water use behaviour, leading to variability in productivity (Matheny et al., 2017; Roman et al., 2015). These species-specific variations in hydraulic responses to water stress can provide valuable information by filling the gap in coarse-scaled SDMs. In particular, recent advances in plant hydraulics have sought to explain water use strategy within the framework of the iso-anisohydric continuum. This approach aims to classify plants into two broad categories:

isohydry, which denotes conservative water use by maintaining relatively constant leaf water potential through stomatal closure, and anisohydry, which represents a more acquisitive water use allowing for continued transpiration through open stomata despite restricted water availability (Martínez-Vilalta et al., 2017). This approach is especially appealing as it simplifies complex biological processes and applies them as predictive measures such as in selecting suitable species for specific environmental conditions (Gillner et al, 2017; Szota et al., 2018). However, the application is more elusive, owning to the use of differing definitions in evaluations that lead to conflicting interpretations, compounded by intraspecific variability (Feng et al., 2019; Hochberg et al., 2018; Martínez-Vilalta and Garcia-Forner, 2017). In addition, these challenges have become particularly pronounced given that most of the empirical evidence relating to plant hydraulics are fragmented over spatio-temporal scale with limited species.

2.3. Niche dynamics in space and time

The intrinsic challenge within predictive modelling based on niche is highlighted by the reality that species' niches are not necessarily static; they may expand, contract, or shift over time or across various habitats (Pearman et al., 2007). Such variability can potentially compromise the conclusions of niche-based SDMs unless the dynamics of niche evolution are adequately incorporated. The distinction between FN and RN becomes paramount in understanding these dynamics, as shifts might stem from alterations in ecological processes affecting the realised niche or from evolutionary modifications influencing both niches. The ability of a species to expand its RN could involve plastic responses to novel environmental conditions. Especially, phenotypic plasticity allows populations to endure environmental shifts without the need for immediate genetic adaptation. Moreover, these adaptations occur at different spatial scale. For example, local adaptation, where populations evolve traits that are specifically suited to their local environments, is another crucial factor influencing species responses to climate change (Valladares et al., 2014). The interaction between local adaptation and plasticity can vary across populations within a species, especially at the biogeographic margins of their ranges. Ideally, incorporating both phenotypic plasticity and local adaptation into models may result in more accurate predictions although this is beyond the scope of this thesis.

Parallel to the discussions on niche dynamics, the exploration of "evolvability"—the capacity of organisms to evolve over time—introduces a new dimension to our understanding of biological evolution (Lehman and Stanley, 2013). While conventional theories attribute increased evolvability to natural selection pressures, such as fluctuations in mutation rates or species' adaptability to new environments, this discourse suggests a simpler explanation. It posits that evolvability might inherently be a part of an organism's genetic constitution, passed down through generations. This perspective implies that organisms with naturally higher evolvability might spontaneously become more diverse and occupy a broader range of ecological niches, challenging the notion that external pressures are the sole drivers of adaptability.

In essence, niche dynamics is an open-end premise that requires further exploration. Attaining a deeper understanding of niche dynamics is also crucial for enhancing predictive capacity of SDMs amidst changing environmental conditions. Therefore, it necessitates a comprehensive approach that combines niche-based SDMs with not only environmental data but also with phylogenetic insights or other biological attributes to delineate the timescales and circumstances under which niche shifts manifest. Furthermore, acknowledging the significance of scale in the examination of niche dynamics, —whether spatial, temporal, populations or phylogenetic—impacts the ability to discern and comprehend niche shifts, and necessitates a multi-scalar approach that effectively capture the change across these scales.

CHAPTER 3

Niche breadth

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Ross Cameron: conceptualization, supervision, critical review
Franziska Schrodt: methodology, review & editing
Kevin Martin: data curation, critical review
Robert Cubey: data curation, critical review

3.1. Abstract

The heightened vulnerability of urban trees under changing climate has spurred the need to reevaluate their suitability. To assess species suitability, predictive models based on applied niche theories are increasingly used. In particular, the concept of NB, the range of environmental conditions that species can tolerate, is 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 native 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 analysed 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 the warmest quarter led to an 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 modelling.

3.2. 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 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 modelling 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 realised 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 modelled species distributions and the theoretical niche (Guillera-Arroita 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 realised niche (Peterson and Soberón, 2012). Species could also occupy 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 realised niche. Typically, the occurrence of species in urban environments is excluded during the data preprocessing stage of niche modelling (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, this 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. The study also incorporated the drought index and heatwave trends over the study period to examine the influence of climate change on the mortality trend. This is to evaluate the combined effect of severe drought and unusually warm temperature on mortality as so-called “hotter drought” is known to be the key driver for tree decline whether it is urban or rural (Allen et al., 2015; Nitschke et al., 2017; Settele et al., 2014)

3.3. Research questions and hypotheses

According to the NC hypothesis, it is hypothesised that those species beyond their native NB would be more vulnerable than those within their native NB. In particular, the combining effect of warmer temperature and long-term drought would further increase the mortality risk for those species positioned below the lower limits of their NB.

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?

3.4. Material and methods

3.4.1. Study sites

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 3.1). These botanic gardens not only represent distinct regional climate characteristics of the UK but also hold largest living collections, which enable the calculation of long-term mortality rates. Acquiring long-term mortality rates is quite important to match the temporal scale in this analysis, especially when climate data used in extracting NB are aggregated means over 30 years.

Table 3.1. 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

3.4.2. Selections of species and NB

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 (Appendix A). Species with a minimum of six specimens in at least one botanic garden were selected. Taxonomy of all species was standardised 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.

Four bioclimatic niche variables were selected as potential indicators for mortality response to heat and drought stress; they are 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, the occurrences of each species from the Global Biodiversity Information Facility (GBIF; Appendix A) were obtained and filtered 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 (Appendix B - Figure 1). 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 categorised 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 Appendix A.

3.4.3. Mortality data

Mortality records of all *Acer* and *Quercus* species were obtained for the period between 2000 and 2021, along with all living records as of the 2021 year-end. All mortality records were filtered, excluding all deaths 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. Any deaths identified as physical damage such as storm damage, over-competition, or deaths in a nursery were also excluded. Lastly, trees with unknown accession years or those with accession years before 1900 were excluded, 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 response to climate stress in a specified time interval following as in (1),

$$\mu_o = D_t / R_t \qquad (1)$$

where mortality μ_o 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 summarised in Table 3.2.

Table 3.2. Summary of tree mortality data by botanic gardens.

Genus	Status	KEW	WESB	RBGE
All *Acer*	Number of live trees (end of 2021, *n*)	537	1034	1024
	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 annualised mortality rate (%)	2.0	1.3	2.2
All *Quercus*	Number of live trees (end of 2021, *n*)	1425	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 annualised mortality rate (%)	0.4	1.1	1.4

3.4.4. 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, the standardised precipitation and evapotranspiration index (SPEI) were used. SPEI is a widely used meteorological drought index that utilises monthly climatic water balance information (Vicente-Serrano et al., 2010) as in the Eq. (2).

$$D_i = P_i - PET_i \qquad (2)$$

The difference (D) between precipitation, P and potential evapotranspiration at month i, PET_i is accumulated over a specified time scale and standardised to represent deviations from the mean values. To account cumulative effects, 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, SPEI5yr were used. All monthly SPEI values were calculated using SPEI package v.1.8.1 (Vicente-Serrano et al., 2010).

For heatwave, the total number of heatwave days for each year, HW_{days} were calculated. 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).

3.4.5. Statistical analysis

The mortality analysis was conducted at both genus and species-level. To associate climate anomalies with annual mortality rates, all individuals within a genus were considered 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 (Gompertz, 1833; 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), (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 is expressed in the covariate X of the individual i at a time period of s, with coefficient β and the intercept α. Gompertz regression uses complementary log-log transformation of the probability of mortality μ as expressed in (4). This probability of mortality μ is then rewritten as the inverse log-log function in equation (5). 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 (Appendix B - Table 1).

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). Kruskal-Wallis test was used to assess the difference in mean cumulative mortality rates between groups categorised as 'in' and 'out' of the selected NB, given that the mortality rates represented non-parametric data.

All analyses were performed using the R statistical language (version 4.1.0; R Core Team, 2021). Gompertz regression was run with 'glm' function from R base package, 'stats'. The 'jtools' package version 2.2.2 was used for the summary of hazard models (Long, 2022), and the 'effects' package version 4.2-2 was used for the visualisation of models (Fox, 2003).

3.5. Results

3.5.1. 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 (Figure 3.1-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 (Figure 3.1-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 (Figure 3.1-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 (Figure 3.1-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 its lowest point three years later in 2006 and 2007 (Figure 3.1-b, f, j). When the SPEI$_{5yr}$ reaches its lowest point and coincides with another short-term drought, it creates a 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 SPEI5yr 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).

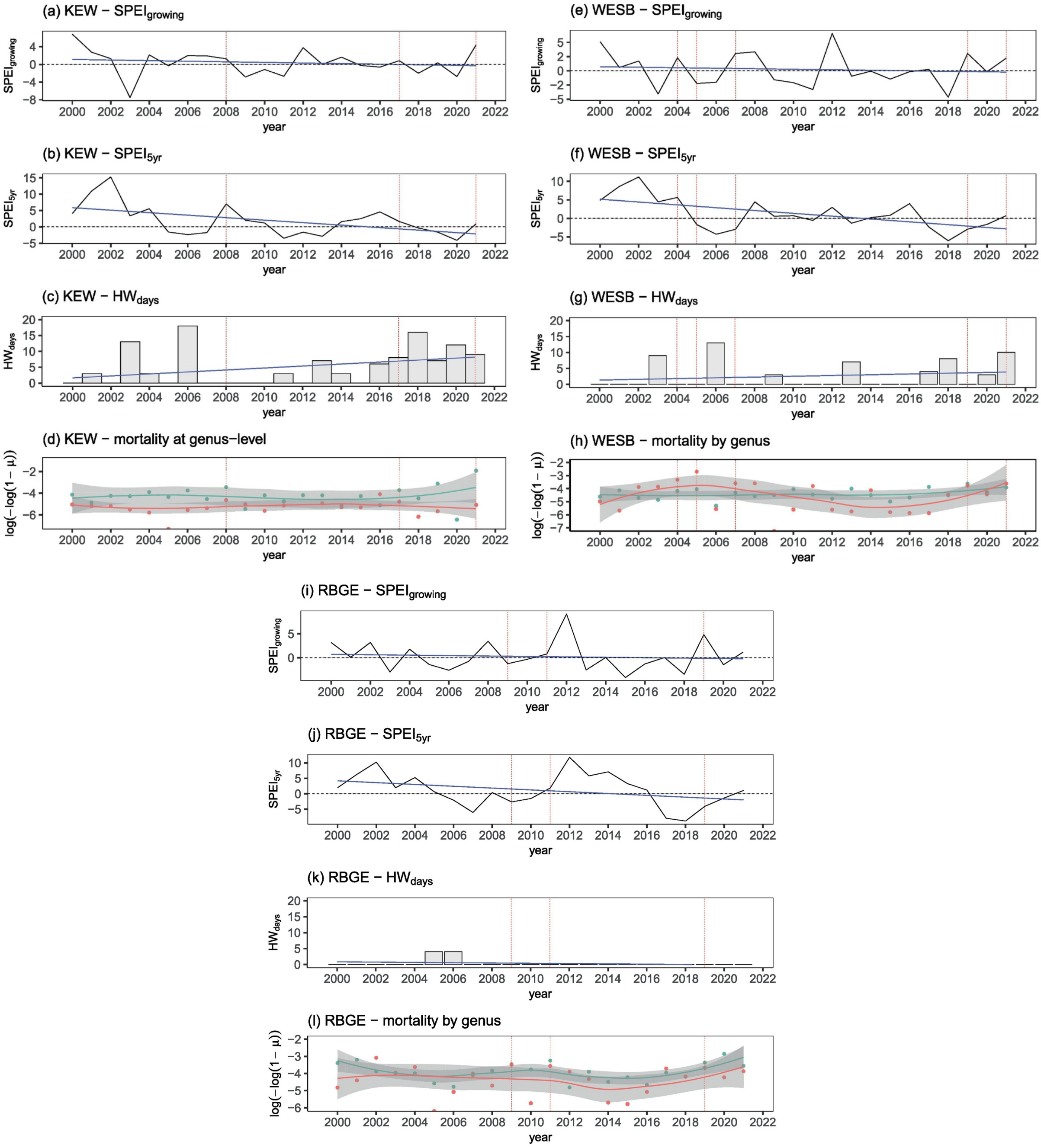


Figure 3.1. The climate trend over the period of 2000 to 2021. The regression fit for KEW, (a) SPEI$_{growing}$ (slope=0.07, p=0.5) (b) SPEI$_{5yr}$ (slope=−0.38, p=0.01) (c) HW$_{days}$ (slope=0.31, p=0.1); for WESB (c) SPEI$_{growing}$ (slope=−0.04, p=0.66), (f) SPEI$_{5yr}$ (slope=−0.38, p=0.004) (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.

3.5.2. The effects of niche positions on the mortality risk

The 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 3.3). 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 (Appendix B - Fig. 2 and Fig. 4). 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 3.3). This is also translated to a 0.9 % decrease in the predicted annual mortality (Appendix B - Fig. 4). 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 3.3), this increased risk corresponds to only a 0.6 % increase in the predicted annual mortality (Appendix B - Fig. 5).

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 lowest when compared to the rates at the other two botanic gardens (Table 3.2). 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 contrasts with *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).

Table 3.3. 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 4,317 (*Quercus*) for RBGE; 8,964 (*Acer*) and 4,363 (*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**
Acer	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
Quercus	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

3.5.3. 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 3.4). 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 (Appendix B - Table 2). 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 (Figure 3.2). While mortality rates within each species vary in a similar range, these variations often correspond to geographical locations, represented here by BGs. Many *Acer* species exhibit a slightly higher mortality rate in the order of KEW > RBGE > WESB (Table 3.4). 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 3.5).

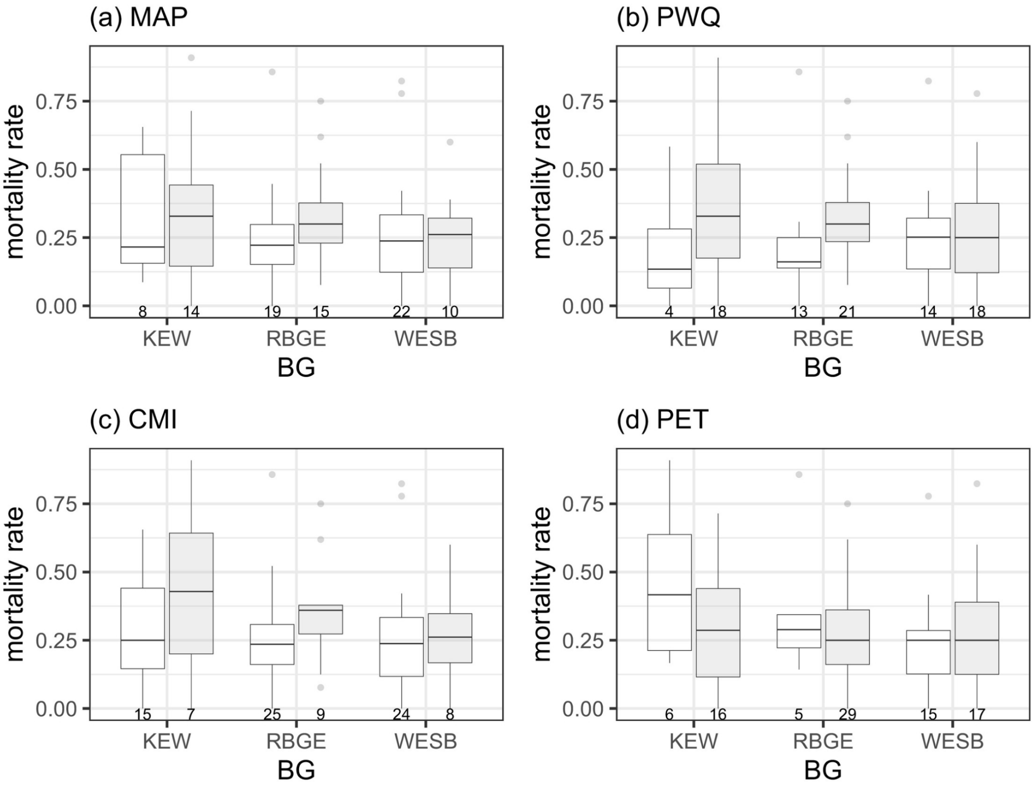


Figure 3.2. The cumulative mortality rates at species-level for *Acer* by their niche positions of the respective NBs. The difference in mean between the "in" (white) and "out" (grey) positions for each bioclimatic niche variable (a) MAP (p = 0.19), (b) PWQ ($p < 0.05$), (c) CMI (p = 1.0), and (d) PET (p = 0.65) was tested using Kruskal-Wallis test (see also Appendix B - Figure 7). However, when the same test was performed within each BG group, no significant difference was found except for PWQ at RBGE.

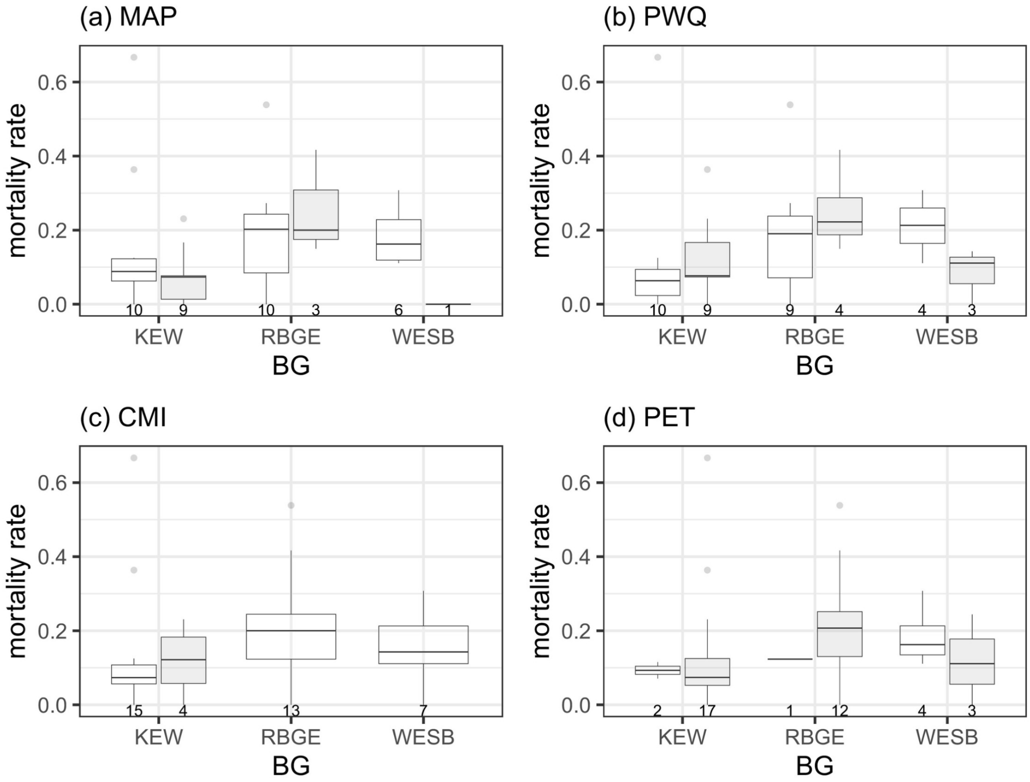


Figure 3.3. The cumulative mortality rates at species-level for *Quercus* by their niche positions of the respective NBs. None of the bioclimatic niche variables exhibited significant difference in the mean between the “in” (white) and “out” (grey) positions with Kruskal-Wallis test (see also Appendix B - Figure 8).

Table 3.4. Cumulative mortality rates within-species for selected *Acer*. 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. 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	*A. campestre*	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
	A. platanoides	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
	A. pseudoplatanus	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	*A. pensylvanicum*	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
	A. negundo	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
	A. rubrum	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
	A. saccharum	WESB	In	**Out**	In	In	0.25	5/20
		RBGE	**Out**	**Out**	In	**Out**	0.27	3/11
	A. sacharinum	KEW	**Out**	**Out**	In	**Out**	0.36	5/14
	A. spicatum	WESB	In	**Out**	In	In	0.78	7/9
		RBGE	In	**Out**	In	**Out**	0.21	3/14
Asia	*A. buergerianum*	WESB	In	**Out**	In	**Out**	0.16	2/12
		KEW	**Out**	**Out**	In	**Out**	0.00	0/7
	A. cappadocicum	WESB	In	In	In	**Out**	0.14	7/50
		RBGE	In	In	In	**Out**	0.16	5/31
		KEW	In	In	In	**Out**	0.09	2/23
	A. crataegifolium	WESB	**Out**	**Out**	**Out**	**Out**	0.60	6/10
		RBGE	**Out**	**Out**	**Out**	**Out**	0.75	18/24
		KEW	**Out**	**Out**	**Out**	**Out**	0.57	5/7
	A. davidii	WESB	In	**Out**	In	**Out**	0.41	16/39
		RBGE	In	**Out**	In	**Out**	0.45	25/56
		KEW	In	**Out**	In	**Out**	0.54	43/79
	A. heldreichii	RBGE	In	In	In	**Out**	0.00	0/17
		KEW	**Out**	In	In	**Out**	0.00	0/8

	A. japonicum	WESB	**Out**	**Out**	**Out**	In	0.27	2/16
		RBGE	**Out**	**Out**	**Out**	**Out**	0.13	6/22
		KEW	**Out**	**Out**	**Out**	**Out**	0.00	0/13
	A. pictum	WESB	In	**Out**	In	In	0.05	1/22
		RBGE	In	**Out**	In	**Out**	0.24	12/51
		KEW	**Out**	**Out**	**Out**	**Out**	0.27	6/22
	A. palmatum	WESB	**Out**	**Out**	**Out**	**Out**	0.39	37/95
		RBGE	**Out**	**Out**	**Out**	**Out**	0.30	33/110
		KEW	**Out**	**Out**	**Out**	**Out**	0.13	22/173
	A. stachyophyllum	WESB	In	**Out**	In	**Out**	0.00	0/16
		RBGE	In	**Out**	In	**Out**	0.26	6/23
		KEW	**Out**	**Out**	In	**Out**	0.30	3/10
	A. tataricum	WESB	In	In	In	In	0.13	2/15
		RBGE	In	In	In	In	0.29	13/45
		KEW	In	Out	In	In	0.66	19/29

Table 3.5. Cumulative mortality rates within-species for selected *Quercus*. 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. 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	*Q. canariensis*	KEW	**Ou**t	In	In	**Out**	0.07	1/15
	Q. cerris	RBGE	In	In	In	**Out**	0.00	0/8
		KEW	**Out**	In	In	**Out**	0.01	1/73
	Q. faginea	RBGE	In	In	In	**Out**	0.00	0/18
		KEW	In	In	In	**Out**	0.08	1/13
	Q. ilex	WESB	In	In	In	**Out**	0.08	1/13
		RBGE	In	In	In	**Out**	0.07	1/14

		KEW	In	In	In	**Out**	0.05	8/164
	Q. pubescens	RBGE	In	In	In	**Out**	0.21	3/14
		KEW	**Out**	In	In	**Out**	0.00	0/10
	Q. robur	WESB	In	In	In	In	0.18	30/165
		RBGE	In	In	In	In	0.12	10/81
		KEW	In	**Out**	In	In	0.07	25/353
	Q. petraea	WESB	In	In	In	In	0.31a	4/13
		RBGE	In	In	In	**Out**	0.19	4/21
		KEW	In	**Out**	In	In	0.12	3/26
	Q. suber	KEW	In	In	In	**Out**	0.05	1/19
North America	*Q. agrifolia*	WESB	In	In	In	**Out**	0.11	1/9
		KEW	In	In	In	**Out**	0.00	0/14
	Q. rubra	WESB	In	**Out**	In	In	0.14	1/7
		RBGE	**Out**	**Out**	In	**Out**	0.20	4/20
		KEW	**Out**	**Out**	In	**Out**	0.07	5/68
Asia	*Q. mongolica*	WESB	In	**Out**	In	In	0.11	1/9
		RBGE	In	**Out**	In	**Out**	0.24^b	11/45
		KEW	In	**Out**	In	**Out**	0.36^a	8/22
	Q. glauca	RBGE	**Out**	**Out**	In	**Out**	0.41^c	5/12
		KEW	**Out**	**Out**	**Out**	**Out**	0.17	1/6
	Q. serrata	RBGE	**Out**	**Out**	In	**Out**	0.15	3/20
		KEW	**Out**	**Out**	**Out**	**Out**	0.08	1/13

3.6. Discussion

3.6.1. Cumulative drought as inciting factor, heatwaves as contributing factor

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 summarised 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 (Figure 3.1). 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 plays 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. 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 (Appendix B - Figure 2 and 3).

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 - characterised 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 3.4). A recent study also reveals that shade-tolerant species 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 maintained 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).

3.6.2. A niche perspective on mortality of *Acer*

The hazard model reveals that, among the selected bioclimatic niche variables, the niche position of PWQ had a 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 (Appendix B - Figure 10), 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 (Appendix B - Figure 6). 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 3.4). Given that this study only assessed four selected bioclimatic variables and classified niche positions 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 (Appendix A). 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 3.4 and Appendix B - Figure 6). 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 responses. 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 favourable 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. carpinifolium* (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 behaviour, 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.

