Can Trait-Based Schemes Be Used to Select Species in Urban Forestry?

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Urban forests in northern Europe are threatened by climate change and biosecurity risks, and in response, city planners are urged to select a wider portfolio of tree species to mitigate the risks of species die-off. However, selecting the right species is a challenge, as most guidance available to specifiers focuses on ecosystem service delivery rather than the information most critical to tree establishment: the ability of a species to tolerate the stresses found in a given place. In this paper, we investigate the potential of using ecological techniques to describe ecological traits at the level of species selection, and the potential of functional ecology theories to identify species that are not widely discussed or specified at present but might be suitable. We collected trait data on 167 tree species across 37 genera, including 38 species within a case study genus, *Magnolia* L., and tested four theories that posit ways in which traits trade off against each other in predictable ways. We found that at this scale, most species recommended for urban forestry tend to be ordinated along an axis of variation describing pace of life and stress tolerance, and that most Magnolia species are described as being fast-growing rather than stress-tolerant, although there is a degree of inter-specific variation. Further, we found that only one theory offers a succinct and reliable way of describing physiological strategies but translating ecological theory into a form appropriate for urban forestry will require further work.

Keywords: urban forestry, species selection, functional ecology, plant traits, ecological theories and technologies

INTRODUCTION

It is widely acknowledged that urban forestry's challenge of optimising the fit between a tree and a site is likely to become increasingly difficult (Conway and Vander Vecht, 2015; Esperon-Rodriguez et al., 2019; Núñez-Florez et al., 2019) as the rate and extent of global urban tree habitat decline is likely to be uneven under climate change (Burley et al., 2019). To address this challenge, growing bodies of ecological and arboriculture literature identify different causes and types of environmental stress (Sack and Buckley, 2020; Mertens et al., 2021), accompanied by an increasing understanding of the physiological responses to these different stresses (Morgenroth et al., 2016). However, a substantial gap exists between our understanding of these stress-response processes and the methods that urban foresters use to apply this knowledge when it comes to selecting species for urban environments. In this paper, we attempt to close this gap by exploring the potential of ecological trait-based theories to improve species selection in urban environments.

Ecological traits are plant characteristics that fulfil functional purposes (*functional traits*) or describe ontological stages (*life history traits*) and are used for a wide range of purposes, including assessments of plant development, ecosystem services, and interactions between plant individuals and communities. Large bodies of literature have grown around both schools of trait ecology (Franco and Silvertown, 1996; Salguero-Gómez et al., 2015; Díaz et al., 2016; Kunstler et al., 2016) and the links between them are currently being explored (Adler et al., 2014; Struckman et al., 2019) but common to both are quantitative methods for describing plant functioning and the interactions between an individual and a community or a site. Recent research has shown that reproductive trait trade-offs scale from cell to population (English and Bonsall, 2019), strengthening the argument that relatively simple physiological processes can be used to describe complex strategies for resource allocation and community dynamics. As such, these fields hold significant potential for urban forestry, not only regarding species selection but also for improving many other aspects of urban forest management such as the quantification of ecosystem service provision or preparing management plans.

A central tenet of trait-based theory is that plants are constrained from performing alternative functions simultaneously (Law, 1979; Lavorel et al., 2007; Funk et al., 2017), such that they are traded-off against each other in predictable ways. For example, isohydric and anisohydric physiologies represent two viable but alternative strategies for a species to persist in stressful environments (Skelton et al., 2015) by either avoiding or tolerating drought. Building on this, broad principles for the coordination of traits within an individual or community have been developed, with numerous hypotheses proposed that describe strategies for coordinating resource allocation within a plant (Schimper, 1898; Herms and Mattson, 1992; Gitay and Noble, 1997; Westoby, 1998), structuring community dynamics (MacArthur and Wilson, 2001; Franco and Silvertown, 1996), and linking these processes to environmental variability (Grime, 2001; Southwood, 1988). Today, trait-based approaches are becoming increasingly made use of with functional traits being used to rank or ordinate species within schemes across international boundaries (Cerabolini et al., 2010) or map community successional stages (Chai et al., 2016). A major advance by Díaz et al. (2016) identified six key traits that explain the majority of variation in plant form and function, of which plant height and seed mass were among the most significant. This study was seminal in that it covered a global range of herbaceous and woody plants, identifying that some traits (such as Specific Stem Density and Leaf Mass per Area) are decoupled from height or size, showing instead that these traits describe the metabolic pace of an organism. Moreover, the functional hotspots identified in this study show that most plants occupy intermediate positions along trade-off boundaries, with relatively few species occupying extreme positions of variation.

The potential for using traits to understand global trends in plant ecology is increasingly supported through new capabilities in data sharing (Kattge et al., 2020), statistical analysis and computation power (Moles, 2018) alongside genetic studies

that map traits to stress tolerance (González-Martínez et al., 2008). Traditionally, trait data have been used by ecologists to assess habitat changes, plant responses to climate change or the delivery of ecosystem services (Asner et al., 2016), or by researchers to identify superior phenotypes in forestry and cereal crops. However, methodological advances (Moreno-Martínez et al., 2018; Verbeeck et al., 2019) open new opportunities for researchers to collaborate across disciplines and identify new applications for this knowledge.

Nevertheless, there remain major barriers that need to be overcome in order to apply trait-based strategies to designed landscapes such as the urban forest. Firstly, finding global support for functional strategies remains elusive, with ongoing disagreements over fundamental issues such as what a trait is, for example (Walker et al., 2017) or the scale at which they operate (Messier et al., 2017). Even traits that are well-recognised, such as Specific Leaf Area (SLA) present paradoxes in that they can be highly plastic but nevertheless repeatedly trade off against or correlate with other traits (such as Relative Growth Rate or Leaf Lifespan) (Sancho-Knapik et al., 2020) and explain fundamental dimensions of plant variation (Pierce et al., 2013). Further, traits appear to vary in the extent to which they are plastic or under genetic control (Saccone et al., 2017; Walker et al., 2017), whilst others have been shown to vary in significance over time (Gray et al., 2019) leading to changing relationships between traits as plants age (Gibert et al., 2016; Falster et al., 2018). These conceptual challenges are compounded by the characteristics of data that are used to develop theoretical advances: whilst major databases are being developed (Kattge et al., 2011, 2020; Salguero-Gómez et al., 2015; Maitner et al., 2018) that can advance macro-ecological questions, data are patchy in terms of species covered and traits measured, making it difficult to find sufficient traits for a species in order to ordinate them within a scheme. Further, inconsistent recording methodologies are used in spite of accepted protocols (Pérez-Harguindeguy et al., 2013), limiting the confidence with which we can interpret the results.

Alongside the barriers presented by working with an emerging theoretical field, the silo thinking that exists within urban forestry research needs to be overcome. Practitioners still place considerable emphasis on the heuristic literature (i.e., based on experience rather than standardised trials *per* Watkins et al., 2020), resulting in a slow feedback loop between research and practise, with tree nurseries yet to report changing sales patterns in spite of recent advances in the scope and focus of species selection guidance (e.g., Hirons and Sjöman, 2018). Where attempts have been made to use Plant Functional Types (PFT) in urban forestry, these have predominantly used traits that describe hypothetical ecosystem service delivery (Baraldi et al., 2019; Núñez-Florez et al., 2019) or include aesthetic criteria (Conway and Vander Vecht, 2015; Goodness et al., 2016; Goodness, 2018) rather than the fundamental ability of a tree to persist in an environment, which is the prerequisite for any other values that a tree might provide once it is mature. In this study, we seek to overcome this barrier by exploring whether quantitative, trait-based approaches can be used to identify potentially appropriate species for urban forestry by providing predictions of the fit between a tree and a planted environment. To do this, we evaluate

four widely-discussed theories of functional ecology that describe how different traits are integrated using a large dataset, covering species that are currently used in north European urban forestry or recommended for this purpose as well as a case study genus that is not well-understood in this context. As a case study, we selected *Magnolia* L. as it has a wide distribution across a range of geographic and climatic zones and in theory, should display a range of adaptations. Finally, we use the findings of this research to propose a simple scheme for integrating PFTs and functional traits in urban forestry.