3.6.3. 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 3.3). The results largely relied on its species composition which was dominantly selected from warm temperate regions (Appendix B - Figure 6). 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 3.5). 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* (Appendix B - Figure 13). 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 3.5), 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 the 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 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* (Figure 3.3) and the mortality rate within species (Table 3.5) 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 favourable 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 (Figure 3.1-l), 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.

3.6.4. 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.

Firstly, 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 pre-emptively removed by horticultural decision, especially if they are in poor health conditions, to prevent the spread of diseases. We attempted to minimise this discrepancy by excluding those specifically identified as ‘early removal of poor specimens’ at the data filtering stage as described in Section 3.4.3. On the other hand, records of death caused by pathogens were not removed intentionally, as they were interpreted 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 (Figure 3.1). 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, 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 modelled niche and the realities of how these niches manifest in urban environments. In doing so, the critical role of urban botanic gardens and their underutilised inventory data are underscored (Hirons et al., 2020). 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 initiatives. 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 stocktaking 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.

3.7. 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 a population accumulate over time and exhibit consistent patterns within a 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.

Chapter 4

Species distribution models

This chapter has been submitted but is not yet accepted. Major methods and research framework remain unchanged, but much of introduction, data formats/presentation and discussion are subject to change according to reviewers' feedback.

Kim, E.H., Hitchmough, J.D., Cameron, R.W., Bahn, V., and Schrodt, F., 2024. Relating survival rates to habitat suitability in the phylogenetic context.

Each author has contributed to the following areas:

Eun Hye Kim: methodology, formal analysis, writing – original draft, visualization
James Hitchmough: conceptualization, supervision, review & editing
Ross Cameron: supervision & critical review
Volker Bahn: methodology, critical review & editing
Franziska Schrodt: methodology, critical review & editing

4.1. Abstract

The term 'transferability' refers to the ability of a predictive model to maintain its accuracy beyond the known spatial or temporal extents. In a period marked by profound uncertainties of climate change, model transferability becomes increasingly important for making informed decisions in conservation and land use planning. While ecological niche models essentially aim to predict the unknown, the predictive accuracy largely depends on the environmental similarities between the trained and the projected environments. The study aims to investigate the relationship between niche similarity and habitat suitability (HS) and the relationship between HS and the actual survival rates (SRs). Three introduced *Acer* species, *A. davidii, A. palmatum* and *A. pictum*, were selected for this study and compared their niche with native European species, *A. campestre* and *A. platanoides*. As hypothesized, high niche similarity resulted in the high HS although niche similarity alone did not determine HS. However, *A. davidii* with the highest HS counterintuitively demonstrated the most vulnerability in the UK. Moreover, *A. pictum*, which resulted in poor model transferability with low HS, demonstrated higher SR. Our study further discovers a notable correlation between SRs and phylogenetic proximity; the high SR of *A. pictum* was associated with its closer phylogenetic relationship to native species rather than niche similarities. These results highlight the importance of incorporating basic physiological response data to complement predictive ecological niche models to balance between intrinsic biological factors and extrinsic environmental factors.

4.2. Introduction

Global land-use change and anthropogenic climate change have jointly become the most profound drivers of ongoing transformation in the natural landscapes today (Hoffmann et al, 2019; Scheffers et al., 2016; Winkler et al., 2021). This period of uncertainty has prompted a shift in study of focus from ‘explanatory’ to ‘anticipatory predictions’ of complex ecology systems (Mouquet et al., 2015). In particular, increasing needs in predicting the potential impacts of climate change on species’ distribution pattern to support informed conservation decisions and risk assessment has propelled the popularity of the correlative species distribution models (SDMs) (Pearson and Dawson, 2003). Essentially, SDMs are projected based on the inferred relationship between species occurrences and the environmental characteristics of specific sites they occupy (Elith et al., 2011). However, despite significant advancement in accessible species survey data and global-scale environmental databases, data deficiency still remains a major hurdle in many cases (Sequeira et al., 2018; Elith et al., 2010). Moreover, the changing climate has begun to weaken the stable correlations between extant climate and species occurrences (Williams et al., 2007). This situation may further exacerbate the challenges of already data-deficient discipline, highlighting the critical need for transferable models.

The term 'transferability' refers to the capacity of a model to predict species response beyond the observed spatial and temporal bounds (Sequeira et al., 2018; Yates et al., 2018). While the potential of transferable models lies in maximising the utility of limited sampling, our current knowledge gap hinders reliable transferability, which is the subject of ongoing discussions (Rousseau and Betts, 2022; Thuiller et al., 2008; Yates et al., 2018). Among the challenges, a key limitation arises from the environmental dissimilarities between the sampled and the target regions to be projected: the predictive accuracy diminishes as the novelty of the environment in the target regions increases (Qiao et al., 2019). Further, accounting this environmental dissimilarity into modelling process is even more challenging with increased complexity due to (1) non-equilibrium, absence of species in suitable habitats (Hannemann et al., 2016; Schurr et al., 2012), (2) a choice of variables (Gardner et al, 2019; Petitpierre et al., 2017), and (3) a shift in collinearity (Elith and Leathwick, 2009; Feng et al., 2019).

Another critical challenge with transferring SDMs is model validation. Generally applied validation methods such as split samples, cross-validation, and bootstrapping (Elith and Leathwick, 2009) are more suitable for validation of projections within the sampled biogeographic range. While alternate approaches, such as using independent empirical observations in projected environments (Araujo et al., 2005), comparing predictions with cross-training models (Randin et al., 2006), or identifying spatial patterns in uncertainty (Pearson et al., 2006), have been proposed, testing model transferability and thus dealing with extrapolation of unobserved data remains inherently challenging. Moreover, even a well-fitting model based-on observed distributions does not necessarily imply accuracy, necessitating cautious interpretation.

Considering these challenges, this research seeks to bridge the gap in intricate triangular relationships among niche similarity, modelled projections and actual survivorship. For this analysis, the mortality rates from chapter 3 are used to calculate SR and to compare with extrapolated HS values. HS is the conditional probability of occurrence at the projected site, which is calibrated between 0 and 1 (Elith et al., 2011). Although the HS index does not explicitly reveal how extensive the potential occurrence may be, HS and survivorship link closely in concept (Kearney and Porter, 2009). As such, it can be reasonably assumed that any species is more likely to survive and to grow closer to optimal conditions with a high HS (> 0.8) (Hirzel et al., 2006). Although SRs are restricted to selected sites and not integrated into mechanistic models as outlined by Kearney and Porter (2009), examining if the SR over a specified period of time correlates with the projected HS, especially for those introduced species, is insightful.

4.3. Research questions and hypotheses

The study aims to investigate the relationship between niche similarity and HS and the relationship between HS and the actual survival rates (SRs). Based on the NC hypothesis, it is assumed that phylogenetically related species show ecological niche similarity due to shared ancestry (Warren et al., 2008). Therefore, it is hypothesised that (a) species with high niche similarities to native species will result in high HS and therefore (b) correspond to high SR.

The research aims to answer the following questions.

(1) How closely does niche similarity correlate with HS across different species?

(2) Can HS projections be explained in terms of a species' physiological tolerance to a given climate?

(3) Can phylogenetic signal be detected in niche similarity analysis or SR?

4.4. Material and methods

4.4.1. Study area

The study area includes eastern Asia (China, Japan, and Korea) as training sites to build models, and the United Kingdom as the novel environment where the trained model is transferred to project predictions.

4.4.2. Species occurrence data

Three *Acer* species were selected, *A. davidii*, *A. palmatum*, and *A. pictum* as each species characterises a distinct geographical range (Figure 4.1). Occurrences of *A. davidii* is primarily concentrated in Sichuan, extending to Southern China, which ranges from subtropical zones to cooler montane areas (Su et al., 2021). In contrast, *A. palmatum* is more prominently distributed throughout southwest of Korea and from Honshu to Kyushu in Japan (Chang, 1990). *A. pictum* exhibits a broader distribution, predominantly in more northern regions and higher elevations across all three countries.

All occurrence data were retrieved from the Global Biodiversity Information Facility (http://www.gbif.org; GBIF, 2023) and filtered for invalid occurrences (e.g., non-terrestrial) using the CoordinateCleaner R package v2.0-20 (Zizka et al., 2019). From the downloaded data, only those sources of natural distributions such as herbariums or national survey were selected, and any occurrences outside known native ranges, referenced from the Plants of the World Online (POWO: https://powo.science.kew.org), were excluded. In addition, given the importance of occurrence density in niche modelling and equivalency tests (Warren et al., 2008) and to account for an unequal number of occurrences across countries, all occurrence data were rarefied to the resolution of environmental variables so that a minimum 1 km distance between occurrences were maintained using the spThin R package v0.2.0 (Aiello-Lammens et al., 2015).

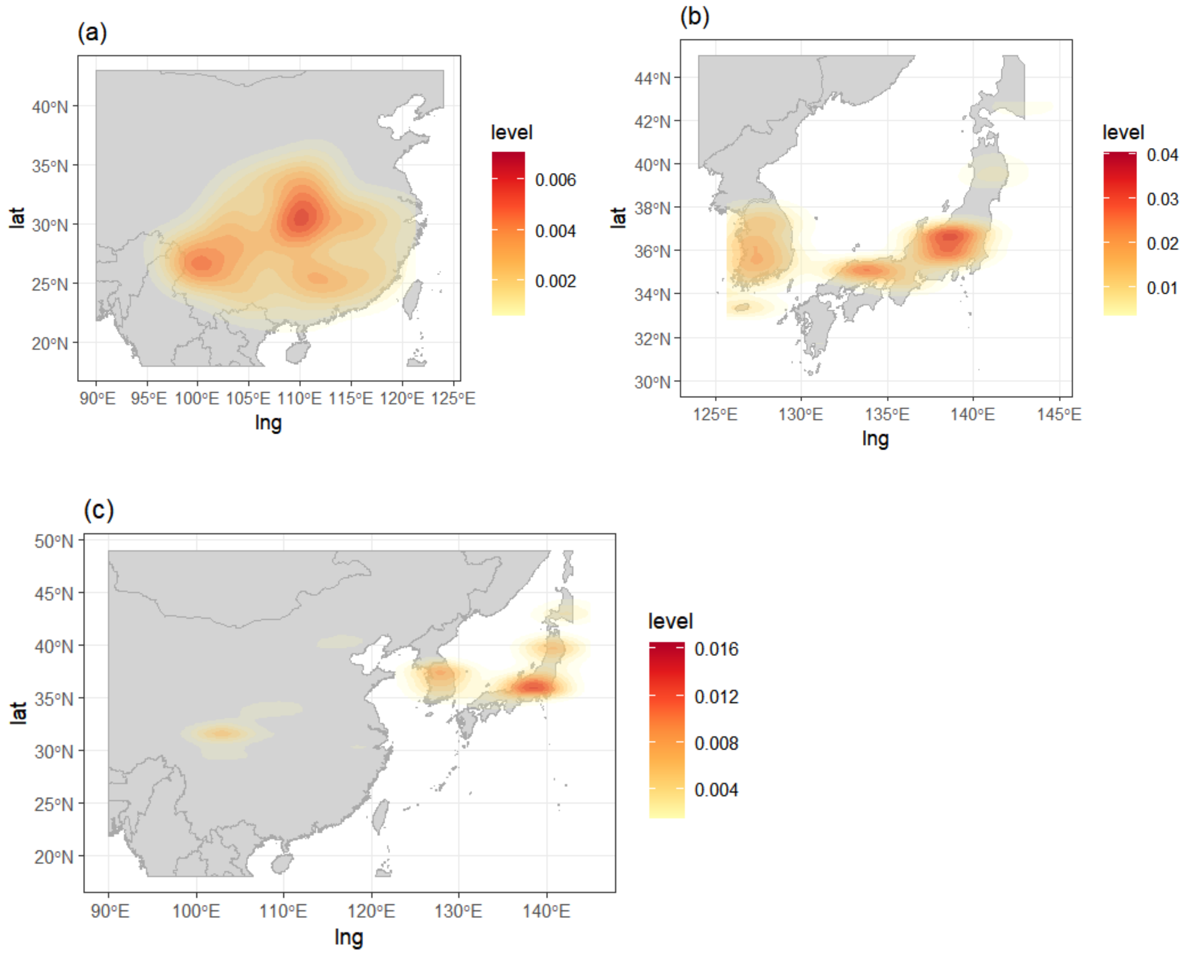


Figure 4.1. Distributed density map of *A. davidii* (n=222), *A. palmatum* (n=925), and *A.pictum* (n=2,671) in their native range

4.4.3. Environmental variables

Climate, soil, and land cover variables were derived from multiple global databases (Appendix C - Table 1). Within the climate category, bioclimatic variables were categorised into three groups based on distinct criteria for each group. The first group, 'bioclim selection A ', is composed of filtered variables based on a paired correlation test with its correlation coefficients < 0.70 (Dormann et al., 2013) out of all 19 bioclimatic variables. The 'bioclim selection B', is again determined based on a paired correlation test but is drawn from a larger pool of variables. In addition to 19 bioclim variables, we selected bioclim+ variables (Brun et al., 2022), which are considered as having more direct influences on plant physiological response (Gardner et al., 2019; Guisan and Zimmermann, 2000). These additional variables include climate moisture index (CMI), potential evapotranspiration (PET), solar radiation (rsds), and the growing degree days above 5°C. Monthly means of CMI, PET, and rsds were aggregated to calculate growing season mean from April to October. The final group, ‘bioclim selection C’, consists of variables that reflect seasonal effects which can link to biophysical tolerance. For example, the growing season CMI is segmented into spring (March to May) and summer (June to August), based on its respective 3-months mean values. Also, regardless of any correlations, bioclim variables were switched to ones that directly reflect plant physiological tolerance, such as bio6, mean minimum temperature of the coldest month and bio9, mean daily temperature of the driest quarter. All bioclim and bioclim+ data were obtained from CHELSA v2.1 climatologies at a spatial resolution of 30 arc sec (~1 km at the equator) (Brun et al., 2022; Karger et al., 2021). All correlation tests were performed using the ‘caret’ package (Kuhn, 2008).

For soil variables, selections were made based on their ecological relevance to nutrient availability and water-holding capacity (Dodd and Lauenroth, 1997; Eyre, 2017). Global soil profile data, including soil acidity (pH), clay, silt, and bulk density of the upper soil layer (0-5 cm), were downloaded from SoilGrids 2.0 (Poggio et al., 2021) at a resolution of ~ 250m. Among them, sand content was excluded due to its strong correlation with clay and silt content. The downloaded profile data were then averaged over 30-arc-second pixels to align its resolution with bioclim rasters. Lastly, remote-sensed land surface characteristics, such as enhanced vegetation index (EVI) and EVI dissimilarity index derived from the Moderate Resolution Imaging Spectroradiometer (MODIS), were download from the EarthEnv (Tuanmu and Jetz, 2015) at a spatial resolution of 30 arc sec (~1 km at the equator). These vegetation indices are indirectly influencing ecosystem attributes such as soil moisture, land surface temperature, and intercepted light amount (Regos et al., 2022). Given that the selected *Acer* species are generally known to be shade-tolerant subcanopy species, we included these vegetation indices to test if these variables would improve our models. However, both EVI and EVI dissimilarity indices are heavily dependent on temporal factors, making it crucial to establish the appropriate temporal condition. In this study, annual EVI dissimilarity and the maximum monthly EVI for each year were averaged across the preset period from 2001 to 2005.

4.4.4. Species distribution modelling

Among the various modelling methods available, MaxEnt v3.4.4 (Phillips et al., 2006) was chosen because it was generally known to exhibit good transferability with presence-only data and is able to handle more complex models (Elith et al., 2006; Heikkinen et al., 2012; Phillips and Dudík, 2008). MaxEnt also shows relatively higher sensitivity compared to other modelling methods. While high sensitivity could potentially lead to over-predictions, it has the advantage of identifying potential niches beyond the calibrated range (Barbet-Massin et al., 2012; Qiao et al., 2019). Prior to modelling, we delineated the training regions for each selected species by generating polygons around each occurrence with a buffer radius of 200 km. The distance was determined based on the previous research demonstrating optimal performance of areas under the receiver operating characteristic curve (AUC), under different strategies of random pseudo-absence points (VanDerWal et al., 2009). A geographic-exclusion strategy has been shown to provide more realistic pseudo-absences than random locations in several studies (Barbet-Massin et al. 2012; Chefaoui and Lobo, 2008). In this research, several test-runs were performed under different settings of minimum distances and the final distance was determined based on optimal balance between AUC performance and transferability. It was noted that the AUC was highest when the minimum distance was set to approximately one degree (~110 km). However, this configuration resulted in poor model transferability, characterised by extreme predictions (data not shown). Such a trade-off between model accuracy and transferability is not uncommon (Heikkinen et al., 2012) and necessitates a mediating approach. We thus created a smaller buffer of either 10 km (for *A. palmatum*) or 30 km (*A. davidii* and *A. pictum*) around occurrences to avoid generation of pseudo-absences in close proximity to known occurrences whilst balancing model accuracy and transferability. The number of pseudo-absences were also an important factor (Barbet-Messin et al., 2012). For *A. palmatum* and *A. pictum,* a total of 10,000 pseudo-absences per species were drawn, while it was reduced to 5,000 for *A. davidii* to balance with a lower count of observed occurrences. This random sampling was repeated 5 times.

For other model configurations, model evaluations were performed using 'ENMeval' v2.0.4 (Muscarella et al., 2014). Four feature combinations ('Linear + Quadratic', 'Linear + Quadratic + Hinge', 'Quadratic + Hinge + Product + Threshold', 'Linear + Quadratic + Hinge + Product + Threshold'), each paired with regularisation multiplier (RM) values of 1.0 and 2.0, generated 8 candidate models for evaluation. In evaluating candidate models, ΔAIC scores were used instead of AUC as proposed by Muscarella et al. (2014). As a result, the full feature combination of 'LQHPT' with RM value of 1 was selected for all species.

Occurrences were split for training and cross-validation, setting aside 20% for cross-validation. With 5 different sets of random samples and 10-fold cross-validations, a total of 50 models were trained and cross-validated. Based on the results of cross-validation, only models with True Skill Statistics (TSS) > 0.5 were used to project distributions in the UK. All resulting model projections of HS were then converged into a single projection by the mean value. The raw HS data was multiplied by 0.01 to standardise highest suitability (1) to lowest suitability (0). The complete modelling process including masking studied regions, random sampling, training, projections, and cross-validations was performed using 'dismo' v1.3-9 (Hijmans et al., 2017) and 'biomod2' v4.2-4 (Thuiller et al., 2023) and run on the high-performance cluster at the University of Sheffield.

4.4.5. Niche identity and similarity test

In addition to SDMs, niche identity and similarity tests were performed to check if there are any coherent patterns in HS and niche similarities between the three selected ex-situ species and native species within the UK (Broennimann et al., 2012; Warren et al., 2008) using 'ENMTools' v1.1.1 (Warren et al., 2021). We selected two widely distributed *Acer* species in the UK, *A. campestre* and *A. platanoides* (Fig. S1) for this comparison. It is noted that *A. platanoides* is selected even though it is not strictly native to the UK. However, as a European species that has extensively naturalised across the UK comparable to 'near-native', its distribution extent was deemed to be adequate for niche comparison. First, the niche identity tests were conducted to test a null hypothesis of equivalency if the environmental niche overlap between two disjunct species remained constant within the 95% density. On the other hand, the niche similarity test evaluates the niche overlap between the two species in comparison to the overlap observed within the available ecological environments. The null hypothesis — that the observed niche overlap does not differ from what would be expected by chance — can be rejected if the *p*-value is below 0.05 after 100 simulation runs. Both tests are primarily based on the metrics, Schoener's D (Schoener, 1970) and Warren's I (Warren et al., 2008). A score of one indicates complete overlap, while a score of zero indicates no overlap.

4.4.6. Habitat suitability and survival rates

Mortality rates for the selected species were obtained and converted into SR (1 - mortality rate) based on previous research (Kim et al., 2023). These retrieved SRs were originally collected from the three urban botanic gardens in the UK; the Royal Botanic Garden, Kew (KEW), Westonbirt, the National Arboretum (WESB), and the Royal Botanic Garden Edinburgh (RBGE). For the comparative analysis, HS scores were aggregated for each local district where these urban botanic gardens are located. Specifically, these local districts are Richmond upon Thames for KEW, Cotswold for WESB and Midlothian and West Lothian for RBGE. For Edinburgh, surrounding counties were selected rather than the city itself as soil variables were only available for non-urban areas.

4.5. Results

4.5.1. Niche identity and similarity

Overall, *A. davidii* demonstrated the highest environmental overlap with *A. campestre* among the three species. It also showed greater niche similarities with the UK distributions than with the whole distributions of Europe, particularly significant on the bioclim selection A and C (Table 4.1). This contrasts with *A. palmatum* which exhibited no environmental overlap with neither *A. campestre* nor *A. platanoides* in the UK on all three sets of bioclim variables. *A. palmatum*, on the other hand, showed some degree of environmental similarities with *A. platanoides* ($p < 0.1$), when tested across broader distributions (Table 4). In case of *A. pictum,* greater environmental similarities with *A. platanoides* across the broader European region were observed, with notable statistical significance on the bioclim selection C and EVI. All of the species on niche identity tests rejected the null hypothesis of equivalency, indicating an ecological niche divergence in the given environmental range.

Table 4.1. Test results of niche identity and niche similarity with *A. campestre* across the UK and Europe. Bold fonts indicate statistical significance as in **, P < 0.01, ∗, *P* < 0.05, ‘, *P* < 0.1. Metrics for Schoener's D (D) and Warren's I (I) were calculated by variable types; Bioclim (bio A, bio B, and bio C), soil (pH, clay, silt and bulk density), and EVI (EVI and EVI dissimilarity).

UK												
	A. davidii - A. campestre				*A. palmatum - A. campestre*				*A. pictum - A. campestre*			
Var.	Identity		Similarity		Identity		Similarity		Identity		Similarity	
	D	I	D	I	D	I	D	I	D	I	D	I
bio A	**0.07****	**0.20****	**0.06***	**0.20***	**0.00****	**0.00****	0.00	0.00	**0.02****	**0.06****	0.02	0.05
bio B	**0.06****	**0.20****	0.06	0.19	**0.00****	**0.00****	0.00	0.00	**0.15****	**0.33****	0.14	0.32

bio C	0.16**	0.36**	0.16*	0.35*	0.00**	0.00**	0.00	0.00	0.12**	0.30**	0.12’	0.30’
Soil	0.26**	0.42**	0.25	0.40	0.26**	0.45**	0.24	0.43	0.19**	0.35**	0.17	0.32
EVI	0.48**	0.74**	0.49	0.74	0.54**	0.77**	0.52*	0.75*	0.58**	0.81**	0.56’	0.80’
Europe												
	A. davidii - A. campestre				*A. palmatum - A. campestre*				*A. pictum - A. campestre*			
Var.	Identity		Similarity		Identity		Similarity		Identity		Similarity	
	D	I	D	I	D	I	D	I	D	I	D	I
bio A	0.11**	0.24**	0.22	0.44’	0.19**	0.38**	0.18	0.36	0.08**	0.17**	0.08	0.16
bio B	0.26**	0.49**	0.25	0.49	0.19**	0.36**	0.18	0.35	0.11**	0.30**	0.12	0.31
bio C	0.27**	0.53**	0.27	0.53	0.09**	0.25**	0.09	0.24	0.13**	0.36**	0.13	0.36
Soil	0.33**	0.55**	0.32’	0.54’	0.21**	0.40**	0.21	0.40	0.16**	0.33**	0.17	0.34
EVI	0.50**	0.76**	0.49	0.76	0.45**	0.70**	0.37	0.62	0.55**	0.79**	0.59’	0.82’

Table 4.2. Test results of niche identity and similarity with *A. platanoides* across the UK and Europe. Bold fonts indicate statistical significance as in ∗∗, P < 0.01, ∗, $P < 0.05$, ‘, $P < 0.1$. Metrics for Schoener’s D (D) and Warren’s I (I) were calculated by variable types; Bioclim (bio A, bio B, and bio C), soil (pH, clay, silt and bulk density), and EVI (EVI and EVI dissimilarity).

UK												
	davidii - platanoides				*palmatum - platanoides*				*pictum - platanoides*			
Var.	Identity		Similarity		Identity		Similarity		Identity		Similarity	
	D	I	D	I	D	I	D	I	D	I	D	I
bio A	0.07**	0.22**	0.07’	0.21*	0.00**	0.00**	0.00	0.00	0.01**	0.04**	0.01	0.04
bio B	0.06**	0.17**	0.06	0.18	0.00**	0.00**	0.00	0.00	0.19**	0.37**	0.19	0.36
bio C	0.20**	0.40**	0.20*	0.41*	0.00**	0.00**	0.00	0.00	0.16**	0.38**	0.16	0.37
Soil	0.09**	0.22**	0.07	0.19	0.23**	0.40**	0.23	0.40	0.10**	0.21**	0.10	0.20
EVI	0.47**	0.71**	0.48	0.71	0.53**	0.75**	0.54’	0.76	0.63**	0.80*	0.62**	0.79*
Europe												
	davidii - platanoides				*palmatum - platanoides*				*pictum - platanoides*			
Var.	Identity		Similarity		Identity		Similarity		Identity		Similarity	
	D	I	D	I	D	I	D	I	D	I	D	I
bio A	0.08**	0.18**	0.08	0.19	0.35**	0.61**	0.34	0.60	0.23**	0.48**	0.24’	0.50’

bio B	**0.23****	**0.48****	0.23’	0.48’	**0.45****	**0.71****	0.45’	**0.71***	**0.35****	**0.65****	0.36’	**0.67***
bio C	**0.23****	**0.46****	0.23	0.46	**0.28****	**0.54****	0.28’	0.54’	**0.39****	**0.69****	**0.39***	**0.68***
Soil	**0.07****	**0.25****	**0.07***	**0.25****	**0.08****	**0.24****	0.08	0.24	**0.14****	**0.34****	0.14	0.33
EVI	**0.43****	**0.72***	0.47	0.75	**0.36****	**0.60****	0.38	0.62	**0.52****	**0.76****	**0.54***	0.78’

4.5.2. Habitat suitability

The overall performance of the trained models was good with mean AUC value of 0.80, 0.90, and 0.92 for *A. davidii*, *A. palmatum*, and *A. pictum* respectively (Table 4.3). The corresponding mean TSS was 0.68, 0.64, and 0.73, all averaged above 0.6. Among them, *A. davidii* showed an increase in performance as the model added variables to the full set of available variables. On the other hand, the performance of the model for *A. palmatum* was highest with bioclim selection A and soil variables. *A. pictum* showed AUC values > 9.0 regardless of variables while it yielded the highest TSS with all bioclim-only sets.