MATERIALS AND METHODS

Experiment Design

When it comes to applying ecological theory, one of the differences between urban forestry and the fields of restoration ecology or eco-evo where much of this theory originates, us that

urban forestry is more concerned with the fit between a plant and a site and characteristics such as stress tolerance rather than other processes such as reproduction, or population dynamics. As such, we focus on aspects of plant functioning relating to how quickly a tree might establish and the ability to tolerate stresses arising from nutrient, oxygen or water deprivation. Whilst there is general agreement over the conceptual premise that the traits that reflect the pace of growth are traded off against plant size and the "investment" of resources in producing tissue (Wright et al., 2004; Salguero-Gómez et al., 2016), a consensus has yet to be reached over which of several competing theories is most effective at describing this trade-off and identifying species that might then be appropriate for species selection. To explore which (if any) theories might be most appropriate for use in urban forestry, four of the most widely discussed theories were studied (**Figure 1**): Universal Adaptive Theory, originally proposed by Grime (2001) as CSR theory and expanded in Grime and Pierce

FIGURE 1 | Conceptual summary of the four trait-based schemes evaluated in this study.
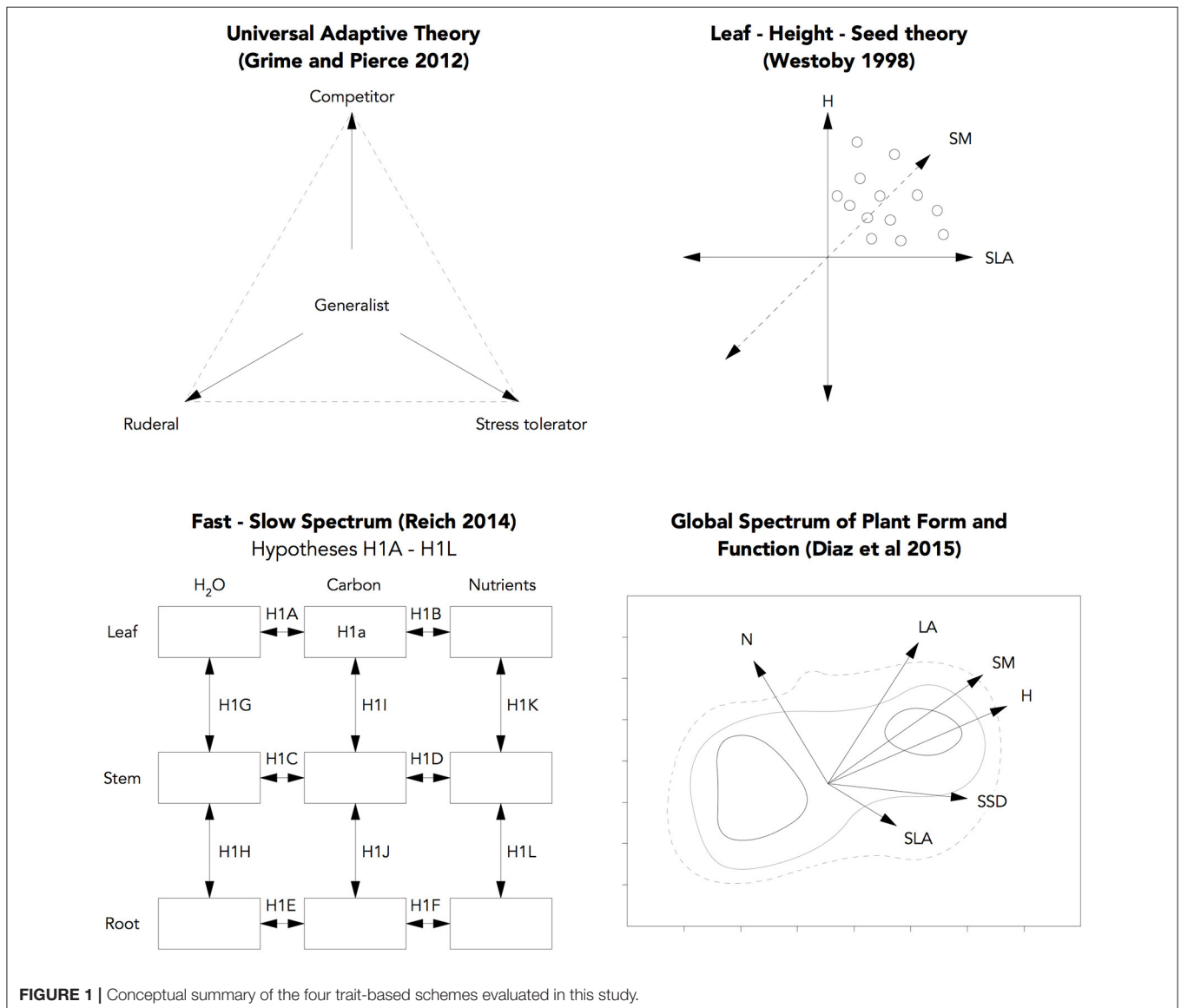
(2012), the Leaf-Height-Seed Scheme proposed by Westoby (1998) in response to Grime's CSR theory, the Fast-Slow spectrum formalised by Reich (2014) and the Global spectrum of plant form and function (Díaz et al., 2016).

Each of these theories aims to explain trait relationships that scale from the level of the organ to the whole plant and in turn to population and ecosystem, with the promise of providing elegant insights into complex functional relationships using simple, easy-to-measure traits. As can be seen in **Table 1**, the theories deploy similar traits: most rely upon a trade-offs between "soft" traits (e.g., Leaf area, *per* Hodgson et al., 1999), with only the Fast-Slow spectrum incorporating hard traits, and the varying emphasis on relationships between them and the ways in which they are correlated. Note that hereafter, the following abbreviations are used to identify traits: LA (Leaf Area), LDMC (Leaf Dry Matter Content), SLA (Specific Leaf Area), SSD (Specific Stem Density), WP-TLP (Leaf Water Potential at turgor loss-point), SM (Seed Mass), and H (Height). In this experiment, we collected trait data for the traits above with the aim of testing the extent to which (a) these relationships hold true at this scale and (b) they can be used to inform species selection. As such, a successful scheme would be based on strong and significant relationships and also provide an interpretable framework for ordinating species.

Species Selection

An increasing diversity of species are proposed for use in urban forestry in response to existential threats such as biosecurity risks and climate change (Kim et al., 2019; Hanley et al., 2021). To test whether trait schemes can aid selection of novel species or identify species that are currently used but that are likely to be inappropriate under climate change, we selected species that are discussed in current industry guidance (see **Supplementary Table 1**) and used a case study genus (*Magnolia* L.) to explore the potential of different schemes to identify species

(shown in **Table 2**) that would be appropriate for different urban forestry purposes such as street trees, parks, or swales.

Magnolia L. is a flagship genus with active programmes in conservation and horticulture but is largely unused in high stress environments such as streets or urban podium planting, presenting opportunities for urban forestry to diversify the range of species that are currently used. In spite of its reputation of being non-robust and drought-prone, *Magnolia* L. is a potentially interesting genus, partly due to its high ornamental qualities but also due to the wide range of genotypic variation and the wide range of environmental niches it occupies, as shown in **Table 2**. Further, the ornamental qualities of *Magnolia* L. offer an opportunity to address concerns that the aesthetically striking trees that are preferred by residents do not generally possess the traits needed to survive in harsh environments (Pataki et al., 2013; Conway, 2016).

Data Collection

A number of sources were needed to collect sufficient trait data for this research. The TRY database (Kattge et al., 2020) and unpublished data from Hirons and Sjoman provided the baseline data, complemented by experimental research on genus *Magnolia* L. collected in the summers of 2017 and 2018, as shown in **Table 3**. A request was submitted to TRY for the traits in **Table 1** across all the species listed in **Supplementary Table 1**. These data were filtered to remove juvenile plants (Data ID 413), non-healthy plants (Data ID 1961), records with a high error risk (>3) or those that were too small (H <5 m).

This research highlights the logistical challenges of evaluating novel species for urban forestry as many of the species in **Table 2** are found only in specialist collections in northern Europe, where restrictions exist over the type of trait data (e.g., SSD) that collection managers permitted to be collected.

Magnolia trait data were collected in the summers of 2017 and 2018, using sites listed in **Table 3**. Mature, healthy trees

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TABLE 1 | The traits and trait-based schemes evaluated in this study.

Trait	Ecological significance	Functional trait schemes
Leaf area	Photosynthetic organ size; response to soil resources; climate adaptation	• Global spectrum of plant form and function (Díaz et al., 2016), hereafter GSPFF • Universal Adaptive Theory (Grime and Pierce, 2012), hereafter UAT
Specific leaf area	Plasticity; response to disturbance; stress avoidance	• Fast-Slow spectrum (Reich, 2014), hereafter FSS • GSPFF • Leaf—Height—Seed scheme (Westoby, 1998), hereafter LHS • UAT
Leaf dry matter content	Index of conservatism in life history; plant defence; and protection	• UAT
Height	Competitive ability; CO_2 response; response to disturbance	• GSPFF • LHS
Specific stem density	Longevity; resistance to embolism; tolerance of chemical toxicity	• GSPFF • FSS
Seed mass	Dispersal in time and space; Seedling establishment; plant defence and protection	• GSPFF • LHS
Leaf water potential at turgor point	Tolerance of drought	• FSS