The projected mean HS in the three selected regions was consistently high in the order of *A. davidii* > *A. palmatum* > *A. pictum* across different sets of variables (Figure 4.2 and Appendix C - Figure 2). Richmond yielded the highest mean HS of 0.91 for *A. davidii* while in Cotswold, it decreased to 0.73. *A. palmatum* finds both Richmod and Cotswold similar with mean HS of 0.69 and 0.68 respectively. For all selected species, Midlothian and West Lothian region was projected not suitable with a mean HS of < 0.5. It is noted that the resulting HS for *A. pictum* appear overfitted, yielding projections of extremely low values with either extremely high or null uncertainty values (data not shown) in many regions. The projected HS improved when EVI variables were added to modelling. Nonetheless, such results contradicted the expectation as *A. pictum* showed the highest AUC and TSS.

Table 4.3. Performance of the trained models for selected *Acer* species: *A. davidii*, *A. palmatum*, and *A. pictum*. AUC (Areas under receiving operating curves) and TSS (true skill statistics) were evaluated by different groups of variables. Bioclim variables was selected with criteria of bio A (filtered out of 19 variables), bio B (filtered out of 19 and bioclim+ variables that relate with physiological response), and bio C (filtered out of 19 and seasonal bioclim+ variables). Soils include pH, clay, silt, and bulk density of the topsoil. EVI (enhanced vegetation index) include both EVI and EVI dissimilarity. See Fig. S1 for specific list of variables.

Variable selections	*A. davidii*		*A. palmatum*		*A. pictum*	
	AUC	TSS	AUC	TSS	AUC	TSS
bio A	0.67	0.51	0.89	0.63	0.91	0.78
bio B	0.74	0.60	0.88	0.60	0.90	0.77
bio C	0.74	0.59	0.89	0.61	0.92	0.78
bio A + soil	0.79	0.67	0.94	0.75	0.89	0.62
bio B + soil	0.83	0.73	0.89	0.62	0.91	0.69
bio C + soil	0.82	0.71	0.90	0.64	0.92	0.70
bio A + soil + EVI	0.83	0.73	0.89	0.63	0.92	0.70
bio B + soil + EVI	0.85	0.75	0.90	0.64	0.94	0.74
bio C + soil + EVI	0.90	0.83	0.90	0.65	0.94	0.75

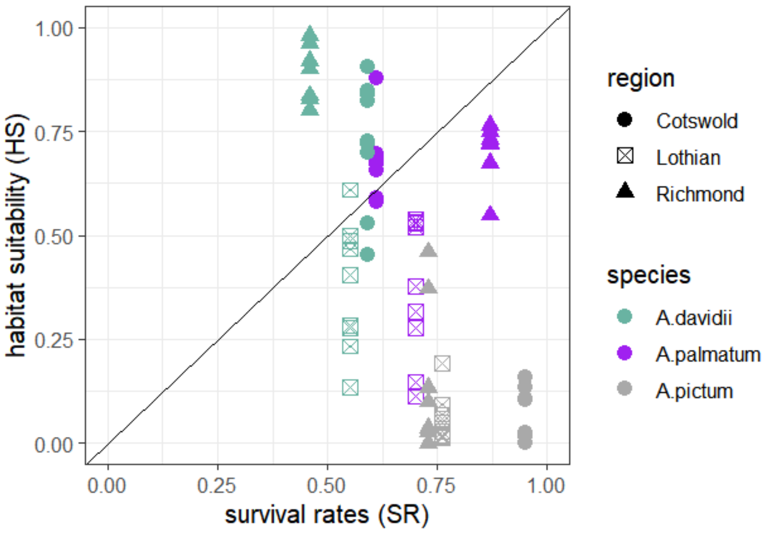


Figure 4.2. Resulting modeled HS and the measured SR from botanic gardens. Each species is represented in the colors of green (*A. davidii*), purple (*A. palmatum*), and grey (*A.*

pictum). Selected UK regions are in the shape of circles (Cotswold), rectangles (Midlothian and West Lothian), and triangles (Richmond).

4.5.3. Survival rates

Contrary to our hypothesis, overall HS and SR are not in agreement. While the overall mean HS was high in the order of *A. davidii* > *A. palmatum* > *A. pictum*, the SR followed exactly the reverse order. Among the three species, *A. davidii* showed the lowest range of SR, all under 0.6, while *A. pictum* demonstrated the highest SR, all above 0.7, in the selected botanic gardens (Table 4.4). The SR of *A. palmatum* varies by region, exhibiting relatively high SR of ≥ 0.7 in KEW and RBGE but a lower SR of 0.6 in WESB.

Table 4.4. Survival rates (SR) by botanic gardens. All SR ≥ 0.7 is in bold font.

garden - region	*A. davidii*	*A. palmatum*	*A. pictum*	*A. campestre*	*A. platanoides*
KEW - Richmond	0.46	**0.87**	**0.73**	**0.84**	**0.75**
RBGE - Mid and West Lothian	0.55	**0.70**	**0.76**	**1.00**	**0.86**
WESB - Cotswolds	0.59	0.61	**0.95**	**1.00**	**0.85**

4.6. Discussion

4.6.1. Niche similarity in the context of phylogenetic relations

Acer is a highly diverse genus, comprising approximately 152 species, with its ancestral biogeographic region traced back to Eastern Asia (Wolf and Tanai, 1987). While majority of these species are still predominantly distributed in Eastern Asia, it is inferred that about a dozen species native to Europe had migrated from Eastern Asia to Europe via ecological corridors of China and Western Asia (Li et al., 2019). In this study, all the selected non-native species originated from Eastern Asia while their biogeographical range size and coverage differ (Figure 4.1). According to the phylogenomic analysis conducted by Li et al. (2019), each species belongs to a different section, *A. davidii* to section *Macrantha*, *A. palmatum* to section *Palmata*, and *A. pictum* to section *Platanoidea*. Interestingly, it is section *Platanoidea* that includes both of the selected UK species in niche comparison. Based on this phylogenetic tree, *A. pictum* is most closely related to these UK species while *A. palmatum* is most distantly related.

These phylogenetic relations are partly reflected in the results of niche similarity tests. The results of the niche identity test evidently indicate that all species occupy in non-equivalent niches, suggesting a pattern of ecological divergence. Nonetheless, the environmental niche overlaps between *A. pictum* and *A. platanoides* were more similar than the given environments available to them, which aligned with their close phylogenetic relationship. This pattern, niche similarity but not identity, is commonly seen in other studies (Peterson et al., 2011), given that the diversification process begins with allopatric speciation, i.e., occurrence of species in isolation due to geographic barriers, while maintaining similar environmental tolerance (Warren et al., 2014). In contrast, other disjunct species exhibiting significant or even non-significant environmental similarities can be interpreted more as differences between their respective environments (Melton et al., 2022). This is because we have limited information on what factors truly influenced speciation beyond environmental filtering as noted by Losos (2011).

4.6.2. Niche similarity and HS

In the general ecological modelling approach, density of the distributions play the key role (Broennimann et al., 2012; Elith et al., 2011; Warren et al., 2008). More precisely, the probability of occurrence is estimated by the probability density function of environmental conditions of occurrence with respect to the probability density function of environmental conditions across the whole background. As a result, *A. davidii,* of which distribution is relatively densely concentrated in the warm temperate regions of Southwest China, exhibits significant niche overlap with *A. campestre* concentrated in the Southern UK (Table 4.1, Appendix C - Figure 1). The resulting niche similarity also correlated with projections of high HS for the selected regions within the UK. In contrast, the models for *A. pictum*, of which environmental distribution density is more analogous to that of *A. platanoides* stretching to Northern Europe, yielded poor HS. However, environmental dissimilarity may not be the single factor that explains poor model transferability in this study. *A. palmatum*, exhibiting zero niche overlap with distributions of both *Acer* species within the UK, still yielded reasonable projections, albeit relatively high mean uncertainty - coefficient of variation about 60% - with the best model. Instead, it may be attributable to more species-specific issues with the model-choice, configurations, complexity of algorithms and selections of variables which need further assessments (Guisan et al., 2007; Yates et al., 2018). For example, species distributions characterised as broad and dispersed across a range of varied physiographic and bioclimatic conditions, such as in case of *A. pictum,* may lead to the development of an overly complex model. With the input of multiple variables, these models may be too tightly fitted to calibration data, exhibiting high accuracy in interpolating within known conditions, but poor predictions for extrapolation beyond the calibration range (Moreno-Amat et al., 2015).

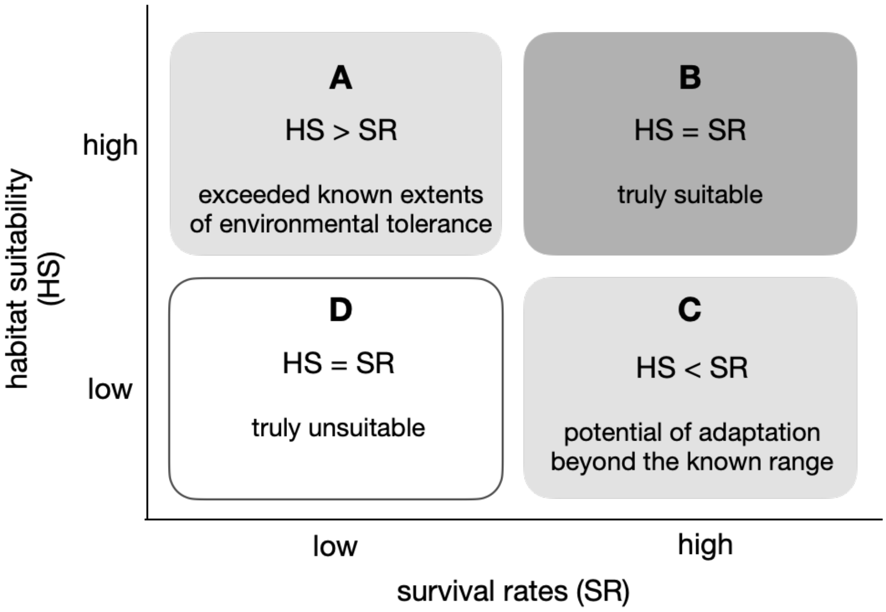


Figure 4.3. A schematic diagram of the relationship between habitat suitability (HS) and survival rates (SR).

Box 1. Relating SR in niche models

There have been continued efforts made to improve accuracy of the predictive niche models by integrating traits and mechanistic processes into SDMs (He et al., 2019; Hülsmann et al., 2018; Morin et al., 2007; Swab et al., 2012). Linking individual biological responses to ecological scale can be exceedingly complex, owing to its non-linear relationship with environments, biotic interactions, and hidden compounding variables (Maschler et al., 2022; Trugman, 2022; Venturas et al., 2021). Nonetheless, employing even a simplified approach of checking biological plausibility can provide complementary perspectives to niche models (Merow et al., 2014; Thuiller et al., 2014). While HS or the probability of occurrence, as a general concept, is projected based on the probability density function of environmental covariates across locations of observed occurrences, high HS does not necessarily translate into high abundance (Thuiller et al., 2014). The discrepancy is inevitable due to imperfect sampling (Elith et al., 2011; Royle et al., 2005). Moreover, many of these observed occurrences are based on herbarium records of which temporal extents are often too broad to reflect changing climate. In this context, SR, by reflecting demographic performance over a specified time period, can be particularly useful in assessing responses to abnormal climate events. While SR can be assessed on a large scale, such as across extensive forested landscapes, it is more often assessed within a more confined and restricted spatial extent, especially for ex-situ species. Conducting assessment in more controlled environments such as common gardens, plantations, or, as in this study, botanic gardens can streamline the process, which is more advantageous for species-specific monitoring. Considering all these differences, comparing SR to HS can yield additional insights especially when these two factors are not in agreement (Figure 4.3). When SR is low and HS is high (SR < HS), it is more likely that sites previously considered suitable have experienced adverse environmental changes, potentially contributing to species declines. In case of extrapolation, given that the projected HS cannot be validated, it raises reasonable doubts about the presence of other unaccounted but significant variables for decline, yet omitted in the models. Conversely, when SR is high and HS is low (SR > HS), the inference is reversed. Sites that were previously considered less suitable or not occupied might be potentially suitable environmental conditions despite, or because of climate change. Similarly, there also exists the potential of unaccounted variables leading to higher SR.

4.6.3. Interpreting SR based on the environmental niche and beyond

While HS is derived from the models trained on the bioclimatic conditions spanning from 1981 to 2010 across a broad geographical area (Karger et al., 2021), our previous research (Kim et al., 2023) details species-specific mortality events tied to specific locations from 2000 to 2021. The disagreement between HS and SR may propose two distinct potential scenarios as described in Box 1. When SR is lower than projected HS as in the case of *A. davidii*, it suggests a potential exceedance of the known extent of environmental tolerance in response to recent transitions toward warmer and drier climate in the UK as evidenced by heatwave becoming an annual occurrence in the Southeast UK from 2010 onwards (Kim et al., 2023). Further, the number of annual mortality events of *A. davidii* at KEW evidently reached a dramatic peak in 2021 (data not shown), which is interpreted as an indication of accumulated heat and drought stress. Another case is when SR is higher than projected HS as observed in *A. pictum* at all three sites and *A. palmatum* at KEW and RBGE. This suggests that these species may have higher potential for adapting to the changing climate in the UK compared to *A. davidii*. The discrepancy arises primarily because species distributions are closely tied to geography rather than biological processes (Warren et al., 2014). In other words, the environmental tolerance inferred from species native distributions might not accurately reflect the true physiological tolerance of these species.

The disparity in HS-SR can be further explained by examining its phylogenetic relationships rather than focusing solely on the environmental niches. Interestingly, it has been observed that sister species belonging to the same section display similar SRs among themselves. For example, within section *Platanoidea,* to which *A. pictum* belongs, other sister species such as *A. cappadocicum* (0.84~0.91), *A. platanoides* (0.77~0.80), and *A. campestre* (0.84~1.0) exhibit a similar range of high SRs. On the other hand, those species within section *Macrantha*, to which *A. davidii* belongs, have shown relatively lower SRs as observed in *A. pensylvanicum* (0.29~0.59) and *A. crataegifolium* (0.25~0.40). Lastly, *A. palmatum* belonging to section *Palmata* also shows a similar range of SRs with sister species within this section such as *A. japonicum* (0.73~1.0) and *A. circinatum* (0.72~0.86). Such patterns are not only evident in the interspecific SRs but also evidenced in the variations of intraspecific SRs among the botanic gardens. For instance, the SRs of those species from section *Macrantha* are similarly lowest at KEW and highest at WESB, whereas those species from section *Palmata* exhibited the opposite patterns, lowest at WESB and highest at KEW. These coherent patterns of variations observed within sections suggest the presence of the "phylogenetic signal i.e., the tendency that more closely related species show similar characteristics" (Pearman et al., 2008). Furthermore, phylogenetic distance hints us that there are other ecological processes involved in speciation beyond just environmental filtering. Specifically, phylogenetic relationships — *A. davidii* being closer to North American species and *A. pictum* to European species — prompt an exploration into other common phenotypic or ecotypic traits that might contribute to similar survivorship, beyond just realised niche similarities.

4.7. Conclusions

Most predictive SDMs rely on correlative relationships between environment-occurrences. However, the discrepancies between true population density and sampling density, as well as between these densities and the optimal environmental growth conditions, lead to intrinsic limitations of correlative models especially for extrapolated projections. These findings, as an exemplary case of such limitations, highlight the significance of incorporating physiological response data. While more similar physiological responses, SRs, were observed among phylogenetically closer species in the novel environment, the actual range of environmental conditions in their natural distributions are not necessarily more similar to each other than those species less related. This leads to the conclusion that projection of HS solely based on the environment-occurrence correlation would invariably reveal only part of the complete picture. The dynamic interactions between intrinsic and extrinsic driving forces in shaping ecological communities is an ongoing fundamental question in the field of ecology. While much research has already underscored the further needs of balancing these two factors in SDMs, addressing realistic logistical issues, such as difficulties in data collections and developing a shared knowledge platform on a global scale, remains a challenge. In this regard, this research presents the potential opportunity of leveraging inventory data from the botanic gardens, whose roles in the times of climate change may extend from local to a broader global community.

Chapter 5

Plant water use strategy

This chapter is currently being prepared for submission. Major methods and research framework remain unchanged, but much of introduction, data formats/presentation and discussion will be revised.

Kim, E.H., Hitchmough, J.D., and Cameron, R.W., 2024. Exploring variability of water use between and within Acer and Quercus species

Each author has contributed to the following areas:

Eun Hye Kim: methodology, formal analysis, writing – original draft, visualization
James Hitchmough: supervision, review
Ross Cameron: supervision, review

5.1. Abstract

Contrasting hydraulic strategies between *Acer* and *Quercus* species have been already well-studied. However, the extent to which those contrasting strategies operate consistently across different environmental contexts remains unclear. Here, we selected a pair of co-occurring species *Quercus rubra* and *Acer rubrum*, and alternatively *Q. alba* and *A. saccharum* to assess the variability of their water use within and between species. We synthesised species-specific sap flux data across 5 different forested US sites from SAPFLUXNET, the first global database of sap flow measurements, which enables retrieval of individual plant level sap flow data. Our analysis reveals that species exhibit their anticipated water use behaviour when they encounter their preferred belowground conditions that fit species-specific functional traits. This is primarily linked to soil water content (SWC) independently and predominantly contributing to the majority of variability in sap flux. For example, where water was not a restricting factor, *Acer* and *Quercus* did not differ in their sap flux density. However, when belowground conditions, such as soil texture

or soil depth, did not support those key functional traits to cope with water stress, their response deviate greatly from their typical behaviour. For instance, anisohydric *Quercus* suppressed transpiration lower than isohydric *Acer*. The result presents potential exacerbated water stress at urban landscapes with hostile soil conditions. Moreover, positive land-atmosphere feedback would further drive a drier environment by suppressing transpiration of urban trees. Our study highlights the importance of synthesising fragmented sap flux data and contextualising species-specific response within a broader biogeographical framework. This is essential to enhance our predictive capacity of plant response to climate change and narrowing the gap between individual plant function and broader ecosystem dynamics.

5.2. Introduction

Transpiration is an integral component of carbon and water cycle as the dynamics of water fluxes through plants extend from the individual organism level to the broader ecosystem level through the soil-plant-atmosphere continuum (SPAC) (Anderson et al., 2003; Fatichi et al., 2016; Stoy et al., 2019). The significance of this subject has been further highlighted by the increasing frequency of drought events driven by climate change in the recent decades, leading to widespread tree declines and shifts in species distributions on a global scale (Allen et al., 2015; Landsberg and Waring, 2017; McDowell et al., 2008). In the context of the urban environment, the examination of transpiration has recently begun to emerge, primarily focusing on its contribution to urban cooling or reduction of stormwater runoff (Rahman et al., 2020; Pataki et al., 2011; Szota et al., 2018; Thom et al., 2022). Given the widely acknowledged significance of canopy transpiration in reinforcing the role of urban trees as a nature-based solution for climate adaptation, efforts to model transpiration as a key proxy metric for assessing ecosystem function and species-specific performance are also on the rise (Winbourne et al., 2020). However, despite the substantial evidence, it remains challenging to translate this knowledge effectively into the real-world design and implementation of multifunctional green infrastructure (Pataki et al., 2021; Sousa-Silva et al., 2023). Plant-water interactions and hydrodynamics are amongst the most variable and uncertain components of the ecosystem, highly dependent on the specific environmental context even among individuals of the same species (Feng et al., 2019; Kannenberg et al., 2022). Given the heterogeneity of urban environments, many studies, often short-term and based on a limited numbers of individual species using inconsistent metrics between studies, restrict capacity to generate informed guidance for practice.

In recent years, a growing number of studies on the conceptual framework of plant regulation in water use under hydraulic stress gained traction for its potential to provide predictive measures (Kannenberg et al., 2022; Roman et al., 2015). It is especially appealing as it simplifies complex biological processes framed into a binary axis of iso- and anisohydric, corresponding to ‘conservative’ and ‘acquisitive’ strategies to guide species selection for stressed urban sites (Gillner et al, 2017; Szota et al., 2018). Yet, differing definitions used in evaluations lead to conflicting interpretations, compounded by evidence of intraspecific variability, which also collectively restrict its application to practice (Feng et al., 2019; Hochberg et al., 2018; Martínez-Vilalta and Garcia-Forner, 2017). These challenges highlight the need for more consistent and continuous in-situ data across a broader range of species and environments (Choat et al., 2012; Novick et al., 2022). The recent introduction of SAPFLUXNET (https://sapfluxnet.creaf.cat) (Poyatos et al., 2021), an initiative that compiled a global database of sap flow measurements, is encouraging. Sap flow, the flow of water through tree stems, is linearly related with canopy conductance (Grainier and Bréda, 1996). These measurements were predominantly collected for estimation of transpiration on a stand-scale or scaled up for analysis of ecosystem water flux. Nonetheless, with the pre-calibrated dataset from SAPFLUXNET, a comparative analysis of species’ individual water use across multiple sites has become more feasible, which would otherwise be costly. This comparative analysis can be particularly significant in urban contexts, where non-native species are often introduced to highly heterogeneous environmental conditions that differ markedly from their native habitats. It is because species can be falsely ‘characterized’ if the evaluation is based solely on the ‘response traits’ and overlooks crucial interacting environmental conditions that actually contribute to species success (Feng et al., 2018). For example, species known as drought tolerant in their native habitats would not necessarily thrive in dry conditions of urban sites of analogous climate if certain environmental conditions are not met. Therefore, this research aims to improve our understanding of species-specific responses at individual-level across a diverse range of environmental conditions and to examine the environment-response interactions using SAPFLUXNET datasets. In particular, the study primarily focuses on two species, *Q. rubra* and *A. rubrum*, and alternatively *Q. alba* and *A. saccharum* as these species are co-occurring species of contrasting water use strategies with wealth of documented literature. *Q. rubra* and *Q. alba* are generally known to exhibit anisohydric behaviours with associated traits such as deep tap roots and ring-porous stems, efficient for rapid hydraulic transport from deep soil (Hacke et al., 2006; Kannenberg et al., 2019). On the other hand, *A. rubrum* and *A. saccharum* exhibit isohydric behaviors with shallow fine roots and diffuse-porous stems, relatively slower water transport but efficient in quick water acquisition from topsoil (von Allmen et al., 2015). Lastly, given that all sap flow data is derived from the native forest stands, it is attempted to reinterpret how these findings from the comparative analysis should be applied in the urban environmental context.

5.3. Research questions and hypotheses

It is hypothesised that two co-occurring species with contrasting water use strategies should exhibit consistently contrasting behaviors across different environmental conditions. In addition, strong confounding effects of heat and water balance-related variables would be expected to characterise the variability of sap flux for both *Quercus* and *Acer* species.

Therefore, this research aims to answer the following research questions.

(1) How consistent are the overarching water use strategies of co-occurring *Acer* and *Quercus* species across different environmental conditions?

(2) Is the response of species-specific sap flux to changing moist levels consistent?

(3) Between heat and water balance-related environmental variables, which environmental variables independently or jointly contribute to the variability of sap flux across different sites?

(4) How can the results of questions (1) ~ (3) be interpreted in the context of urban environments?

5.4. Materials and methods

5.4.1. Sites and species selections

Sites and species were selected based on the downloaded data from global SAPFLUXNET database, version 0.1.5 (Poyatos et al., 2021). The prerequisite for site selection was that it must have sap flow measurements for both co-occurring species from *Quercus* and *Acer* for comparative analysis. A total of 5 sites that have either *Q.rubra* or *Q.alba* and *A.rubrum* or *A.saccharum* were selected (Figure 5.1, Appendix D - Table 1) (Cook et al., 2004; Matheny et al., 2014; Tajchman et al., 1987; Wilson et al., 2001; Yi et al., 2016). It was intended to have at least two replicates per species per site. Moreover, it was ensured that the individual samples of similar sapwood areas were chosen to minimise any size effects on transpiration. The mean annual temperature (1981-2010), T_{annual}, for each site ranges from a low of 5.2 °C in Wisconsin, WI to a high of 14.8 °C in Tennessee, TN, whereas the mean annual precipitation (1981-2010), P_{annual}, ranges from a low of 781 mm in Michigan, MI to a high of 1,493 mm in West Virginia, WV. To compare interannual variations, annual measurements from each site were categorized into either relative 'normal' or 'dry' years. The distinction between normal and dry year was determined by the ratio of actual precipitation during the measurement period to the long-term average precipitation of the corresponding period, represented as P/P_{mean} (Table 5.1). For example, a year would be considered 'normal' when the P/P_{mean} ratio falls within ± 15% or 'dry' when the P/P_{mean} ratio falls between 0.5 and 0.85. Soil textures vary from 92% sand content in MI (Matheny et al., 2014) to silt clay loam in TN (Wilson et al., 2011). WV is a silt-loam soil but in quite distinct condition, with its restricted soil depth of less than 1 m to bedrock (Tajchman et al., 1997).

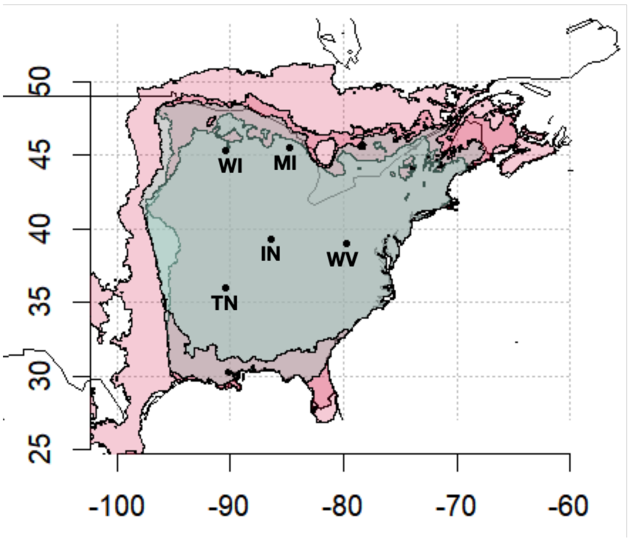


Figure 5.1. Site locations and species range map by colour: *Q. rubra* (light green), *Q. alba* (gray), *A.rubrum* (red), and *A.saccharum* (light red). Sites are abbreviated according to their state names: Indiana (IN), Michigan (MI), Tennessee (TN), Wisconsin (WI), and West Virginia (WV). The range map was obtained from the Botanical Information and Ecology Network (BIEN) database using the BIEN R package version 1.2.6 (Maitner et al. 2018).

Table 5.1. Environmental characteristics of the selected sites. T_{annual} (mean annual air temperature), P_{annual} (mean annual precipitation), $P_{(Jun\text{-}Aug)}$ (Precipitation during the summer), P/P_{mean} (Precipitation of the summer was divided by mean summer precipitation). *a* - Y1 in TN experienced drought during the late summer although overall P/P_{mean} remained within ± 15% (Wilson et al. 2001).

env.	unit	year	IN	TN	MI	WI	WV
T_{annual}	℃		12.0	14.8	6.7	5.2	9.3
P_{annual}	*mm*		1,227	1,427	781	861	1,493
$P_{(Jun\text{-}Aug)}$	*mm*	Y1	261	307	262	370	395
		Y2	131	343	207	217	220
P/P_{mean}		Y1	0.78	0.89^{a}	1.15	1.12	1.11

	Y2	0.39	0.99	0.90	0.65	0.50
soil		silt-loam	silt clay loam	sandy	sandy-loam	silt-loam/stone

5.4.2. Sap flux data

From each individual tree, at each site, data for sub-daily mean sap flow per plant (SF, $cm^3\ h^{-1}$) during the daytime were obtained. The daytime mean was calculated for hours between 9:00 and 18:00. The mean SF data were then normalized using two approaches, (1) the normalized mean sap flux ($cm^3\ cm^{-2}\ h^{-1}$) was obtained by dividing sapwood area (A_{sw}) and (2) the normalized ratio by dividing the seasonal mean sap flux over the entire study period by the seasonal maximum sap flux. The first approach focuses on relative transport capacity negating tree size and sapwood differences, whereas the second approach focuses on the variability between the seasonal mean and the seasonal maximum. All measurements were filtered to the period between 1 June to 31 August in order to minimize the influence of phenological changes in leaf area index. Also, any days with mean daily VPD < 0.1 kPa were removed to exclude extreme values. Sap flow measurements were made using the heat dissipation method at three sites (MI, TN, WV) and heat pulse method at the other two sites (IN, WI) (Appendix D - Table 1).

5.4.3. Environmental variables

A total of six environmental variables were obtained from the SAPFLUXNET database. Although soil water content (SWC) and vapour pressure deficit (VPD) are considered primary factors that drive transpiration, additional variables such as daily averaged values of air temperature (T_{air}), daily averaged soil temperature (T_{soil}), net radiation (R_n), and relative humidity (Rh) were added to expand the scope of environmental interactions. SWC was limited to shallow depth which is typically between 0 and 30 cm.

When there was any period that contains missing data, alternatively, remote sensed environmental variables were retrieved from the latest ERA5 hourly data at a 0.25° horizontal resolution (~28km; Hersbach et al. 2023). ERA5 is the fifth generation ECMWF reanalysis for the global climate and weather, which combines modelled data and observations to provide consistent hourly estimated datasets. All daily values were calculated for the daytime hours corresponding to 09:00-18:00.

5.4.4. Variation partitioning

Environmental variables are interrelated. For instance, 'hotter droughts,' which are often characterized as major climate threats to increasing tree decline across biomes, present complex interplay where the effect of heat and that of moisture deficit are not clearly distinguishable as heat and drying occur together (Allen et al., 2015; Yi et al., 2022). Multicollinearity often complicates the identification of whether the effects are solely due to independent variables or joint effects of multiple variables (Mac Nally, 2000). Ignoring these confounding effects might provide misleading interpretations on the effects of environmental variables. To overcome this issue, variation partitioning was employed following the detailed methods used by Anderson and Cribbles (1998), Heikkinen et al. (2004, 2005), and Wang et al. (2011). This approach allows decomposing variance of selected variables by groups, which helps to contextualize interrelated variables and to outline the relative importance of both independent and joint contribution (Borcard et al., 1992; Peres-Neto et al., 2006; Wang et al., 2011). Environmental variables were broadly categorized into two groups: the heat, denoted as H (T_{air}, T_{soil}, and R_n) and the water balance, denoted as WB (VPD, SWC, and Rh). Variation partitioning would fraction the variance of sap flux into four fractions based on three canonical analysis, the individual effects of H and WB denoted as a and b, respectively, the joint effects of H and WB denoted as c, and finally the undetermined variation denoted as u (Figure 5.2). The sap flux data was regressed collectively with respect to the two groups, which yielded the total explained variation ($a + b + c + u$). Subsequently, regressing sap flux with each explanatory group separately yielded the variation explained by H ($a + c$) and WB ($b + c$). Then, a series of redundancy analysis (RDA) were undertaken to determine the pure fraction of each explanatory group and its joint effects at a time. All RDA runs were performed for each group according to a forward selection option in CANOCO and the associated Monte Carlo permutation tests (involving 9999 permutations) to exclude explanatory variables that did not contribute significantly to variance of sap flux, at $P > 0.05$ (Borcard et al. 1992). Variation partitioning and RDA were performed using 'vegan package' version 2.6-4 (Dixon 2003).

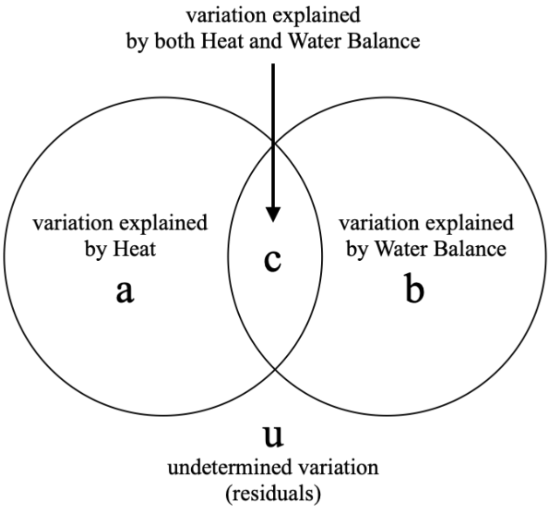


Figure 5.2 – The conceptual Venn diagram of variation partitioning between two sets of explanatory variables, H and WB.

5.4.5. Hierarchical partitioning

To identify individual contributions of environmental variables in the order of significance, hierarchical partitioning method was conducted using 'rdacca.hp package' version 1.1-0 (Lai et al., 2022). In hierarchical partitioning, it computes the increase in the fit, measured in adjusted R^2, of all models with a particular variable compared with the equivalent model without it (Mac Nally, 2000). As a result, it yields an estimate of independent and joint effect of each variable with all the other variables (Heikkinen et al., 2004). VPD data was log transformed to improve linearity. Also, all data was centered and standardized before running analysis, which was performed using the R statistical language (version 4.3.0; R Core Team, 2023).

5.5. Results

5.5.1. Interannual sap flux variations across regions

Among the selected 5 sites, IN, TN, and WV can be grouped together as they fall within the latitude range of 35 and 40 degrees, exhibiting relatively warmer and wetter with loamy soils (Table 5.1 and Figure 5-3). Comparably, MI and WI can be grouped as both are situated above 45-degree latitude, characterized by slightly cooler temperatures, less precipitation, and more sandy soil texture. Despite its relatively lower MAP, WI represented the moist end among the 5 sites with the highest mean daily SWC and the lowest mean daily VPD, mostly under 1.0 (Figure 5.4). On the other end, IN characterized the driest condition marked by the largest reduction in precipitation of 60% with its highest mean VPD reaching up to 4.2 kPa. However, it is noted that MI exhibits the lowest long-term mean summer rainfall among all the sites despite its P/P_{mean} being above 0.9. This factor, in conjunction with sandy soil, accounts for the lowest SWC values.

Although sap flux density varied significantly under different environmental conditions, *Acer* more often exhibited higher sap flux density compared to *Quercus*. This pattern was particularly pronounced during dry years (Figure 5.5 and Appendix D – Figure 1). Even under the driest condition in IN (Appendix D - Figure 1c and h), *A.rubrum* showed a mean sap flux rate of 8.8 ± 1.6 $cm^3\ cm^{-2}\ h^{-1}$, about twice as high as that of *Q.rubra* whereas the difference was marginal at the wettest WI. In WI, both *Q.rubra* and *A.saccharum* exhibited similar daily sap flux density with a mean of 30.4 ± 12.8 and 30.4 ± 12.2 $cm^3\ cm^{-2}$

h^{-1} respectively (Appendix D - Figure 1e and j). Comparably, the sap flux density for *Q. rubra* was lowest with a mean of 3.7 cm^3 cm^{-2} h^{-1} in IN while the lowest mean was 6.0 cm^3 cm^{-2} h^{-1} for *A.rubrum* in WV (Appendix D - Figure 1c and g).

The interannual comparison highlighted a clear pattern: sap flux density generally decreased during dry years, correlating with annual precipitation variability. Specifically, *Acer* reduced sap flux during the second year at all four sites, with the exception of WI, which corresponded to decrease in precipitation. *Acer* also exhibited greater responsiveness to VPD (Appendix D - Figure 1). This greater sensitivity is translated into greater variability within the season, which is reflected in the relatively lower sap flux ratio mostly under 0.5 (Figure 5.6). In contrast, *Q .rubra* selectively reduced sap flux in WV and TN while it slightly increased sap flux in IN, MI, and WI. The most dramatic reduction was observed in WV where the mean sap flux of *Q. rubra* decreased by one sixth from 12.6 ± 3.0 to 2.1 ± 0.9 cm^3 cm^{-2} h^{-1}. Overall, *Q. rubra* tended to maintain low water use during the dry year, remaining relatively constant regardless of changes in VPD in TN, WV, and IN (Appendix D - Figure 1a, b, and c). The lower variability is also reflected in a generally higher sap flux ratio, mostly exceeding 0.5.

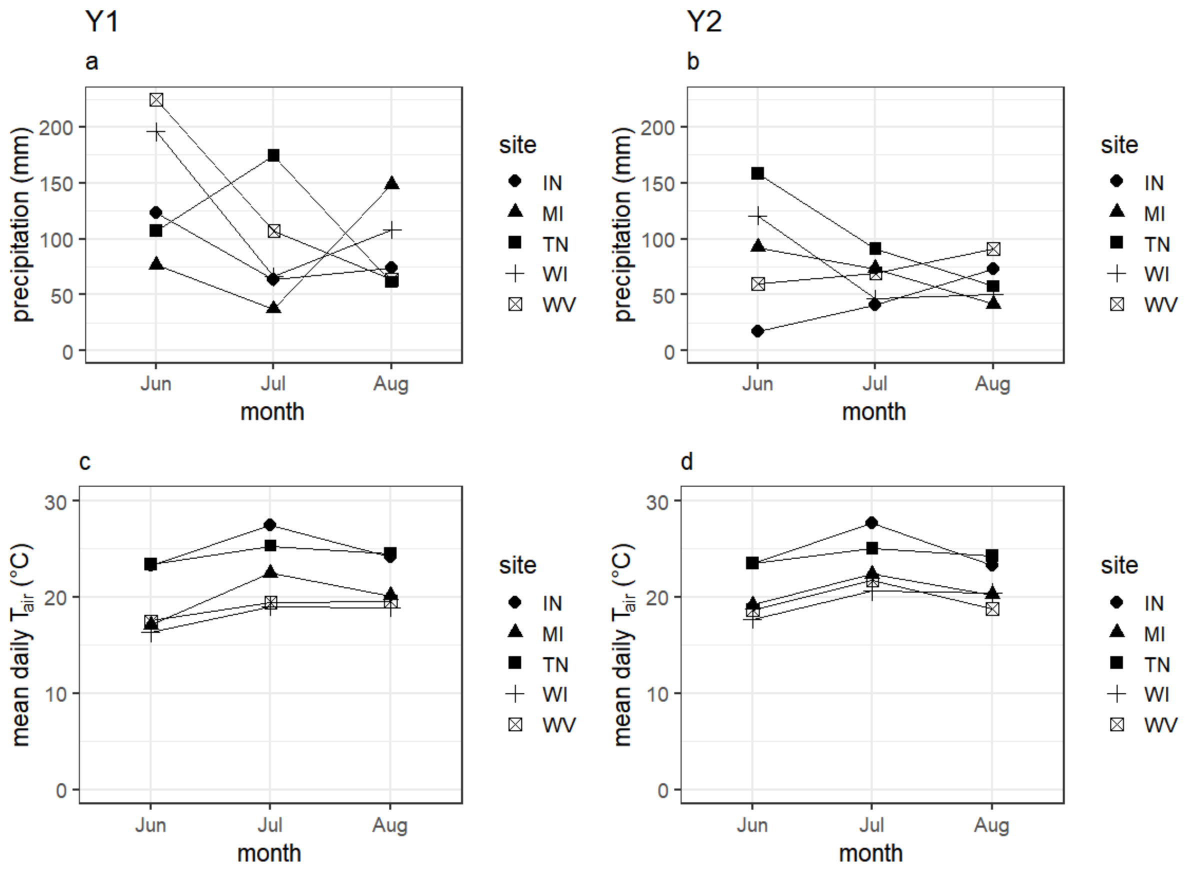


Figure 5.3. Monthly summary of total precipitation for year 1 (a) and year 2 (b) and of mean daily T_{air} for year 1 (c) and year 2 (d). Data are retrieved from ERA5 reanalysis product as described in 5.4.3.

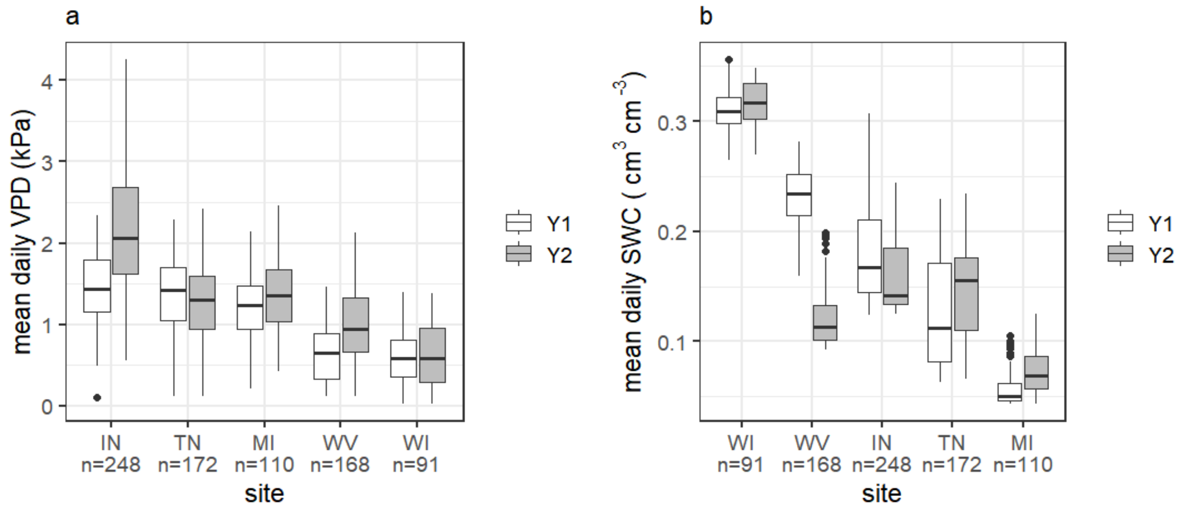
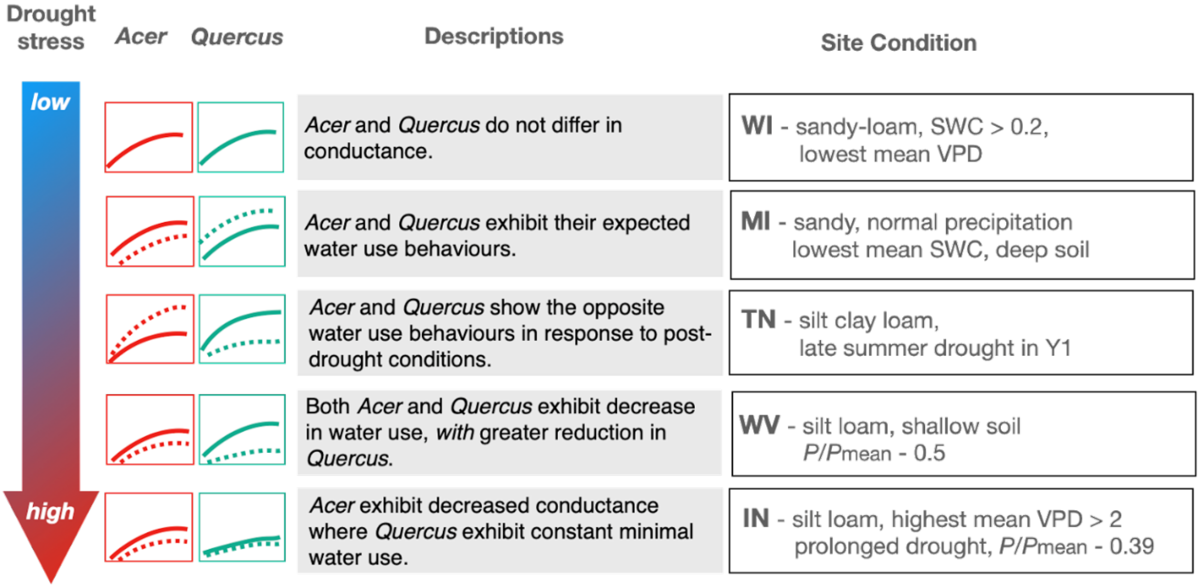


Figure 5.4. Comparison of interannual (a) mean daily VPD and (b) mean daily SWC during the daytime (9:00-18:00). Y1 and Y2 denote year 1 and year 2 respectively. All data are in-situ measurements.



Descriptions	Site Condition
Acer and *Quercus* do not differ in conductance.	**WI** - sandy-loam, SWC > 0.2, lowest mean VPD
Acer and *Quercus* exhibit their expected water use behaviours.	**MI** - sandy, normal precipitation lowest mean SWC, deep soil
Acer and *Quercus* show the opposite water use behaviours in response to post-drought conditions.	**TN** - silt clay loam, late summer drought in Y1
Both *Acer* and *Quercus* exhibit decrease in water use, *with* greater reduction in *Quercus*.	**WV** - silt loam, shallow soil *P*/*P*mean - 0.5
Acer exhibit decreased conductance where *Quercus* exhibit constant minimal water use.	**IN** - silt loam, highest mean VPD > 2 prolonged drought, *P*/*P*mean - 0.39

Figure 5.5. Summary of variability in sap flux across the sites. Simplified plots depict the relationship between sap flux density (in y-axis) and VPD (in x-axis) for *Acer* (in red) and *Quercus* (in green) species. Solid lines indicate Y1 whereas dotted lines indicate Y2. Corresponding detailed plots are illustrated in Appendix D – Figure 1.

5.5.2. Variation Partitioning analysis

The variance in daily sap flux was partitioned into two groups of variables, the H and the WB group (Table 5.3). Apparently, it was the WB group that exerted a more significant independent effect on this variability. Specifically, the variability of *Acer* in IN, TN, and WV was notable, with contribution from the WB group averaging 36.5 ± 6.6%. Comparatively, the influence of the WB on *Quercus* was considerably more modest ranging from only 6% to as high as 25% with the notable exception of WV. Uniquely in WV, the daily sap flux of *Q.rubra* was heavily influenced by the WB accounting for 66% of the variance. In contrast, the H group exhibited a lesser impact, which was almost negligible for *Quercus*. Yet, the influence of the H group was relatively more pronounced in *Acer*, particularly at the sites of IN (9%), WI (9%), and MI (6%). In general, the influence of both H and WB were minimal for *Quercus* as the proportion of U was notably high, amounting to 70% or more for at least one species at all sites with the sole exception of WV.

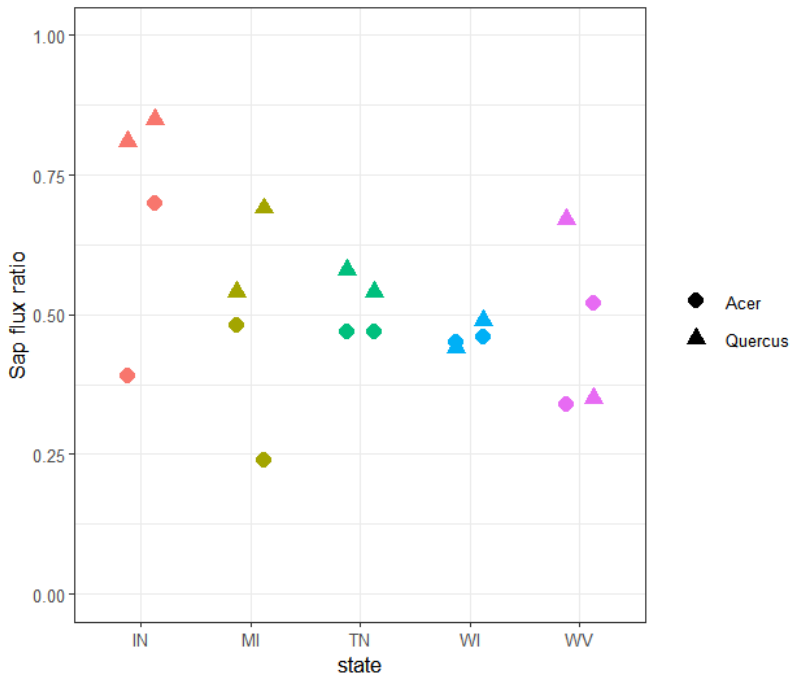


Figure 5.6. Sap flux variability within the season indicated by sap flux ratio. The first point in each state and for each species represents the ratio of year 1 whereas the second point represents the ratio of year 2.

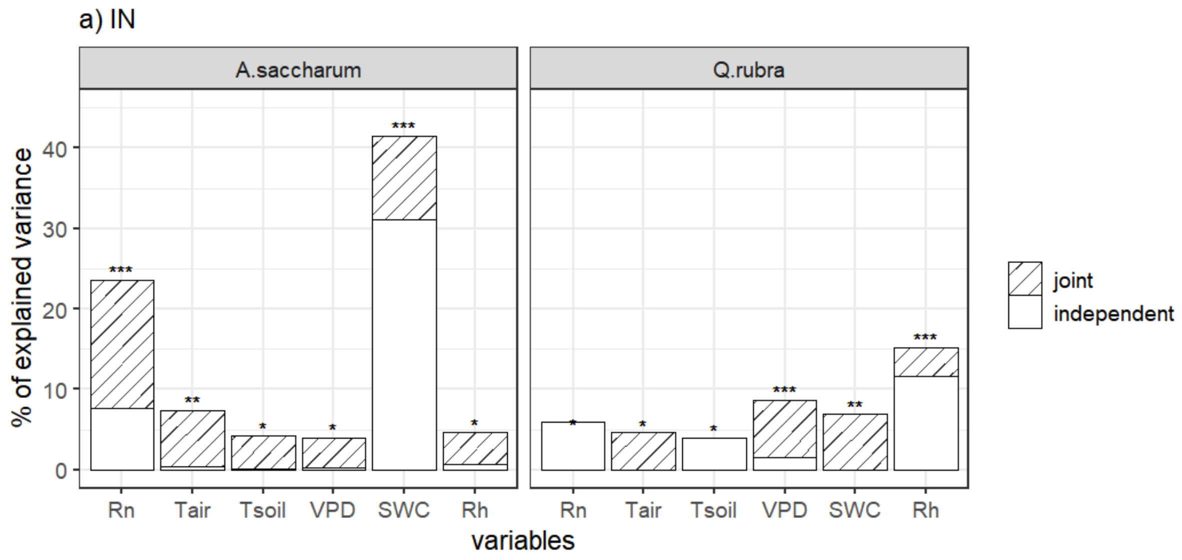
Table 5.3. Relative effects of explanatory variables: H (heat), WB (water balance), H x WB, and U (undetermined) on variance of daily sap flux. * indicates an individual measure while all other values are average.