Species	Environmental niche
M. acuminata	Well-drained valley bottoms or gentle slopes, considered to be the "hardiest" of North American Magnolia species (Kehla, 2014a)
M. biondii	Subtropical or dry tropical forests, growing best in sandy loam around 600 m asl in central/western China (Gibbs and Wheeler, 2014)
M. campbellii	Subtropical and Tropical moist montane forests, between 2,100 and 3,300 m from Bhutan and NE India through Nepal to SW China (Kehla, 2014b)
M. cylindrica	Thickets and forests across a wide altitudinal range (Li et al., 2017)
M. dawsoniana	Steep mountain slopes (Chen et al., 2012)
M. decidua	Subtropical moist lowlands in Subtropical and Tropical moist lowland forests between 400 and 700 m asl in Jiangxi, China (China Expert Workshop, 2014)
M. denudata	Subtropical and Tropical moist montane forests between 500 and 1,000 m asl in central and eastern China (Global Tree Specialist Group, 2014a)
M. fraseri	Temperate forests between 500 and 1,700 m asl in the Appalachian, Blue Ridge, and Cumberland Mountains (Kehla, 2014c)
M. grandiflora	Temperate forests between 60 and 150 m asl in the southeastern USA, growing best on rich, loamy moist, and well-drained soils of the bottoms and low uplands of the Coastal Plains of Southeastern United States, along streams, and near swamps. It also grows on mesic upland sites where fire is rare (Kehla, 2014d)
M. kobus	Temperate thickets and deciduous broadleaved secondary forests at elevations of approximately sea level to 1,700 m asl throughout Honshu Island, Japan (Kehla, 2014e)
M. liliiflora	Subtropical and Tropical moist lowland forest margins between 300 and 1,600 m asl in Yunnan and Hubei, China (Global Tree Specialist Group, 2014b)
M. macrophylla	Temperate forests in the Southern and South-western states of the USA (Global Tree Specialist Group, 2014c)
M. macrophylla var. ashei	Broadleaved or mixed forest on ravine slopes and bluffs in the southern half of the Florida panhandle (World Conservation Monitoring Centre, 1998)
M. obovata	Grows sporadically on damp to mesic places such as margins of deciduous broadleaved temperate forests from sea level up to 1,800 m asl throughout most Japanese islands and Kunashir Island, Russian Federation (Kehla, 2014f)
M. officinalis	Widely distributed through western, central, and eastern China in Subtropical and Tropical moist lowlands and montane broad-leaved forests (Rivers, 2015)
M. rostrata	Between 2,100 and 3,000 m asl in Subtropical/Tropical moist montane forests in Tibet and Yunnan (China) and northern Myanmar (Kehla, 2014g)
M. salicifolia	Wide distribution in Honshu, Shikoku and Kyushu islands, Japan, where it grows in beech and oak forests on mesic to moist mountain slopes from near sea level to 2,000 m asl (Kehla, 2014h)
M. sieboldii	1,600–2,000 m asl in Subtropical and Tropical moist montane forests in south and eastern China, the Korea peninsula and Japan (Kehla, 2014i).
M. sprengeri	Subtropical and Tropical moist montane forests and thickets in central and western China (Kehla, 2014j)
M. stellata	Restricted to a narrow area in Central Honshu around Nagoya, limited to lowland hills, valleys, terraces, riverbeds, or shallow gorges. It occurs primarily in sunny areas which are moist with continuous water flows below 600 m asl (Harvey-Brown, 2019)
M. tripetala	A widespread distribution in the central eastern 23 states, growing in moist soils high in humus found along streams, in ravines and on lower mountain slopes (Kehla et al., 2014)
M. virginiana	Grows throughout southern and south-eastern states in the USA, in sites characterised by acid soils of low base saturation and with poor to very poor drainage and are frequently flooded during the winter or wet seasons. The species is classed as intermediate in its tolerance to shade and flooding (Kehla, 2014k)
M. wilsonii	Subtropical and Tropical moist montane forests and thickets at 1,900–3,300 m asl in Yunnan, Sichuan, and Guizhou (China) (China Expert Workshop, 2015)

were identified, aiming to select six individuals of each species, although in some cases this was not possible. Cultivars were not included, as this study was designed to test inter-specific trait relationships and these selections were not considered to be representative as they are generally selected for outstanding horticultural qualities. Standard protocols were used to collect trait data (Pérez-Harguindeguy et al., 2013).