Y1-Y2	Site	Species	H	WB	H x WB	U
dry-drier	IN	*Q.rubra**	14%	3%	27%	56%
		*Q.alba**	-	4%	4%	94%
		A.saccharum	9%	29%	47%	15%
normal-dry	WI	*Q.rubra*	-	9%	16%	76%
		A.saccharum	9%	7%	4%	79%
	WV	*Q.rubra*	0%	66%	-	34%
		A.rubrum	3%	35%	17%	45%
		*A.saccharum**	2%	45%	17%	36%
dry-normal	TN	*Q.rubra**	2%	2%	15%	80%
		Q.alba	-	25%	23%	52%
		A.rubrum	2%	37%	15%	46%
normal-normal	MI	*Q.rubra*	-	5%	6%	90%

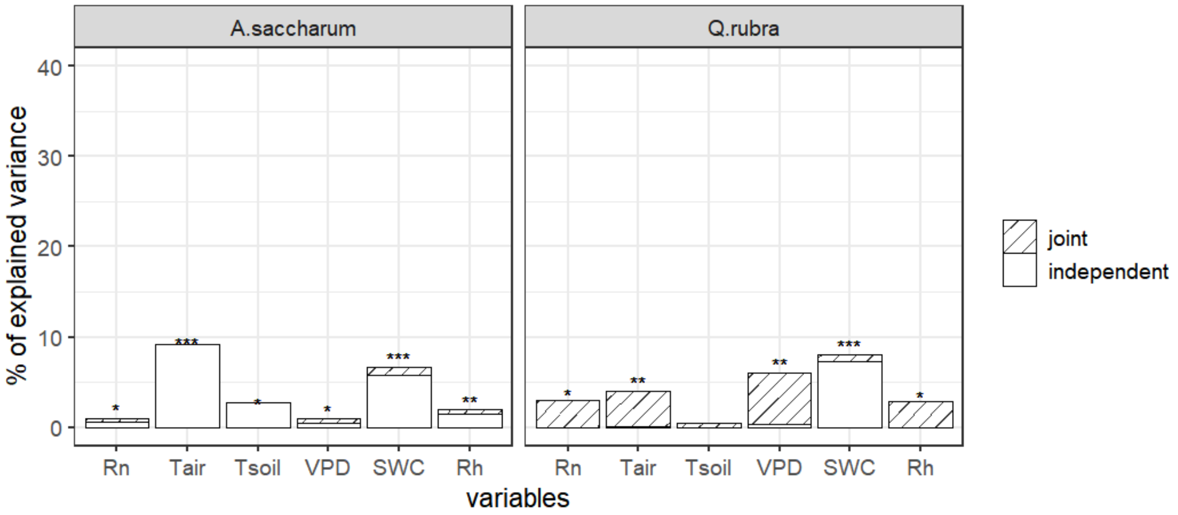
	A.rubrum	6%	6%	37%	51%

5.5.3. Hierarchical partitioning analysis

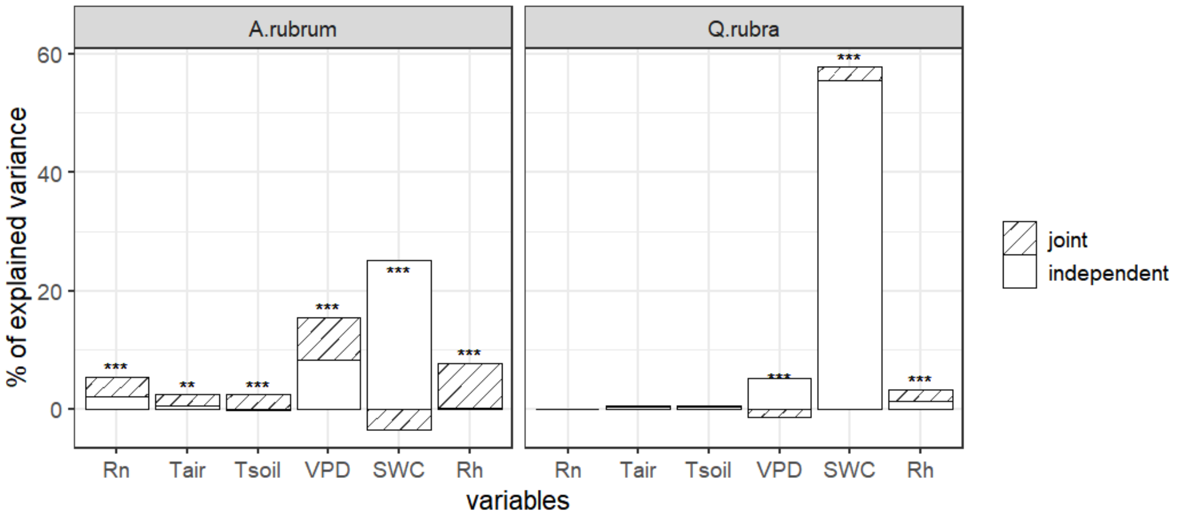
Among the six explanatory variables, variables of the WB group, specifically VPD, SWC, and Rh, consistently made significant contributions across all sites and species, although the extent of these contributions varied (Fig. 5.7). Interestingly, VPD exhibited strong joint effects whereas SWC stood out more often as an independent indicator as observed in IN or WV (Fig. 5.7a and c). Contribution of R_n was generally significant across all sites for *Acer*, while it was only influential at selected sites for *Quercus*. However, in general, the influence of the H group was minimal as discussed in 5.5.2. It was noted that some heat-related variables were found to be exceptionally more influential than WB for *Acer* in cooler regions of both WI and MI. Specifically, T_{air} in WI and R_n in MI showed notable contributions of 9.6% and 16.7% respectively.



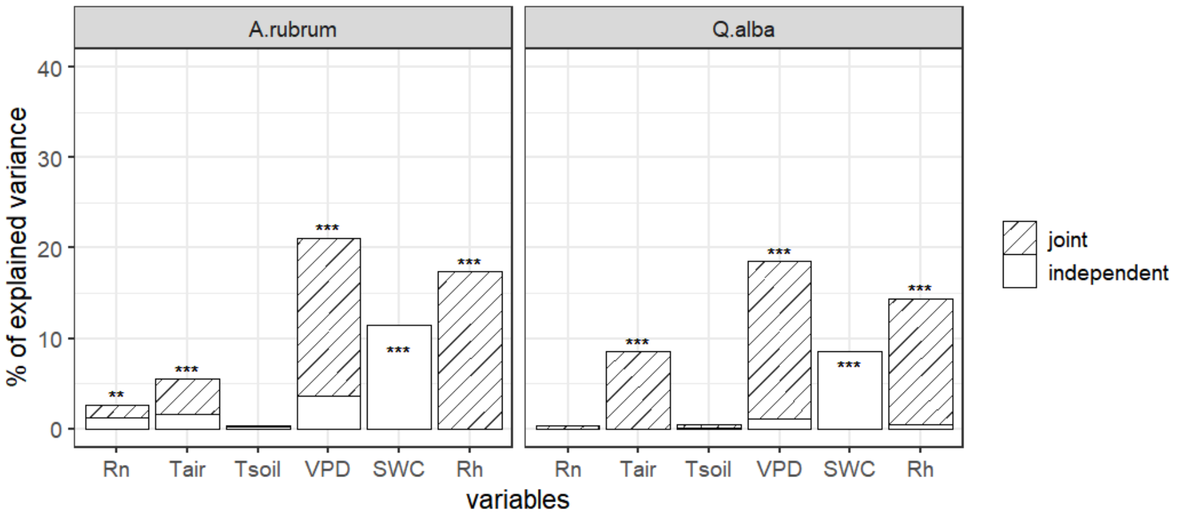
b) WI


A.saccharum
Q.rubra
% of explained variance
40
30
20
10
0
*
***
*
*
***
**
*
**
**
***
*
Rn
Tair
Tsoil
VPD
SWC
Rh
variables
joint
independent

c) WV


A.rubrum
Q.rubra
% of explained variance
60
40
20
0
***
**
***
***
***
***
***
***
***
Rn
Tair
Tsoil
VPD
SWC
Rh
variables
joint
independent

d) TN


A.rubrum
Q.alba
% of explained variance
40
30
20
10
0
**
***
***
***
***
***
***
***
***
Rn
Tair
Tsoil
VPD
SWC
Rh
variables
joint
independent

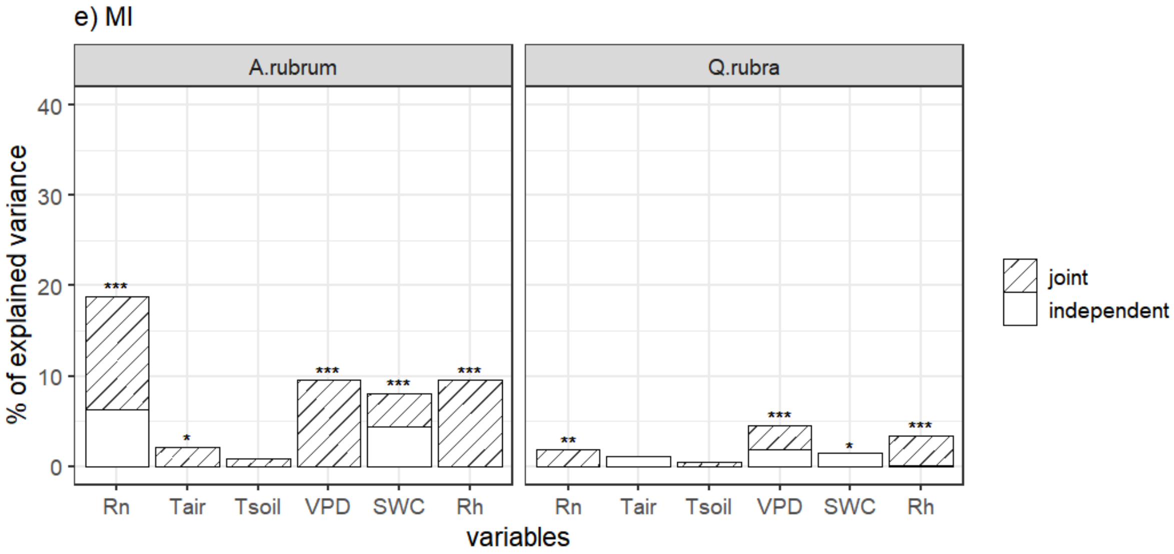


Figure 5.7. Contribution of environmental variables to daily sap flux rate. Significance level: * for $p < 0.05$, ** for $p < 0.01$, *** for $p < 0.001$

5.6. Discussion

5.6.1. Interspecies and interannual variations in sap flux density

Contrary to the general understanding that ring-porous species such as *Q.rubra* exhibit higher efficiency in hydraulic conductance (Hacke et al., 2006; Steppe and Lemeur, 2007; Tyree and Sperry, 1989), our analysis failed to provide evidence showing significant conductance advantage in *Q. rubra* (Figure 5.5 and Appendix D – Figure 1). Notably, at a site such as WI where water scarcity is not a concern and low VPD is maintained, both *Quercus* and *Acer* showed comparable sap flux density (Appendix D - Figure 1e and j). Diffuse-porous species such as *A. rubrum* are adept at facilitating continuous withdrawals of water through their densely arranged vessels with conserved water, which in turn also leads to greater cumulative water usage. This attribute is common characteristics observed in other isohydric and diffuse-porous species, such as *Cryptomeria japonica* (Japanese cedar) and *Chamaecyparis obtusa* (Japanese cypress) (Kumagai et al., 2009). Moreover, *Acer* in our study often exhibited higher sap flux density than *Quercus* under drought conditions. Several other studies have also noted similar observations. For instance, at another site in TN, Wullschleger et al. (2001) reported that the sap flux density of *A.rubrum* was two to three times greater than that of *Q.rubra*. Similarly, at another site in WV, *A.saccharum* was found to consume five times more water than *Q.velutina* (Guillén et al., 2022).

However, this empirical evidence is not static; it is rather dynamic depending on the environmental context. At both of our studied sites TN and WV, *Q.rubra* showed higher sap flux than *A.rubrum* in one year, but the pattern was reversed in the subsequent year (Appendix D - Figure 1). Although initially appearing inconsistent, such variable responses of *Acer* and *Quercus* are distinguished by their species-specific physiological traits and their contrasted interactions with water stress and prevailing environmental conditions. While these interactions between traits and environments are already well-documented, they have been summarized to elucidate the observed variations in sap flux at each site (Table 5.2). Above all, the most fundamental differences in response to water stress lie in the way they extract water from different rooting zones and the way they compensate for water scarcity. *Acer* primarily exploits the upper soil layer for water extraction, with rooting depths of 40 ~ 60 cm (Roman et al., 2015; Thomsen et al., 2013). In contrast, *Quercus,* cohabitating with *Acer*, differentiates its niche by developing a deeper root system which allows access to soil water reserves below 50 cm (Eggemeyer et al., 2009; Tromp-van Meerveld and McDonnell, 2006). This strategy allows *Quercus* to maintain transpiration or to facilitate nighttime rehydration during the water stress, contrasting with *Acer*, which relies on stem water storage to withdraw water during the water deficit (Matheny et al., 2015; Taneda and Sperry, 2008; Yi et al., 2017). Thus, *Quercus* is more likely to withstand drought where it can be deep-rooted. However, the presence of silty clay soil, which increases soil density and resists root penetration in drying soil (Canadell et al., 1996; Gao et al., 2016) or shallow soil depth may restrict the drought tolerance of *Quercus*. Furthermore, ring-porous *Quercus* is known to be more vulnerable to xylem embolism (Klein, 2014; Li et al., 2008). If *Quercus* fails to refill embolized vessels as drought period prolongs, these damaged vessels would become unusable in the following year, resulting in a substantial decrease in hydraulic transport capacity. The decline in sap flux during the post-drought year in TN is an indication that *Quercus* was unable to recover from xylem damage incurred during the drought of the previous year (Figure 5.5a). The sharp decline in sap flux in WV (Appendix D - Figure 1b) can also point to potential damage to xylem as results of intense water stress, but more fundamentally, it is attributed to the shallow soil depth. The average distance to bedrock at this site is known to be only 0.8 m (Tajchman et al., 1997). Such shallow soil depth poses a disadvantage for *Quercus,* which typically develops lower fine root mass (Hertel and Leuschner, 2002), and forces *Quercus* to compete for water in the same rooting zone as more fibrous rooting *Acer*. Moreover, while soil moisture at depth is important for deep-rooted *Quercus*, prolonged drought can facilitate water depletion in deep soil layers while it reduces infiltration of new precipitation (Schlaepfer et al., 2017; Yinglan et al., 2019). The observed low sap flow for *Q. rubra* in IN is an interesting case of prolonged drought. Using the same dataset, Novick et al., (2019) observed indistinguishable predawn leaf water potential for *Q. rubra* compared to other isohydric species, which is contrary to what would be expected for deep-rooted species. In IN where its averaged distance to bedrock is 2.2 m with a minimum of only 0.4 m (Roman et al., 2015), the combination of varying soil depth and prolonged drought may have facilitated depletion of deep soil water and hindered recovery from nocturnal refilling. On the contrary, however, in the environment conditions where *Quercus* can access deep soil water, sap flux density does not decline but increases during the water deficit period, aligning to its classical anisohydric behaviors. For example, despite the soil conditions in MI being excessively well-drained due to high sand content (92%), seasonal snowfall induced by the nearby Great Lake promotes recharge of deep soil water and insulation of soil (Henne et al., 2007; Matheny et al., 2014). This also affects other ecological functions beneficial for rich forest communities. Under these favorable environmental conditions, *Q.rubra* exhibited an increase in sap flux density during the year of higher evaporative demands even at the lowest SWC among all other sites. In another study conducted at the same site (Thomsen et al., 2013), *Q. rubra* was also observed to maintain stable predawn water potential during the drought, indicating active nocturnal refilling. In contrast, *A. rubrum* at the same site not only exhibited a decrease in predawn water potential as SWC decreased, but also showed the greatest reduction in sap flow ratio. These contrasting responses reflect the pronounced sensitivity of *Acer* to topsoil moisture level, which is subject to fast drying in freely drained sandy soil (Figure 5.6).

The contrasting hydraulic strategies between two genera are already well-documented. However, it is crucial to acknowledge that these contrasting traits, when interacting with different environmental conditions, can lead to unexpected behaviours. In some cases, these responses may diverge from the normal responses associated with their traits. Given that these are so intricately linked to site-specific conditions, it complicates efforts to generalize them into a uniform pattern. In particular, the interplay between the belowground conditions and plant traits is highlighted, leading to significant variations in interspecies and interannual sap flux trend.

5.6.2. Between soil water availability and atmospheric evaporative demands

Despite the significant variability in sap flux across different sites, *Acer* in general exhibited a higher degree of variability influenced by the WB compared to *Quercus* (Table 5.3). Among those variables within the WB group, SWC consistently and independently demonstrated a greater influence on *Acer* than on *Quercus* (Figure 5.7). The dependency on SWC was greatest in the order of IN > WV > WI, which is proportional to relative precipitation level, P/P_{mean}, from the lowest to the highest (Table 5.1). The pattern underscores the general concept that the degree of coupling between soil moisture and evapotranspiration is greater at increasing aridity (Koster et al., 2004; Seneviratne et al., 2010); soil moisture becomes the first-order constraint on transpiration when the level of soil moisture falls below the critical threshold. However, the pronounced sensitivity of *Acer* to SWC, more than *Quercus*, can be attributed to the measurement of SWC variables being confined to shallow depth up to 30 cm. Consistent with the earlier discussion, the SWC, corresponding to the ecological boundaries of shallow-rooted *Acer* which primarily extract water from the topsoil, show comparably marked difference in response. Deep-rooted *Quercus*, on the other hand, exhibits higher proportions of undetermined variables, sometimes exceeding 90% at maximum in locations such as in MI. The resulting value in U confirms that there must be other significant latent variables, potentially soil water availability from deeper layers as discussed in 4.6.1. It is noted that in WV where *Q. rubra* encounters conditions of shallow soil depth, dependency on the SWC increases significantly (Figure 5.7).

Another critical factor influencing variations in sap flux is the 'pull' force, namely, atmospheric evaporative demands. Nearly 80% of this demand-side magnitude is determined by solar radiation and air temperature (Penman, 1948; Samani, 2000). Under ideal conditions, the atmospheric evaporative demand would be equivalent to the actual transpiration released into the atmosphere. However, in water-stressed conditions, they shift from a direct correlation to a more compensatory interaction (Brutsaert and Parlange, 1998). Among the sites, *Acer* showed a notable sensitivity to R_n in both IN and MI (Figure 5.7). It was evidenced by a downregulated trend in sap flux in response to the combined conditions of decreasing SWC and increasing atmospheric demand. A substantial correlation was identified between R_n and VPD in IN ($r=0.72$, $p < 0.001$) and MI ($r=0.63$, $p < 0.001$), with an even tighter correlation observed between T_{air} and VPD ($r=0.83$, $p < 0.001$ for IN, $r=74$, $p < 0.001$ for MI). These correlations indicate an operation of potential positive feedback between land surface and atmosphere: downregulated transpiration under limiting soil-moisture regime further facilitate heat transfer to the atmosphere and, thereby, increases atmospheric dryness (Brutsaert and Parlange, 1998; Vincent-Serrano et al., 2019). This is contrasted with TN and WV where *Acer* exhibited heightened sensitivity to VPD than R_n. Here, the correlation between R_n and VPD were weaker ($r=0.32$, $p < 0.001$ for both). This is because increased solar radiation did not lead to atmospheric dryness due to relatively high Rh, with its mean of 66.5 % and 71.8 % in TN and WV respectively. The mean annual precipitation for both TN and WV is well above 1,400 mm and quite evenly distributed throughout the year (Table 5.1). In this relatively moist condition, the VPD predominantly, but jointly with SWC, drives sap flux as in TN, whereas, in the event of drought, the SWC exerts greater influence on transpiration than the VPD as in WV.

5.6.3. Implications for urban landscapes

Contrary to natural forests, urban environments display significant heterogeneity due to extensive anthropogenic modifications. In particular, urban soils are characterized by mixed technogenic substrates and redeposited natural soils, predominantly composed of sands and gravels (Craul, 1992; Jim, 1998). These urban soils are prone to compaction due to human trampling which increases soil bulk density and can reduce infiltration rates by 70 to 99% even in sandy soils (Gregory et al., 2006). Moreover, the relatively shallow depth of urban soil, usually less than 1 m, exacerbates the already dry urban soil, restricting root zones as well as water storage capacity (De Kimpe and Morel, 2000; Jim, 1998). Considering the importance of the belowground conditions in variable sap flux, such hostile urban soil conditions can create synergies with the urban heat island (UHI) effect to cause chronic water stress for plants during the growing season. Under these conditions, a strong coupling of high air temperature and elevated VPD can further drive down transpirations and increase sensible heat flux, creating a positive land-atmosphere feedback loop. Within this loop, urban trees would be forced to maintain minimal transpiration to adapt to new warmer droughts regardless of its inherent hydraulic traits. For example, anisohydric species may suppress their transpiration far lower than the isohydric species as observed in IN. The suppression of transpiration in urban trees affects regional water cycle by reducing moisture reintroduction into the urban atmosphere (Winbourne et al., 2020). This can further lead to drier urban environments, potentially diminishing the critical role of urban trees in mitigating UHI effects. Moreover, it increases the need for additional irrigation to sustain green space, presenting maintenance decisions that weigh benefits of ES against financial cost imposed by additional irrigation. Also, if such dry conditions persist within UHI, certain species will likely become more susceptible to decline. Previous research (Kim et al., 2023) finds higher cumulative mortality rates among *Acer* species from East Asia on the outskirts of London, which is contrasted with relatively resilient *Quercus* species (in general). This was attributed to a prolonged exposure to annual heatwaves from 2010 and onwards and cumulative water deficit, adversely affecting shallow-rooted *Acer* in sandy soils. This insight translates to a dual consideration in plant selections in urban settings: species should be selected by matching key functional traits, especially those traits supporting their water use strategy during water stress, to the specific environmental conditions that these traits interact with. The reciprocal also works. Urban landscapes may need to be tailored to support the successful establishment and growth of selected species in consideration of these key functional traits. Finally, since assessments of ES predominantly rely on standard metrics such as canopy cover density, typified by the leaf area index (Nowak et al., 2008; Natural Capital Project, 2024), the nuanced water usage pattern specific to different species and environmental conditions often remain unaccounted for. This oversight can significantly widen the discrepancy between theoretical ES estimation and actual benefits realised, underscoring the importance of embedding a more process-driven mechanistic approach into ecosystem service evaluations.

5.7. Conclusions

Despite recognising the variability in plant water use, a significant research gap remains due to the limitations in obtaining consistent measurements of water use for single species across a broad spectrum of environments. The study illuminates this gap by detailing the variability of water use between and within species of contrasting strategies, which heavily depended on the environmental context. Under the conditions of severe water restrictions, particularly where species cannot utilise their traits associated with their water use strategy, the responses can deviate markedly, exhibiting constantly suppressed transpiration at minimum. The reduced plant conductance, when coupled with accelerated climate change, could result in a vicious circle, exacerbating drought stress by allowing more heat and drier airs. Hence the study underscores the need to consider both key functional traits supporting their water use strategy and their interactions with the environments in evaluating species' drought tolerance. This is also critical for provisions of healthy ES in heterogenous urban settings. Lastly, synthesising fragmented field data helps to contextualise and to find overarching patterns of species-specific water use within a broader geographical perspective. Interpreting the response of species in one location with respect to its behaviours across various environments, especially, on a global scale, can significantly deepen our understanding of intricate plant-water interactions, and ultimately enhance our predictive capacity, essential for upscaling water flux to broader ecosystems.

Chapter 6

Discussion and conclusions

6.1. Synthesis and implications for urban landscape practice

In assessing the adaptability of urban trees for the future climate, this study delved into some of the niche theories to explore its relevance and applicability on evaluation of urban species, extending beyond their natural distributions. The niche concept has been central to explaining biogeographic distributions of species, with key ecological factors that may set the range limits of species (Hutchinson, 1957; Carscadden et al., 2020). However, the application of niche theories to urban species has been understudied, despite their potential to provide a useful framework. Niche theories are particularly relevant in preliminary assessment of climate suitability before conducting more specialised assessments such as specific stress tolerance or ecosystem quantification. It posits a very fundamental underlining assumption, niche conservatism (Pearman et al. 2007; Wiens et al., 2010), that species conserve their niche. If species are located within the safe bioclimatic range, they are expected to perform well. Once this is met, any discrepancies, e.g., high mortality, vulnerability to disease or even unexpected occurrence, can then be further investigated to identify other hidden causes, which are more likely to be local (Valladares et al., 2014) or non-climatic factors (Soberón and Peterson, 2005). For instance, those introduced species beyond their natural distributions may be seen as expansion of their realised niche (RN) in the absence of competition or local adaptation through maximising plasticity. The thesis specifically focused on three perspectives derived from the niche concept, with each perspective presenting its distinct ecological aspect: (1) testing the effect of bioclimatic NBs on species mortality, (2) relating survival rates (SR) to habitat suitability

(HS) projections based on biogeographic distributions that reflect both climate and terrestrial components, and (3) linking biological interactions within the given geo-ecological and climatic conditions to potential resilience to drought stress. If mortality/survival rates can be explained by the positions of NBs or HS projections based on species distributions, then, it indicates that the ecological/bioclimatic marginality of the species at current locations matches with that of their native distributions. Therefore, niche is conserved in the novel environment. When mortality/survival rates do not align with HS, it suggests that there are hidden variables that may cause this discrepancy. The hidden variables can then be further explored in determining whether it is the realisation of potential niche or just local events, although this is beyond the scope of this research.

From the NB perspective, Chapter 3 questions if the presence of species *x* in a city *y*, beyond their native range of distributions, signify an increased exposure to mortality risk or increased tolerance. In other word, this study uncovered that the impact of NB positions on species performance, survival. The NB presented a general pattern at genus-level; being out of NB increases chances of mortality, yet it also varied among individual species within the genus, each with a different magnitude of influence. In general, *Quercus* species showed more resilience than *Acer* species during the study period of cumulative drought and recurring heat stress. For instance, species locations being far beyond their lower or upper limits of NBs did not affect those *Quercus* from East Asia, such as *Q. glauca* and *Q. serrata*, exhibiting mortality rates similar to those of native UK *Q*uercus. This is contrasted with many introduced *Acer* species from a similar bioclimatic region to these *Quercus*, such as *A. davidii* or *A. crataegifolium*, which exhibited higher mortality rates during the studied period. These *Acer* species are particularly responsive to seasonal climatic variables such as PWQ. On the other hand, being positioned within the NBs did not ensure similar mortality rates. While most European *Quercus* species within their NBs demonstrated expected high tolerance, it was observed that Mediterranean oak species outperformed UK native oaks. These observations suggest that the position of 'climatic' NBs alone may not fully discern species suitability, and also that the correlation between mortality rates and NB relies on the choice of NB variables— those selected variables worked well with *Acer* but not with *Quercus*. Moreover, simplified binary NB position of being 'in' and 'out' helps to grasp the overall suitability of ex-situ species, but not the relative optimal growth conditions for those native species.

Therefore, the study further carried on applying SDMs that incorporated additional land variables, including soil and land cover data, e.g., vegetation index. Chapter 4 questions whether the predicted habitat suitability (HS) based on SDM align with actual survival rates (SR) of species, and how these two metrics might be interpreted. The underlining aim of this second approach was to test if these mortality rates can be explained not only by their NB positions but also by projected HS based on a correlational model with a more inclusive set of environmental factors, encompassing both climatic and land variables. Since correlational models depend largely on environmental similarity between trained and projected sites, niche similarity tests were also conducted to compare this. The results were counterintuitive. Introduced *Acer* species, that exhibited the highest niche similarity to the distributions of native European *Acer* within the UK and yielded the highest projection of HS score, demonstrated the lowest SR. Conversely, species that yielded the poorest HS score demonstrated the highest SR. Instead, species that are phylogenetically more related exhibited a similar range of mortality rates, rather than those species that are more similar in their environmental niche. This contradictory result invites further investigations into the underlying causes of the discrepancy between the modelled projections, HS, and the actual SRs. One potential explanation may be the mismatch in temporal windows between the period used for climate approximation in niche modelling and the period of the mortality survey. A shift towards warmer and drier conditions during the growing season may have led to an increased mortality in species that were previously well-established. However, it points to a more fundamental cause: the existence of other influential factors beyond the environmental variables and inherent limitations in correlative niche modelling. In particular, the evidence of phylogenetic signal suggests that hidden biological attributes must be operating beneath the environmental layers. Furthermore, if these niches were conserved within a lineage, there might be observable heritable features which can be used as surrogates for the assumed underlying biological processes.

The third approach narrows its scope to examine these biological attributes at the individual plant-level. Chapter 5 questions how two co-occurring individual species vary in their water use under moisture stress across varying environmental conditions, and also how species' distinct water use strategy consistent across varying environmental conditions. Co-existing *Acer* and *Quercus* species normally exhibit contrasting water use behaviours along the iso-anisohydric continuum. These contrasting behaviours can be seen as the results of niche differentiation, allowing co-existing species to exploit common resource pools in a non-competitive manner. However, these contrasting behaviours are not consistently observed and can vary depending on the environmental contexts. In particular, species' responses deviate significantly from their normal behaviours when their water use capacity is severely restricted during periods of water scarcity. This is particularly true when their specific phenotypic or morphological traits, which allow them to pursue their water use strategy, are compromised. For example, ring-porous *Quercus* species, known for their xylem that is more susceptible to cavitation, are readily damaged by previous drought. These damaged xylem vessels would then cause significant reduction in water transport capacity, leading to a corresponding decrease in transpiration. If these conditions persist without access to deep soil water, *Quercus* will experience a further reduction in growth, ultimately increasing mortality risk. On the other hand, diffuse-porous and shallow-rooted *Acer* species, which utilise stem water storage to cope with water stress, may withstand drought relying on their reserves while moderating transpiration. This strategy allows *Acer* species to mitigate the immediate effect of drought. However, once these reserves are depleted without subsequent replenishment, these species will quickly encounter water exhaustion, elevating their mortality risk. Without understanding these relationships between plant functional traits and underlying biological processes related to climate adaptation, applying niche models based solely on environmental factors may omit some important information, making it prone to misinterpretation.

With a balanced view of both environmental niches and intrinsic biological attributes, the factors that drove higher mortality rates in *Acer* species compared to *Quercus* species can be better understood. Many *Acer* species, native to the temperate forest of either East Asia or North America — the region where the annual precipitation well exceeds 1,000 mm, are shade-tolerant understorey species that favour moist habitats near streams. These species have developed large, thin leaves to increase opportunities for intercepting lights and shallow roots to rapidly exploit nearby water resources. These traits may have supported fast growth under the conditions of relatively limited light but abundant water; however, they may not confer heat-tolerance and drought stress under more prolonged restrictive water regimes. This is especially the case for many *Acer* species that are open grown in full sun within botanic gardens. In the specific setting of KEW, located near the Thames River, the site condition is characterised by well-drained sandy soil with potential access to deep soil water. *Quercus* can benefit from such site conditions whereas open grown *Acer* is more likely to experience frequent drought stress. This is a particularly relevant scenario as the climate in the Southeastern UK shifts to warmer and drier summers. The resulting mortality rates between these two genera — markedly higher for species within *Acer* than those within *Quercus* — are especially pronounced in those of which NB position below their lower limits. This contrast can be explained by genus-specific biological attributes interacting with environments. However, it is important to note some of the variations in individual species within these genera. There are several *Acer* species that exhibit notably high adaptation to novel environment, distinguishing themselves from other ex-situ species beyond their native range. For instance, despite being disadvantaged in NB position and poorly projected HS values compared to *A. davidii*, *A. pictum* exhibited higher SR than *A. davidii*. Although the findings in Chapter 5 primarily highlighted only the difference between genus in terms of these varying biological interactions, observed phylogenetic signal within *Acer* in Chapter 4 points to the existence of species-specific hidden phenotypes or genotypes that contribute to the varied adaptability. Given the highly fragmented and heterogeneous nature of urban environments, understanding these biological attributes within the broad context of niche is crucial in determining suitable placements for species and assessing ES. This is also why urban species pools are more sensitive to patch-scale habitat features than city-wide ecological gradients (Casanelles-Abella et al., 2021). Misplacement of species in hostile urban environments may inhibit the full functionality of certain key traits as intended, potentially diminishing productivity or even increasing the risk of mortality. Conversely, understanding key functional traits may require altering environmental conditions to ensure these traits can be fully in function.

In summary, discrepancies in species' tolerance at specific site and the estimated niche breadths based on their native distributions vary significantly in magnitude across species. Therefore, when applying niche theories to urban tree evaluation, one must consider the following considerations.

- Niche models primarily operate at macroecological level at continental scale. In heterogeneous urban environment, applying theories at the scale of individual urban patches may not be effective; instead, species can be assessed and screened for the entire region. When adjusting this to smaller scale, it is crucial to ensure that the spatial and temporal scale are coherently aligned.
- Species biogeographic distributions are shaped by specific conditions of the training region. These conditions include non-climatic factors such as interspecies competition, interactions with biotic agents, or specific geological conditions. It means that the degree of analogousness between projection and training region determines the accuracy of projections. When this gap in analogousness between projection and training region is large, additional surrogate measures that can represent these specific conditions can be brought into the model. For example, biological attributes, including plant functional

traits and underlying mechanistic processes, may offer a more direct window into a species' physiological tolerance and growth.

Moreover, records of urban species physiological response can serve as critical evidence to identify this gap between local adaptation and macroecology. While niche models outline the characteristics of broad environmental conditions suitable for species, site-specific mortality records can provide the existence of hidden factors influencing species fitness in local conditions. For example, in this study, it was phylogenetic proximity or physiological traits that explained species' resilience. Further exploration of these hidden factors may facilitate uncover true niche boundaries closer to fundamental niche (FN).

6.2. Limitations and recommendations for future research

The research presented in this thesis should also be considered in the context of several limitations. First, the nature of mortality data used in the analysis has several inherent limitations which are discussed in section 3.6.4. It includes temporal gap between the time of survey and the time of death, lack of supporting biophysical data, and inconsistent irrigation support across botanic gardens. Second, those trees cultivated in botanic gardens may not fully represent the status of urban trees, and their application may be limited to those found in urban forests and parks. It suggests that the results of this research may not be applicable for trees in different contexts. For example, street trees on impervious surfaces with limited water infiltration and shallow soil depth require additional stress assessments for chronic drought conditions, beyond broad climate suitability evaluation. For these street trees, biological attributes and site-specific conditions take on greater importance than climate. Third, the use of secondary sap flux data derived from North American natural forests, without direct measurements of urban species, leads to speculative conclusions in linking biological attributes to niche models.

All these limitations highlight the lack of data availability for urban trees, which would otherwise open new windows for the study of urban ecology. Most public databases on urban trees typically collect basic information, such as taxonomy, locations, dates of placement and removal, limiting their use to inventory purpose rather than extending to interdisciplinary science research (Ossola et al., 2020). Moreover, although the number of urban tree studies related to climate change or ES is increasing, the in-situ measurements collected for these studies are dispersed in fragmented forms. Chapter 5 of this research serves as an exemplary case study using SAPFLUXNET, a global database which integrates and harmonises local measurements. The overarching patterns of variability in sap flux were revealed through the standardised variables and units that ensured consistent quality. In addition, as it is learned that traits reveal species' habitat preferences on a more micro scale, identifying and incorporating these traits may help fill the gap in niche models for future research. However, integrating mechanistic approach into niche models necessitates aligning the scale of biological attributes with that of niche models that employ global climate data. This alignment is crucial and requires access to a corresponding global database that provides consistent and repeatedly measured biophysical data across species and regions. Therefore, future research could further explore this concept by identifying specific attributes and defining methodological approach necessary for the integration of niche models. The approach should be distinguished from those using remote sensing data, yet it could complement them, as it can extend our understanding from individual-level observations to genotypic variations.

In summary, the following recommendations can be provided for stakeholders involved in urban tree assessment for development of urban green infrastructure, which can also be addressed in setting up future research agenda.

- Regional/city municipals

Prioritising ecological criteria in assessing qualities of urban green infrastructure is essential, despite the multiple requirements and concerns related to urban tree selections and ecosystem functions. Following these criteria, combination of niche models and specialised assessment methods can then be tailored to balance general climate/environmental suitability as well as specific site suitability. More importantly, to conduct evidence-based assessments, investments are urgently needed in expanding data collection points and improving data management policies.

- Academia

Application of niche theories in urban environment requires an interdisciplinary approach, integrating ecology, biology, landscape design and statistics/data science. Understanding the discrepancies between macroecology and local adaptation is not only ongoing theme in ecology, but also critical framework to understand species responses across heterogeneous urban environment. Collaborated experiments across different fields of expertise may facilitate to reduce this knowledge gap, particularly found when relating biological attributes to macroecology.

- Landscape Architects

Although designers may find less practicality in application of niche theories, understanding niche is essential for identifying not only climatically suitable species, but also complementary neighboring species that can form resilient communities and enhance urban biodiversity. In particular, contrasting biological attributes of neighboring species often effectively share limited resources as observed in *Quercus* and *Acer* in this study. Integrating these species-specific traits into niche modeling can significantly enhance ecological design.

- Botanic gardens/nurseries

Compared to trees in natural forests, where growth is a major interest for management purpose such as thinning, urban trees are less concerned with growth management. Instead, urban trees are managed as inventories, with a focus on stocktaking. However, the role of botanic gardens and nurseries can be extended to excellent data collection points for urban tree growth studies. As demonstrated in this study, mortality rates from botanic gardens successfully served as ecological evidence of species characteristics. Moreover, urban botanic gardens/nurseries host an incomparably diverse range of species at one site, providing an excellent source for comparable analysis of species response to given environmental condition. The future research can focus on identifying the types of data that needed, the specific methods to collect and database management policies to enhance the data capacity for scientific examination. It should be noted that the data collection should also include information on the extent of irrigation and maintenance provided in order to identify their impacts on species growth response.

6.3. Conclusions

In the context of climate change, moving towards science-based management and assessment of urban green infrastructure necessitates acknowledging cities as urban habitats. Urban environment stewardship based on this recognition facilitates the integration of related ecological theories and models. From a theoretical standpoint, the niche concept provides a robust framework. However, when applying niche theories into practice especially in urban landscape, myriads of issues emerge. These challenges are addressed in this study including, but are not limited to, selecting right niche variables that accurately reflect the ecological needs of species, addressing sampling bias, navigating inherent limitations in modeling techniques, and considering factors related to species biological interactions that facilitate or debilitate species adaptability. These challenges only highlight the potential for further refinement and serve not to diminish but to enrich fundamental values of niche models. The study specifically emphasises the critical importance of integrating biological attributes into niche modeling. The integration is essential to meet evaluation criteria for both future climate and the needed ES provisioning. Ideally, the integration of biological attributes would provide more detailed insights into linking species fitness or productivity with the complex heterogeneity of urban environmental conditions. However, this advancement is only contingent upon access to collective species biological data that corresponds to the scale of niche analysis, which challenges conventional proprietary views on biodiversity knowledge.

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Appendices

Appendix A.

Supplementary data file for Chapter 3

Description: The excel file contains the list of species from each botanic garden matched with reference information of download records from GBIF and basic niche variable characteristics.

File name: list_of_species_with_GBIF_reference.xlsx

Appendix B.

Supplementary tables and figures for Chapter 3

Each species was assigned niche positions either in or out along the axis of selected niche variables; the mean annual precipitation (MAP), the mean precipitation of the warmest quarter (PWQ), the climate moisture index (CMI) and the mean annual potential evapotranspiration (PET).

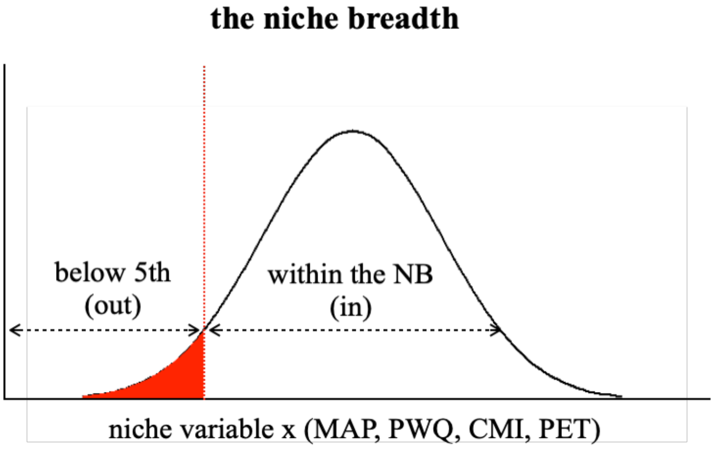


Figure 1. Graphical representation of the NB and its binary classification of niche position for the research

Table 1. Comparison of the candidate models based on ΔAIC_c for each botanic garden.

Genus	Selected variables	KEW	WESB	RBGE
Acer	Full (MAP, PWQ, CMI, PET)	2.7	3.0	3.1
	MAP, PWQ, CMI	1.8	2.4	5.8
	MAP, PWQ, PET	1.0	3.9	1.4
	PWQ, CMI, PET	3.3	2.2	2.0
	MAP, PWQ	**0.0**	3.9	4.0
	MAP, CMI	7.6	0.8	16.8
	MAP, PET	6.2	2.1	16.5
	PWQ, CMI	3.7	1.6	4.0
	PWQ, PET	1.6	2.7	**0.0**
	CMI, PET	7.1	0.9	17.9
	PWQ	2.9	3.5	2.0
	MAP	6.1	1.9	14.9
	CMI	8.3	**0.0**	16.0
	PET	5.1	0.7	20.0
Quercus	Full (MAP, PWQ, CMI, PET)	**0.0**	-	-
	MAP, PWQ, CMI	18.3	-	-
	MAP, PWQ, PET	**0.0**	2.6	2.9
	PWQ, CMI, PET	18.0	-	-
	MAP, PWQ	18.4	0.8	5.5
	MAP, CMI	16.4	-	-
	MAP, PET	14.7	1.5	0.2
	PWQ, CMI	20.2	-	-
	PWQ, PET	16.1	2.3	2.0
	CMI, PET	19.5	-	-
	PWQ	18.6	2.7	4.5
	MAP	16.7	**0.0**	5.0
	CMI	18.5	-	-
	PET	17.8	3.7	**0.0**

The best fit models for WESB and RBGE had *p-value* > 0.05, and therefore were not visualised in plots.

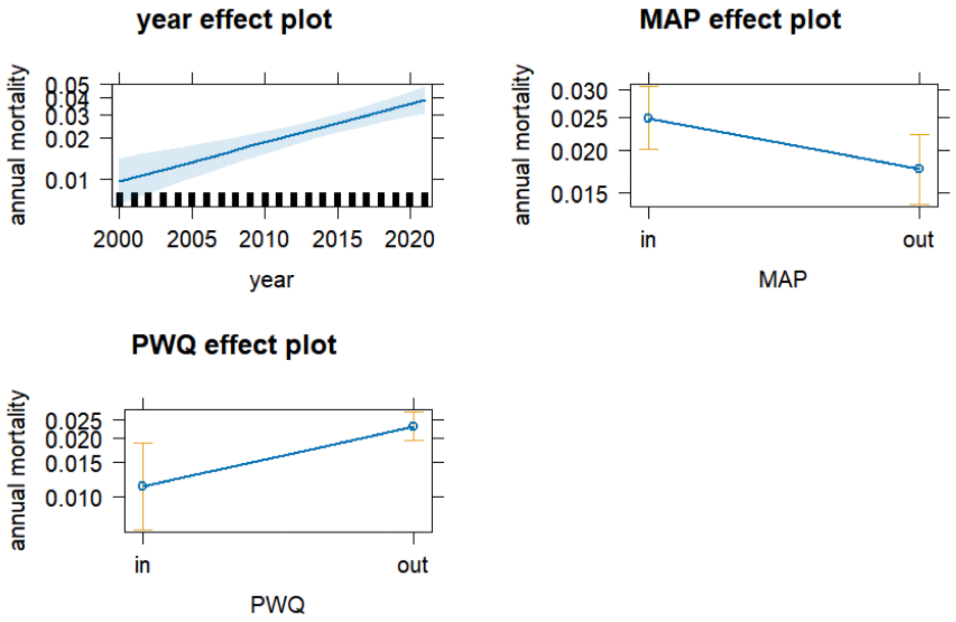


Figure 2. Effects of NB position of the selected bioclimatic niche variables (MAP and PWQ) on the predicted probability of annual mortality of *Acer* for KEW under the best fit model.

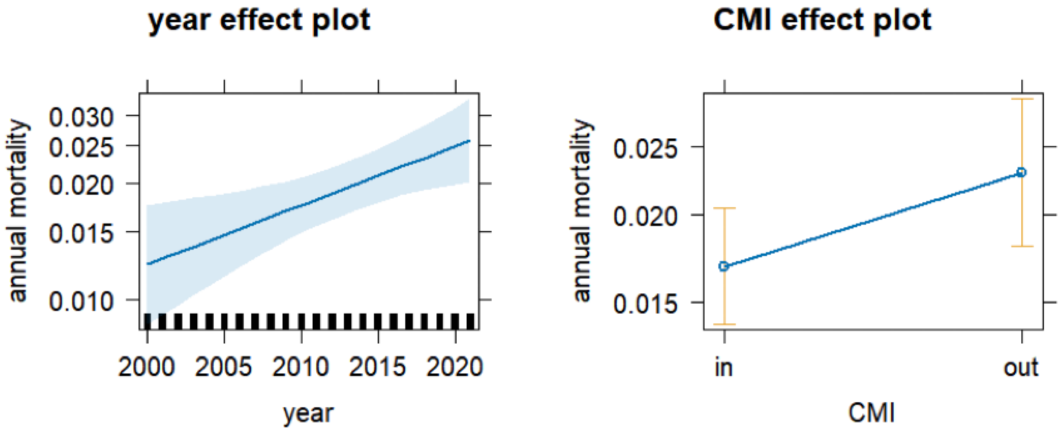


Figure 3. Effects of NB position of the selected bioclimatic niche variable (CMI) on the predicted probability of annual mortality of *Acer* for WESB under the best fit model.

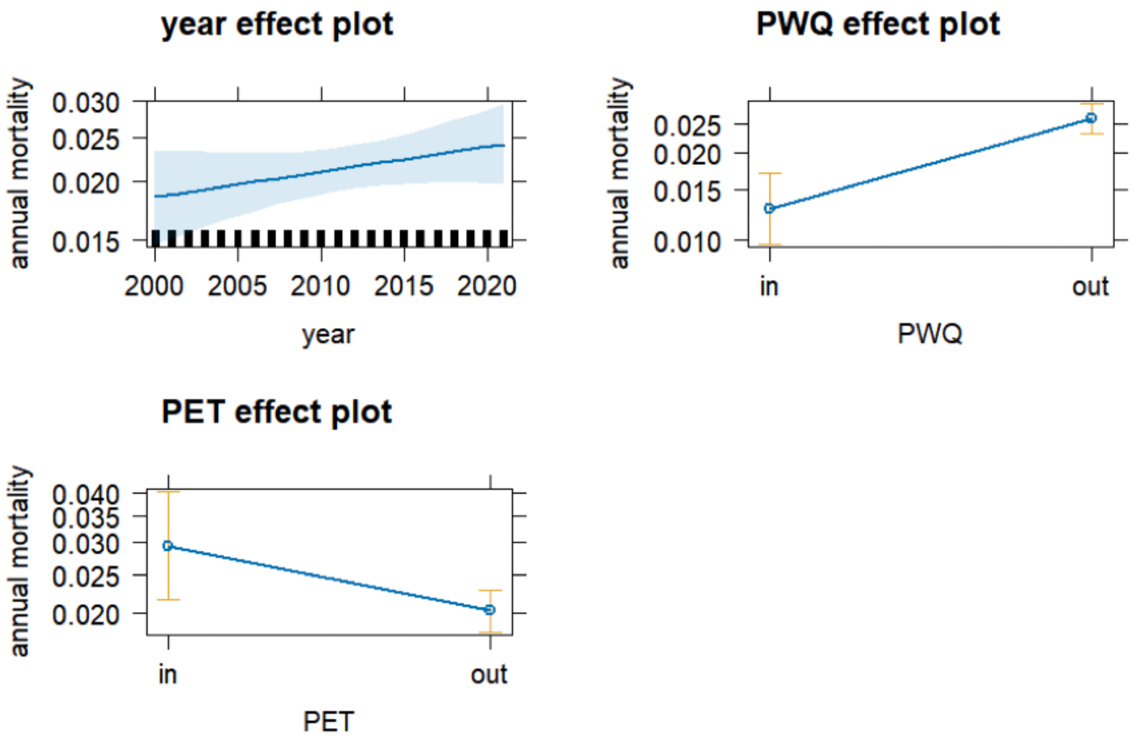


Figure 4. Effects of niche position of the selected bioclimatic niche variables (PWQ and PET) on the predicted probability of annual mortality of *Acer* for RBGE under the best fit model.