Analysis

Statistical analysis was carried out using MS Excel v16.30 and R Studio v3.6.3. Data were checked for normality, and LA and SM data were log transformed. The Pearson correlation coefficient was calculated for each trait relationship and trait distributions were summarised in a matrix using the R packages Hmisc, ggplot2, GGally, and plyr (Harrell, 2020; Schloerke et al., 2020; Wickham, 2020; Wickham et al., 2020).

Using the trait data, species were ordinated within plant functional type schemes using ggplot2 and ggtern (Hamilton and Ferry, 2018). For CSR, the methodology of Pierce et al. (2013) was preferred to that of Hodgson et al. (1999) as it reduces the reliance upon artificial trait categories and can be rapidly calculated using basic morpho-physiological traits. Further, the methodology has been shown to be reliable through replication by Li and Shipley (2017) and can be applied to all vascular plants, rather than merely herbaceous species. CSR ternary plots were created using the C, S, and R values from the StrateFy tool (Pierce et al., 2017). To ordinate species within the Leaf-Height-Seed scheme, species were plotted in a 3 dimensional scatterplot as per Westoby's methodology (Westoby, 1998). Reich's Fast-Slow Spectrum hypothesis (Reich, 2014) does not identify a methodology for ordinating species along the Fast-Slow Spectrum but based on the central hypotheses that (a) being fast at any organ-level at acquiring carbon, nutrients, or

water requires being fast for the other resources at the same organ-level and (b) that being fast for resources at any one organ level requires being fast for all other resources at the other organs, two dimensional scatter plots were drawn for the two trait relationships hypothesised in Reich's Hypothesis 1a (the coordination of Carbon and Water within the leaf) and Hypothesis 1i (the coordination of carbon between leaf and stem) and the trait relationships identified in GSPFF.

TABLE 3 | Magnolia plant material sources.

Plant material source	Coordinates	Trait data collected
Arboretum Wespelaar, Belgium	50.95, 4.63	H, WP-TLP
Caerhays Castle, UK	50.23, −4.84	H, SM
Cornell University, USA	42.45, −76.47	WP-TLP
Florida State University, USA	30.44, −84.29	SM
Mount Congreve, Ireland	52.24, −7.22	H, LA, LDMC, SLA, SSD, SM
Mount Usher, Ireland	53.00, −6.10	H, LA, LDMC, SLA, SSD, SM
Sheffield Botanical Gardens, UK	53.37, −1.49	H, SM
SLU Alnarp campus, Sweden	55.65, 13.08	H, LA, LDMC, SLA, SSD, WP-TLP
Windsor Great Park, UK	51.43, −0.60	H, WP-TLP

For trait data codes, see **Table 1**.

Finally, a table of trait relationships, their Pearson coefficients of correlation and significance was created and ranked according to significance.

RESULTS

Summary

A dataset was built comprising 1,922 Magnolia trait records gathered specifically for this study, 1,309 records of Leaf water potential at turgor loss point from the unpublished Hirons and Sjoman dataset and 26,643 trait records from TRY v6.0 (Kattge et al., 2020), of which 17,570 met the criteria set out above. There were 21 possible trait combinations of the 7 traits in this study, of which 10 show significance at $p < 0.05$ (**Table 4**). Four of these 10 significant relationships represent the same axis of variation (cost of investment in tissue) and are not part of any of the trait schemes considered within this study. Of the 10 trait combinations that were significant, only 2 of the trait combinations (LDMC-SLA and LDMC-SSD) displayed strong trade-offs ($r > 0.5$ or <-0.5), with the relationship between LDMC-SLA supporting Grime and Pierce's hypothesis that the relationship between investment in tissue and metabolic pace represents a fundamental trade-off. The strongly significant positive correlation between LDMC-SSD is not formally discussed by any of the four trait schemes, although this result does support a central tenet of Reich's formulation of the Fast-Slow Spectrum that investment in tissue is controlled at a whole-plant level and is consistent across organs.

TABLE 4 | Significance and strength of correlation between functional traits (significant relationships shown in bold).