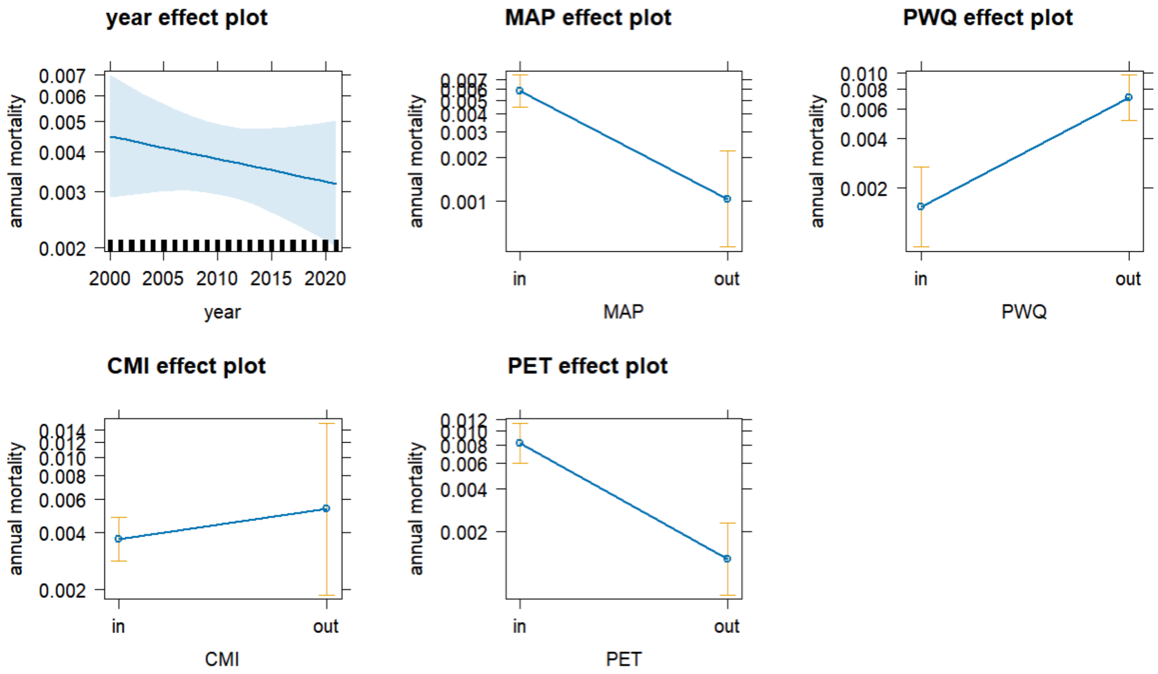
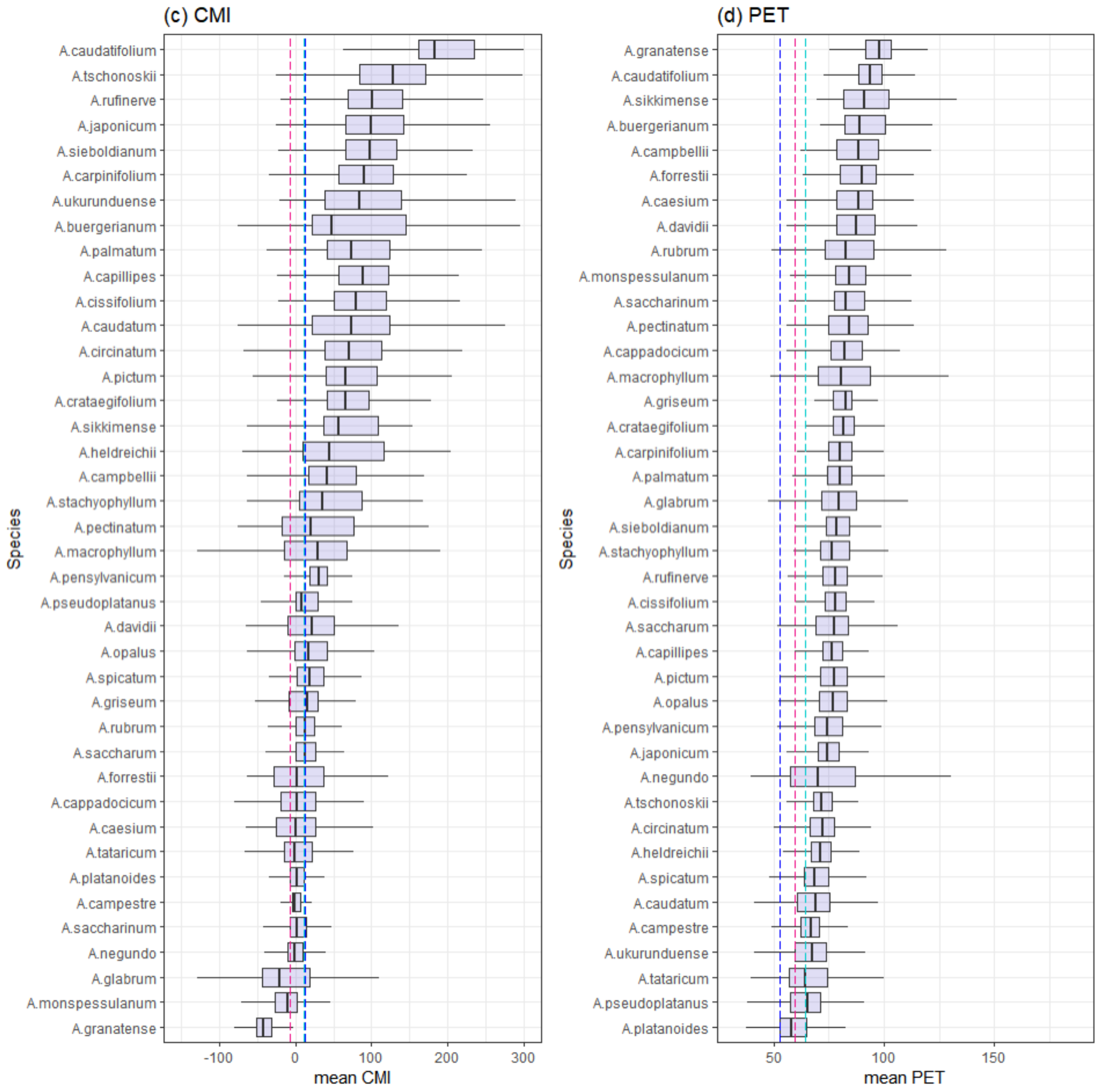


Figure 5. Effects of niche position of the selected bioclimatic niche variables on the predicted probability of annual mortality of *Quercus* for KEW under the best fit model.

Table 2 - The mean cumulative mortality rates at the species-level for *Acer* and *Quercus* in each combination of the selected niche variables, *n* = number of individual species with identical niche positions (The same species are counted independently if found in different BGs). We hypothesised the lowest mortality rate at the combination of niche positions *a*, whereas highest was expected at *b*.

				Acer		*Quercus*	
MAP	PWQ	CMI	PET	Mean cumulative mortality	Species *n*	Mean cumulative mortality	Species *n*
in	in	in	in	0.27	13	0.18	3
in[a]	in[a]	in[a]	**out**[a]	0.21	12	0.11	17
in	in	**out**	**out**	-	-	-	-
in	**out**	**out**	**out**	-	-	-	-
out	**out**	**out**	**out**	0.32	23	0.12	4
out[b]	**out**[b]	**out**[b]	in[b]	0.59	2	0.04	2
out	**out**	in	in	0.20	1	0.12	4
out	in	in	in	0.29	1	0.01	2
out	in	in	**out**	0.07	2	0.00	3
out	**out**	in	**out**	0.29	11	0.11	6
in	**out**	in	**out**	0.27	12	0.30	2
Aggregated mean				**0.29**	**88**	**0.14**	**39**


(c) CMI
A.caudatifolium
A.tschonoskii
A.rufinerve
A.japonicum
A.sieboldianum
A.carpinifolium
A.ukurunduense
A.buergerianum
A.palmatum
A.capillipes
A.cissifolium
A.caudatum
A.circinatum
A.pictum
A.crataegifolium
A.sikkimense
A.heldreichii
A.campbellii
A.stachyophyllum
A.pectinatum
A.macrophyllum
A.pensylvanicum
A.pseudoplatanus
A.davidii
A.opalus
A.spicatum
A.griseum
A.rubrum
A.saccharum
A.forrestii
A.cappadocicum
A.caesium
A.tataricum
A.platanoides
A.campestre
A.saccharinum
A.negundo
A.glabrum
A.monspessulanum
A.granatense
Species
-100
0
100
200
300
mean CMI
(d) PET
A.granatense
A.caudatifolium
A.sikkimense
A.buergerianum
A.campbellii
A.forrestii
A.caesium
A.davidii
A.rubrum
A.monspessulanum
A.saccharinum
A.pectinatum
A.cappadocicum
A.macrophyllum
A.griseum
A.crataegifolium
A.carpinifolium
A.palmatum
A.glabrum
A.sieboldianum
A.stachyophyllum
A.rufinerve
A.cissifolium
A.saccharum
A.capillipes
A.pictum
A.opalus
A.pensylvanicum
A.japonicum
A.negundo
A.tschonoskii
A.circinatum
A.heldreichii
A.spicatum
A.caudatum
A.campestre
A.ukurunduense
A.tataricum
A.pseudoplatanus
A.platanoides
Species
50
100
150
mean PET

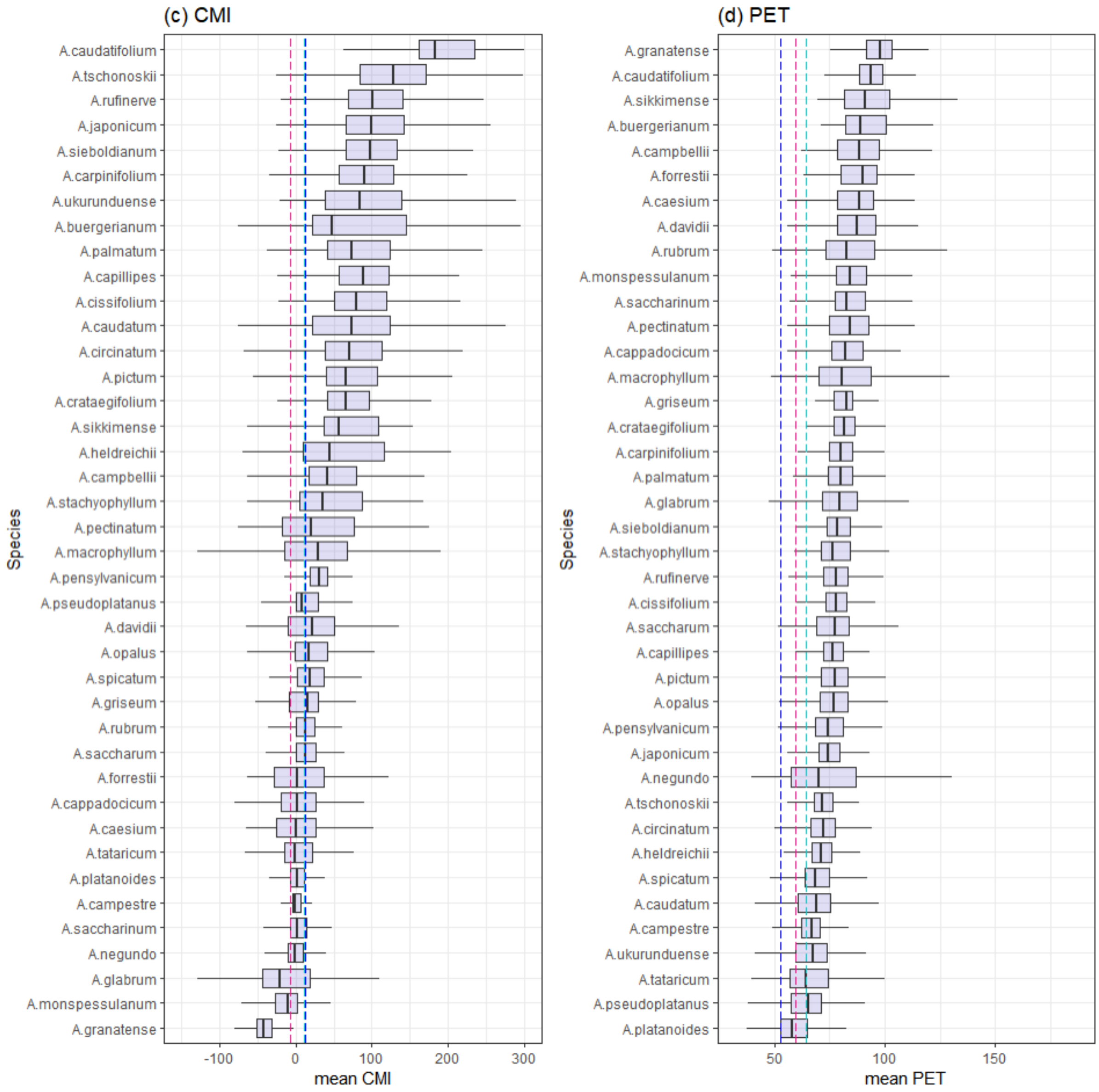


Figure 6. A box plot representing the NB of *Acer* species along the axis of each bioclimatic niche variable. The dotted vertical lines indicate BGs by colours; KEW (red), WESB (green), RBGE (blue)

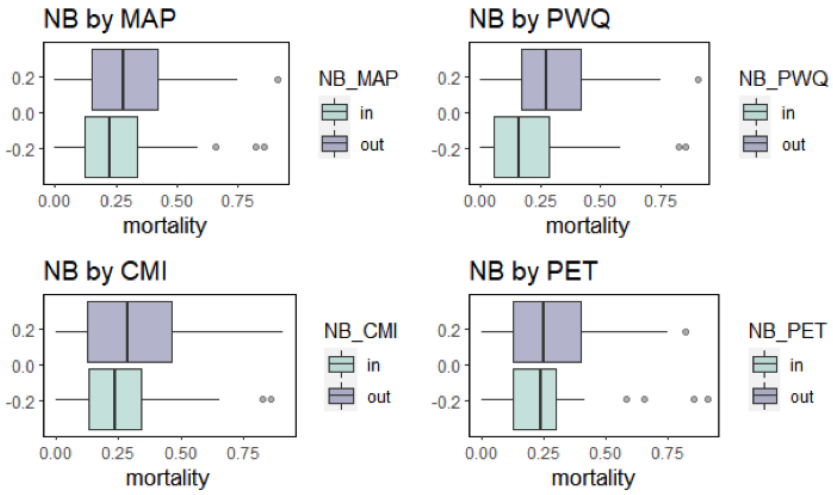


Figure 7. The distribution of cumulative mortality rates of *Acer* was compared between the two groups, in (above the threshold) and out (below the threshold), of the NB. The Kruskal-Wallis test was performed as resulted in MAP (n=47(in), 38(out), p=0.27), PWQ (n=31(in), 54(out), $p < 0.05$), CMI (n=61(in), 24(out), p=0.19), and PET (n=28(in), 57(out), p=0.58), n = number of represented species

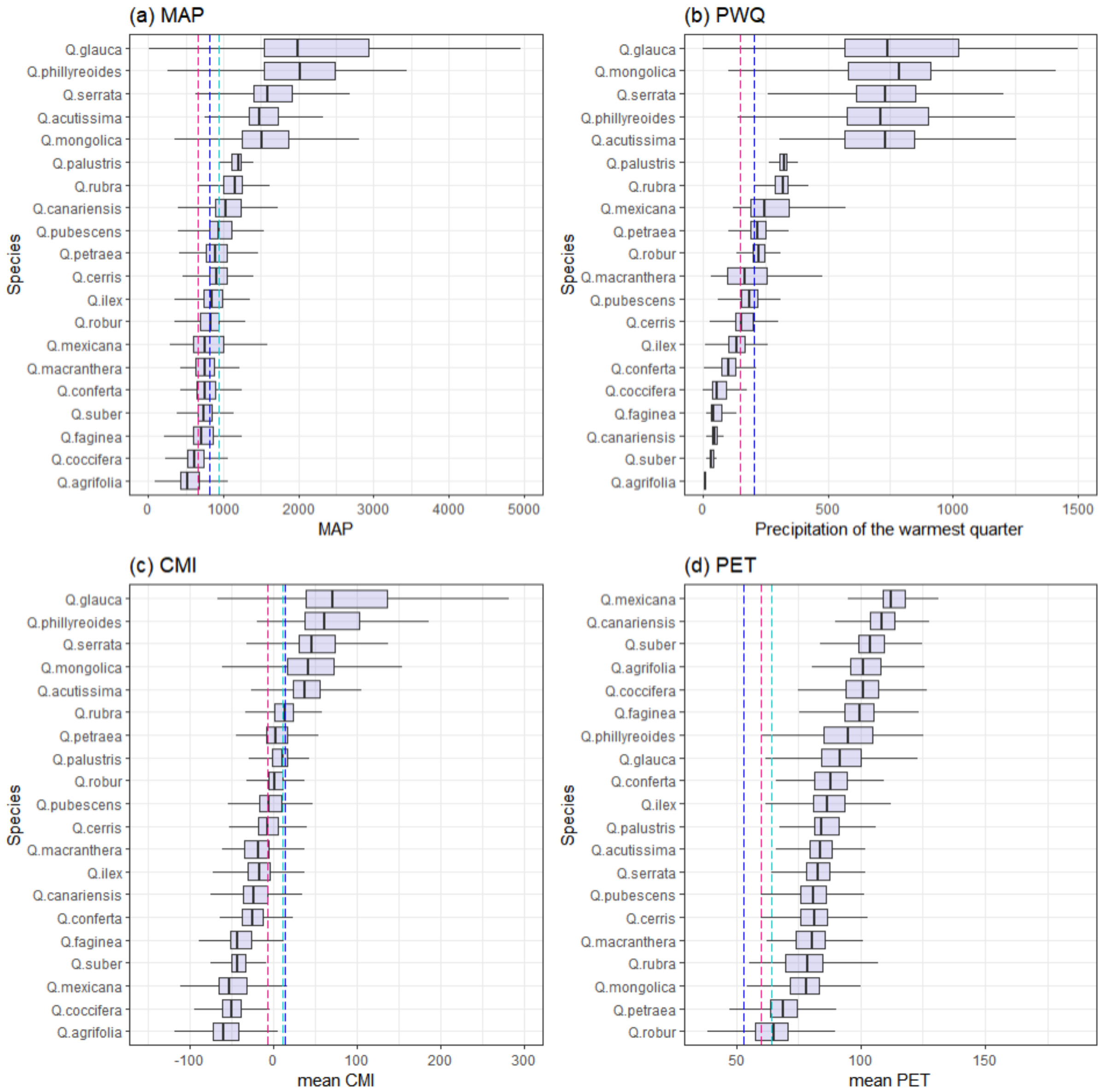


Figure 8. A box plot representing the NB of *Quercus* species along the axis of each bioclimatic niche variable. The dotted vertical lines indicate BGs by colors; KEW (red), WESB (green), RBGE (blue)

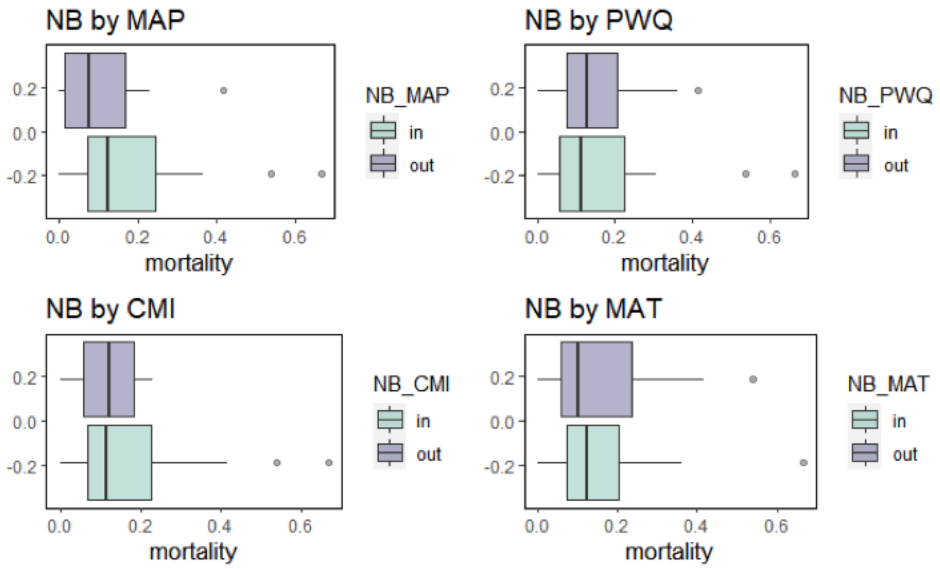


Figure 9. The distribution of cumulative mortality rates of *Quercus* was compared between the two groups, in (above the threshold) and out (below the threshold), of the NB. The Kruskal-Wallis test was performed as resulted in MAP (n=26(in), 13(out)), PWQ (n=23(in), 16(out)), CMI (n=35(in), 4(out)), MAT (n=24(in), 15(out)). All *p-values* > 0.05.

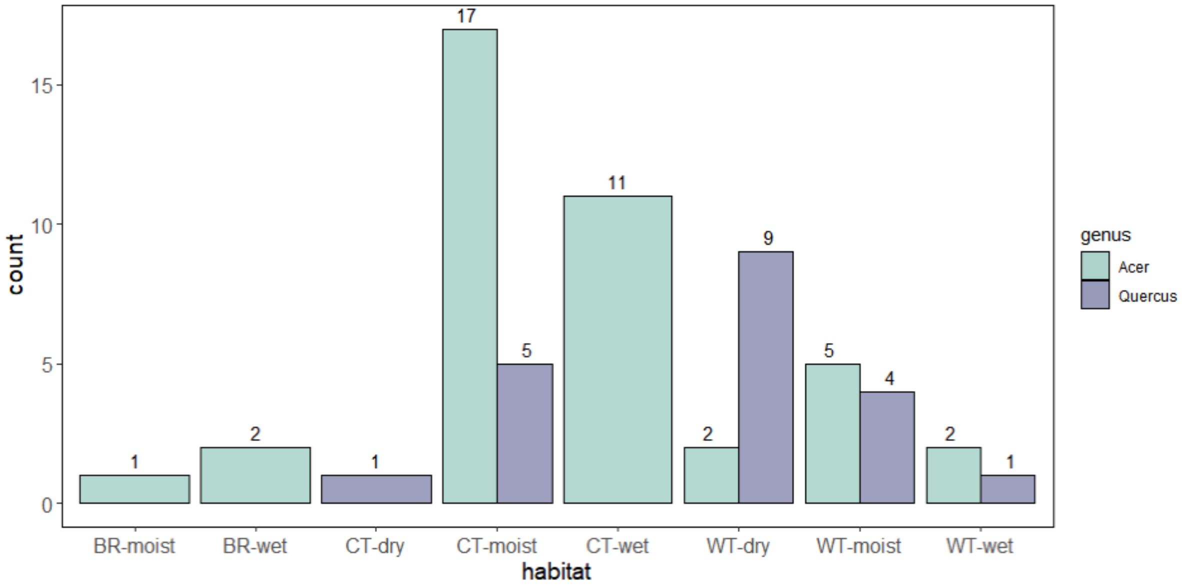


Figure 10. The distribution of species by genus according to their bioclimatic habitats. BR = boreal, CT = cool temperate, WT = warm temperate. The number of species represented is indicated on top of the bar.

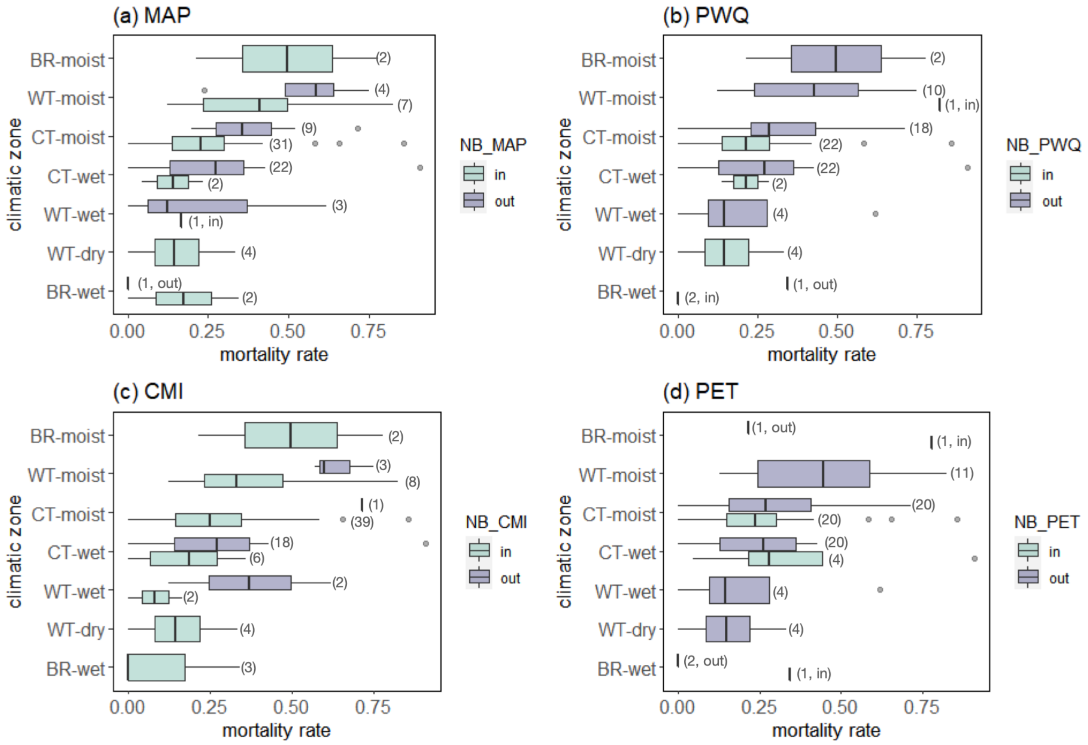


Figure 11. The distribution of cumulative mortality rates at species-level for *Acer* by habitat x NB. BR = boreal, CT = cool temperate, WT = warm temperate. Number of species represented is indicated in the parentheses.

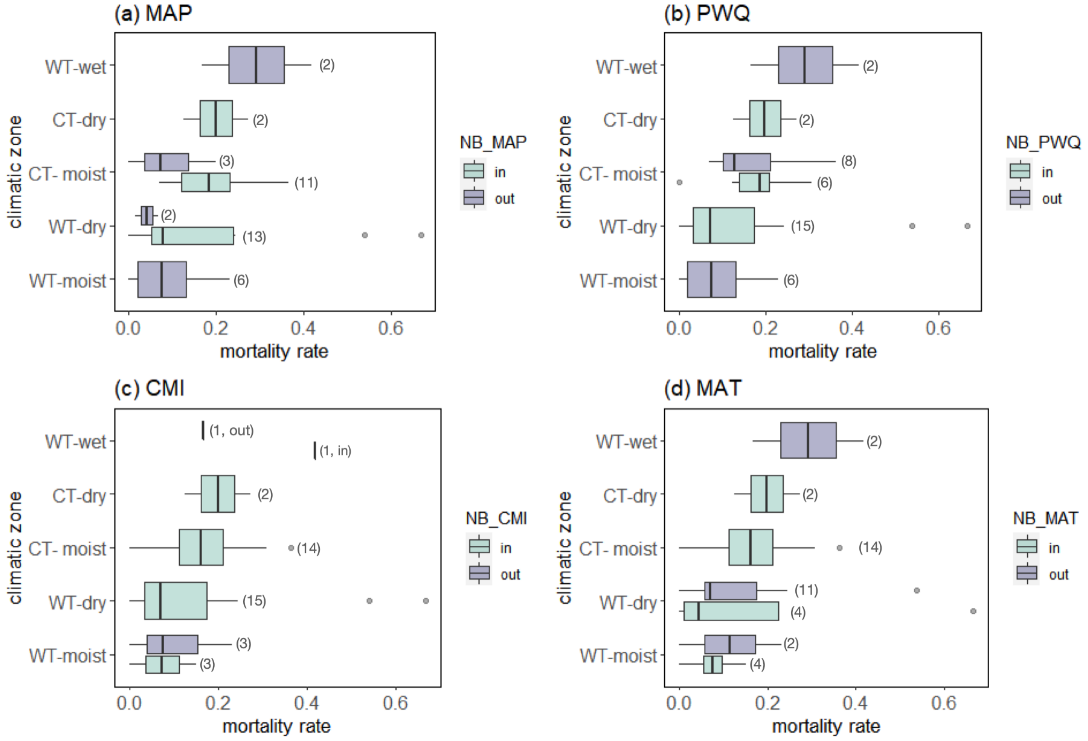


Figure 12. The distribution of cumulative mortality rates at species-level for *Quercus* by habitat x NB, CT = cool temperate, WT = warm temperate. Number of species represented is indicated in the parentheses.

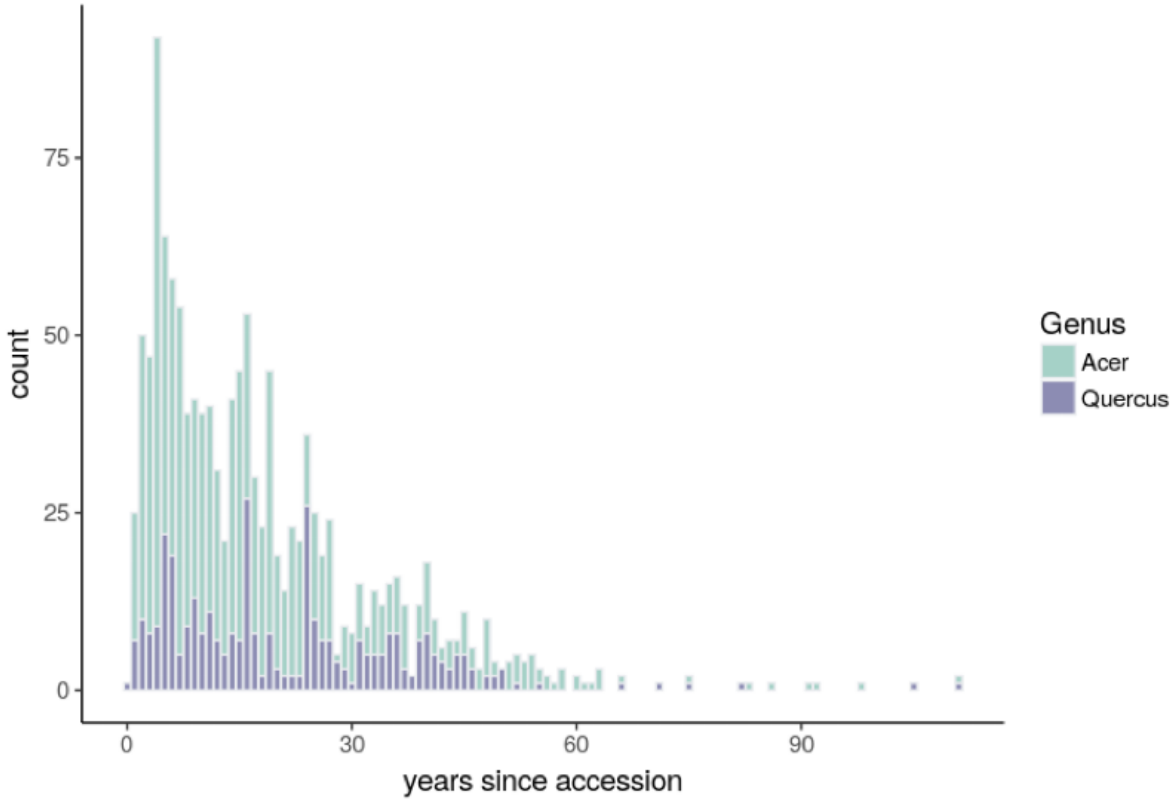


Figure 13. The histogram represents the number of years from the first accession year to the year of the death event. The data is compiled for all *Acer* (*n*=923) and all *Quercus* (*n*=359) across all BGs.

Appendix C.

Supplementary tables and figures for Chapter 4

Table 1. Variables used for bio selection A, B, and C

Variable	Description	*A. davidii*	*A. palmatum*	*A.pictum*
bio2	Mean diurnal air temperature	A, B, C	A, C	A, B, C
bio3	Isothermality	A, B, C	B, C	A, B, C
bio4	Temperature seasonality	A, B	A	A, B
bio5	Mean daily maximum air temperature of the warmest month		A, B	A
bio6	Mean daily minimum air temperature of the coldest month	C	C	C
bio7	Annual range of air temperature		B	
bio8	Mean daily mean air temperature of the wettest quarter		A, B	B
bio9	Mean daily mean air temperature of the driest quarter	C	A, C	C
bio10	Mean daily mean temperature of the warmest quarter	A, B		
bio15	Precipitation seasonality	A, B	A, B	
bio16	Mean monthly precipitation of the wettest quarter		A	A
bio18	Mean monthly precipitation of the warmest quarter	A		
bio19	Mean monthly precipitation of the coldest quarter		A, B	A, B
CMI_gs	Mean monthly climate moisture index during the growing season	B	B	B
CMI_spr	Mean monthly CMI from March to May	C	C	C
CMI_smr	Mean monthly CMI from June to August	C	C	C
PET_gs	Mean monthly potential evapotranspiration during the growing season	B	B	B
PET_spr	Mean monthly PET from March to May	C	C	C
PET_smr	Mean monthly PET from June to August	C	C	C
rsds	Mean monthly surface downwelling shortwave flux in air	B, C	B, C	B, C
ngd	Number of growing degree days at which mean air temperature > 5°C	B, C		B

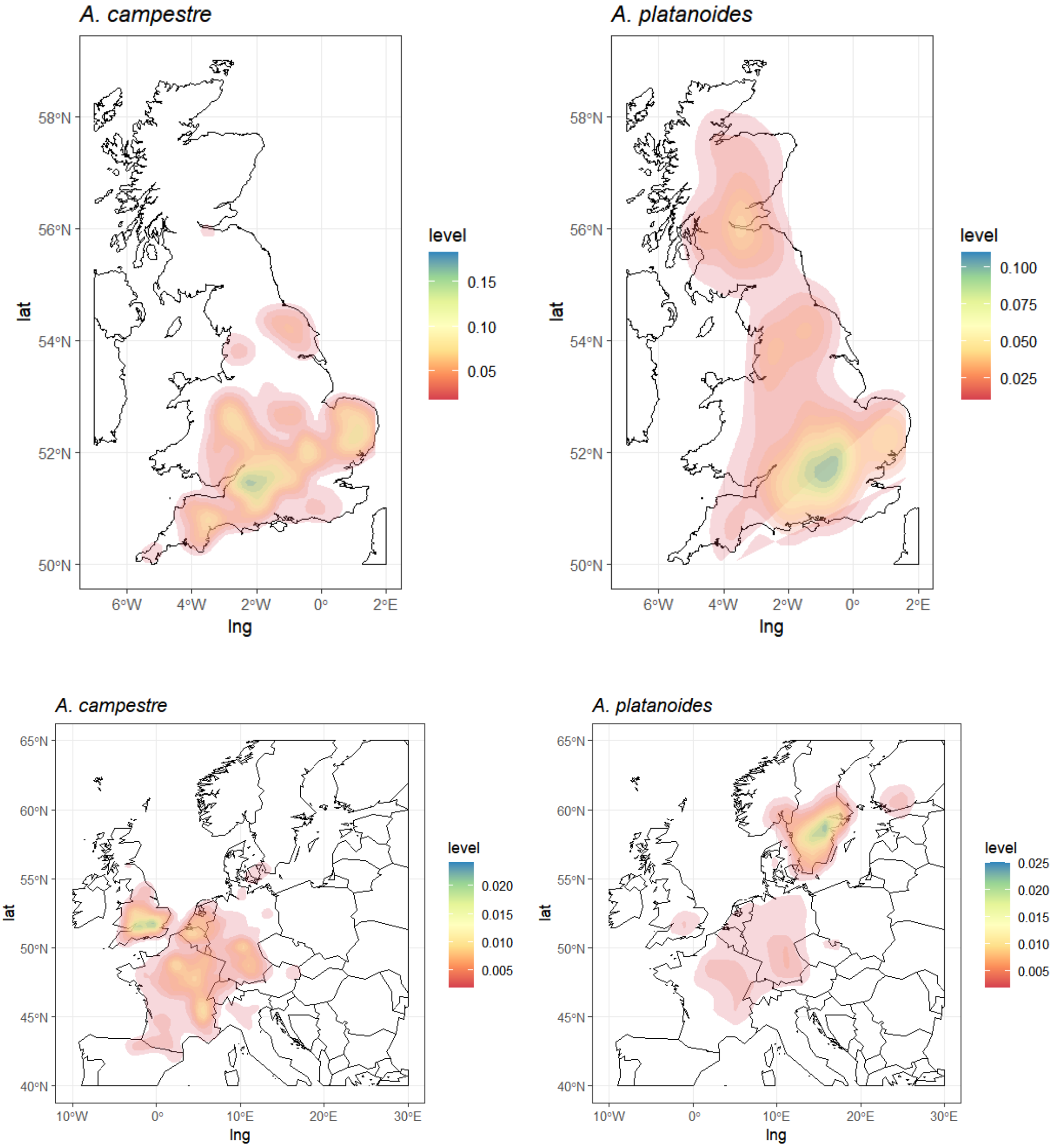
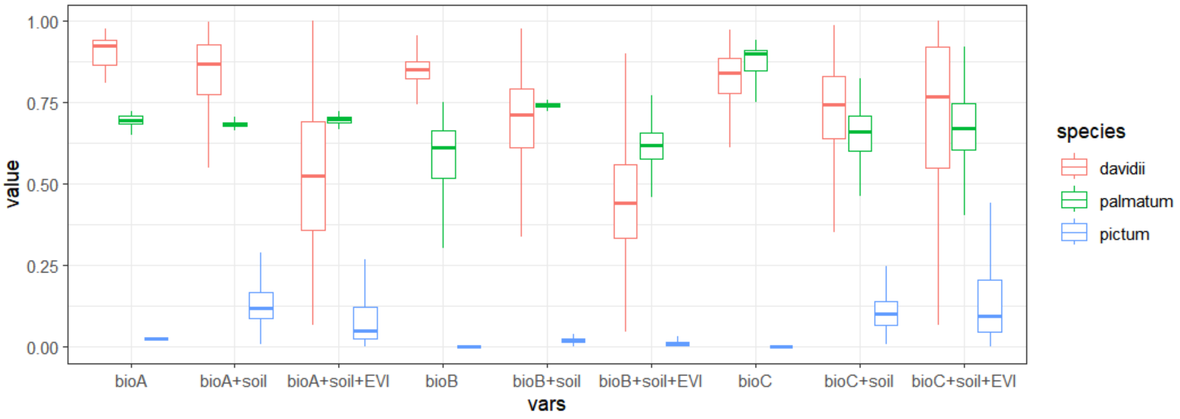
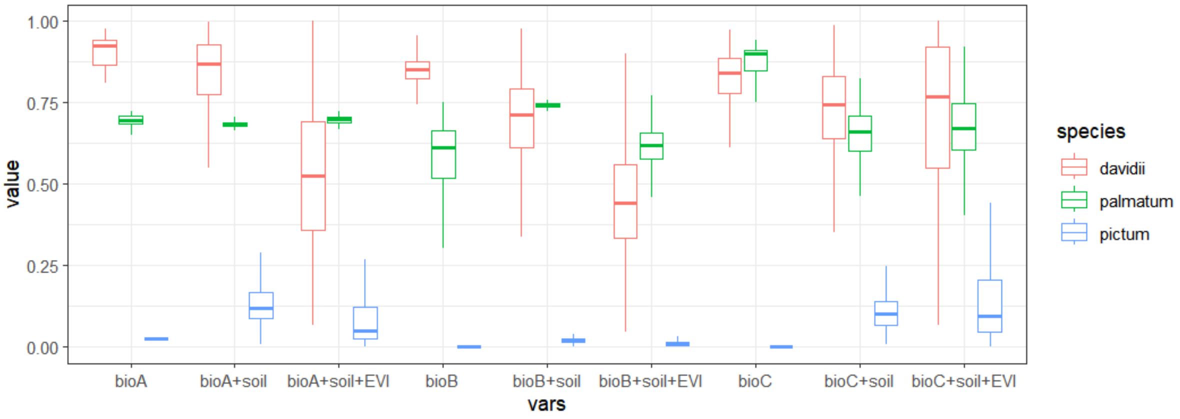


Figure 1. Distributed density map of *A. campestre* (n=14,508) and *A. platanoides* (n=3,036) in the UK (top) and *A. campestre* (*n*=66,712) and *A. platanoides* (*n*=66,482) in the Europe (bottom).


(b) Cotswold


(b) Cotswold

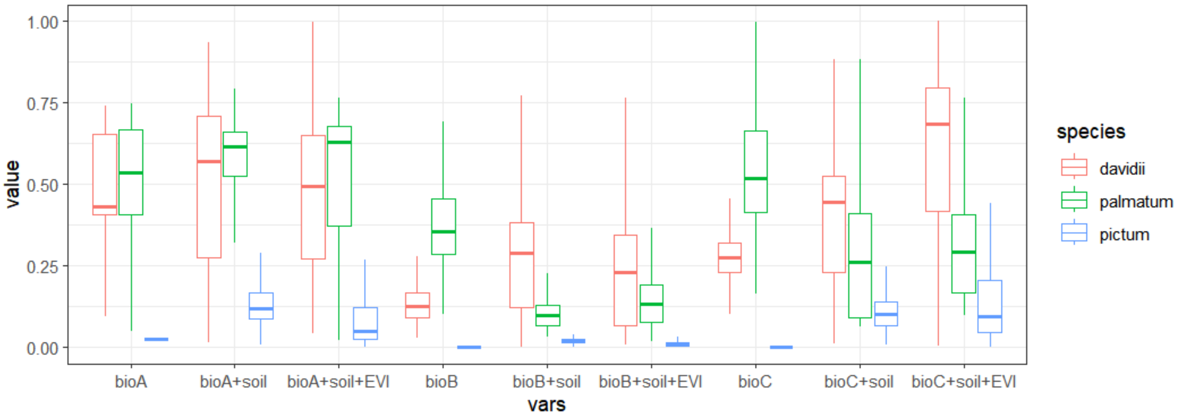

(c) Midlothian & West Lothian

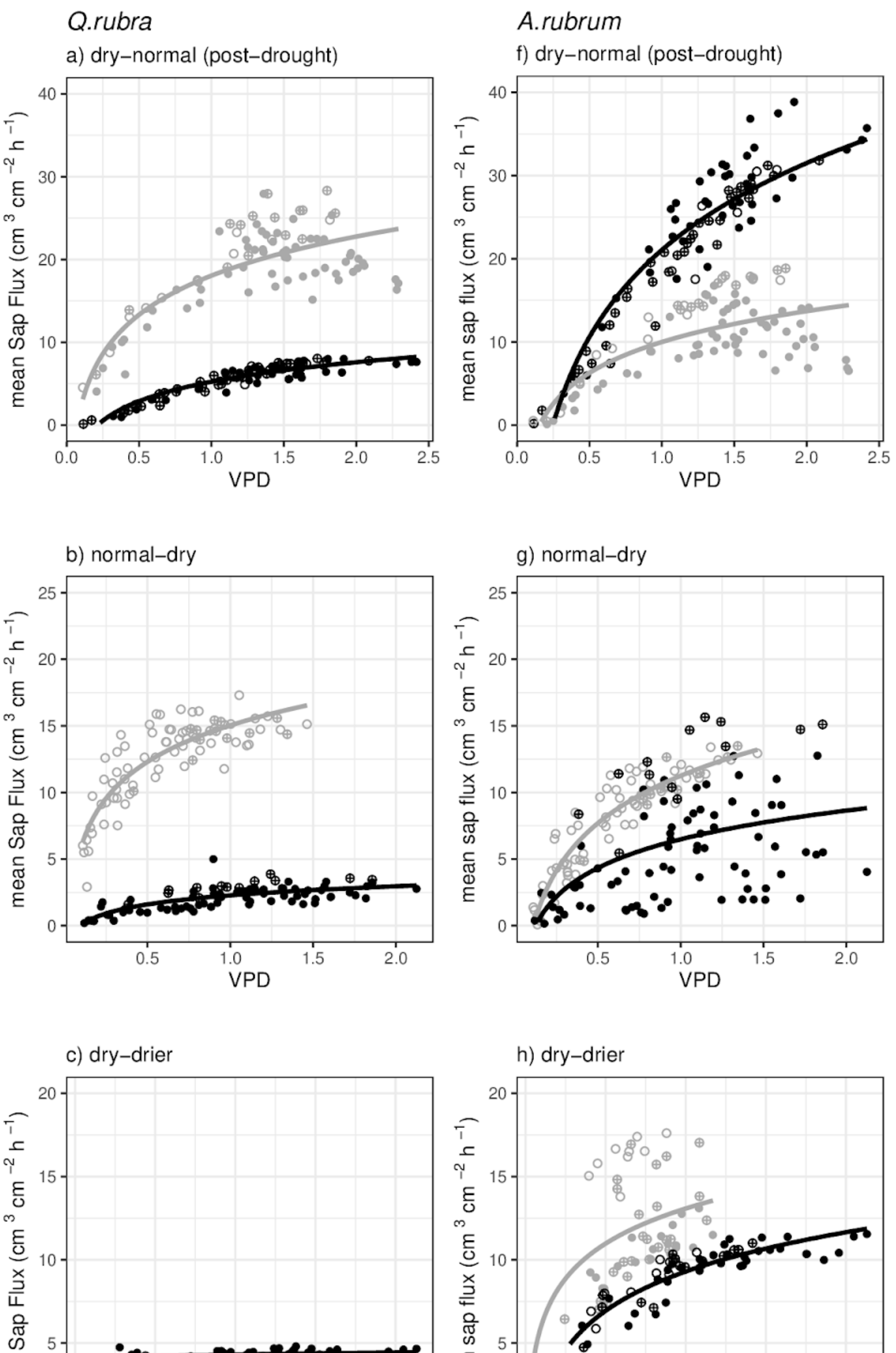
Figure 2. Resulting HS by different combinations of variables

Appendix D.

Supplementary table for Chapter 5

Table 1. Summary of biophysical characteristics and measurements of species for each site. dbh (diameter at breast height), A_{sw} (sapwood Area), *n* (total number of measurements)

Site	Species	unit	dbh (cm)	A_{sw} (cm^2)	Measurements (n)	reference
IN	*Q.rubra*	1	44.6	266.1	114	Yi et al. (2016)
	Q.alba	1	37.5	236.5	114	
	A.saccharum	2	41.2 ± 1.8	1102.5 ± 86.9	223	
TN	*Q.rubra*	1	63.0	537.0	172	Wilson et al. (2001)
	Q.alba	2	44.1 ± 4.5	329.0 ± 2.8	319	
	A.rubrum	2	44.1 ± 11.8	1054.0 ± 606.7	344	
MI	*Q.rubra*	4	31.0 ± 6.0	392.4 ± 156.8	381	Matheny et al. (2014)
	A.rubrum	2	12.0 ± 2.5	93.4 ± 42.7	269	
WI	*Q.rubra*	2	47.8 ± 9.2	188.3 ± 65.9	166	Cook et al. (2004)
	A.saccharum	4	29.2 ± 5.0	526.8 ± 215.5	353	
WV	*Q.rubra*	2	49.8 ± 2.8	375.0 ± 11.3	332	Tajchman et al. (1997)
	A.rubrum	2	18.3 ± 1.9	208.0 ± 42.4	332	
	A.saccharum	1	18.9	249.0	168	


Q.rubra
A.rubrum
a) dry−normal (post−drought)
f) dry−normal (post−drought)
b) normal−dry
g) normal−dry
c) dry−drier
h) dry−drier
mean Sap Flux (cm 3 cm −2 h −1)
mean sap flux (cm 3 cm −2 h −1)
VPD
0
5
10
15
20
25
30
40
0.0
0.5
1.0
1.5
2.0
2.5
1
2
3
4

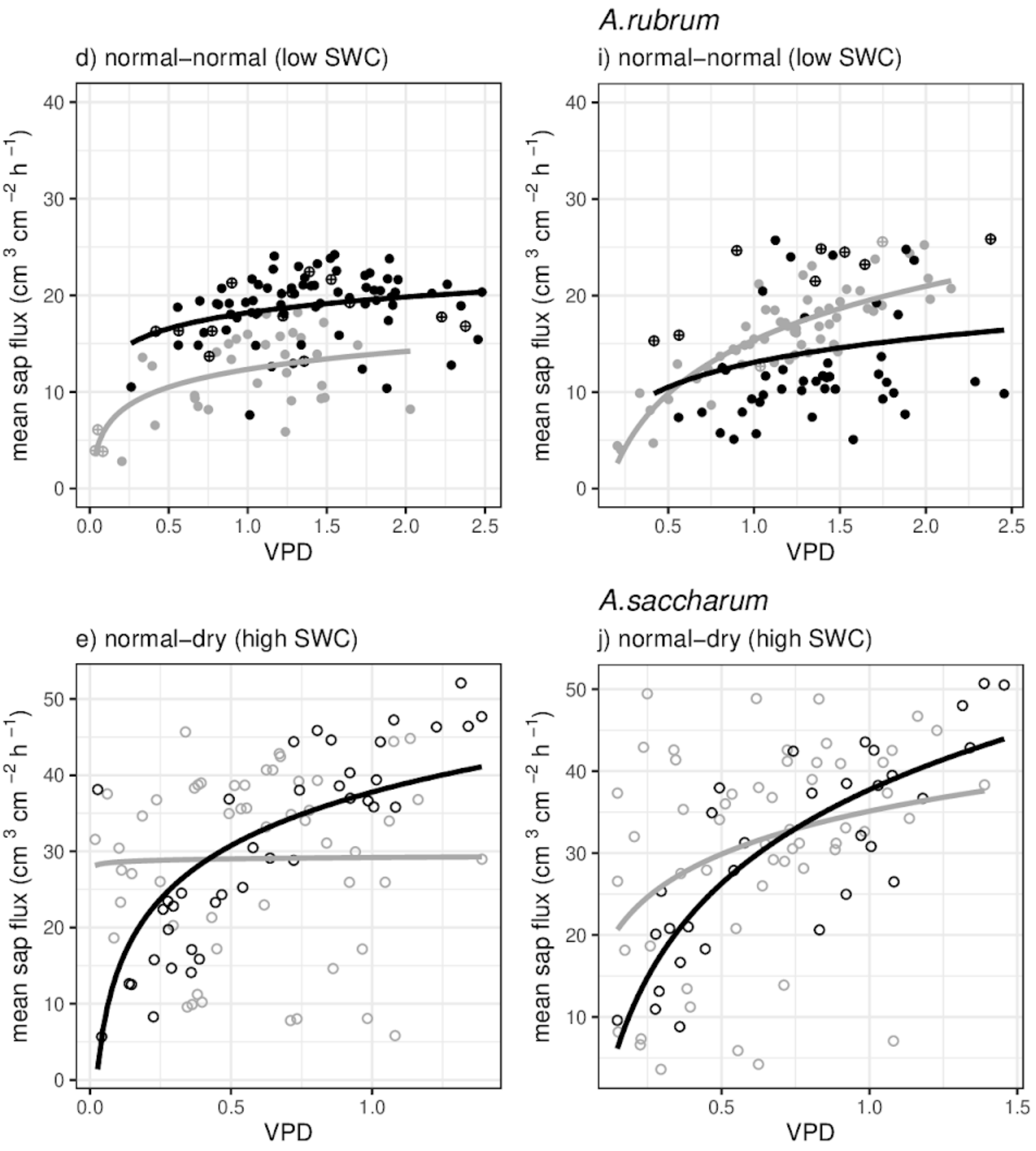


Figure 1. Mean sap flux in relation to VPD for TN (a, f), WV (b, g), IN (c, h), MI (d, i) and WI (e, j). SWC is denoted as ○ for wet (> 20%), ⊕ for mid, or ● for dry (<15%). Logarithmic regression curve for year 1 (Y1) in grey and year 2 (Y2) in black. Each year is classified as normal ($P/P_{mean} \geq 0.85$ & < 1.15), dry ($P/P_{mean} \geq 0.5$ & < 0.85) and drier ($P/P_{mean} < 0.5$).