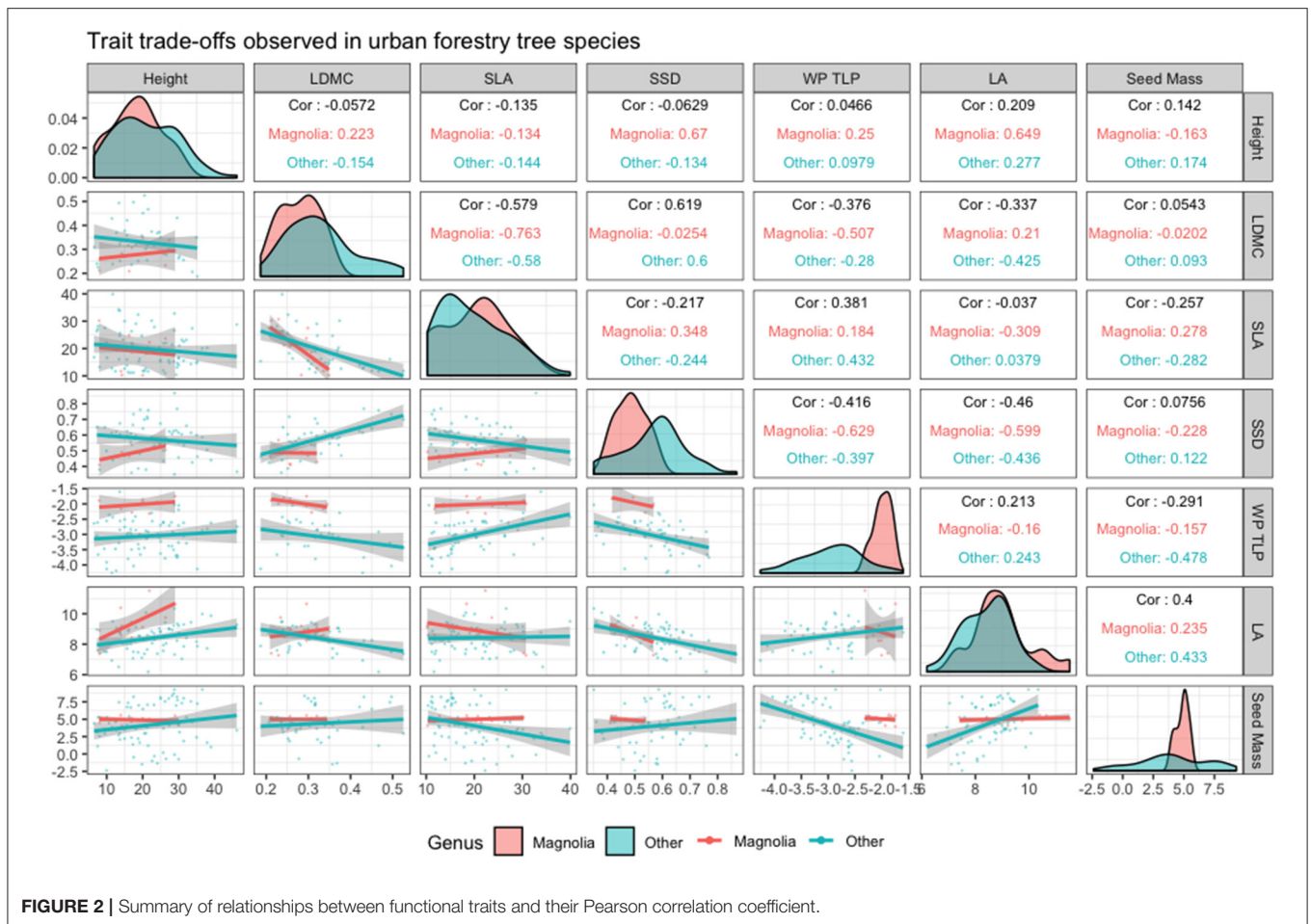| Trait relationship	Scheme	Functional significance	Pearson's correlation	Significance
LDMC–SLA	UAT	Cost of investment vs. metabolic pace	−0.579432	**0.0000010**
LDMC–SSD	None	Cost of investment (same axis of variation)	0.61912911	**0.0000027**
SSD–LA	GSPFF	Cost of investment vs. size	−0.46002281	**0.0000792**
LA–SM	GSPFF	Cost of investment vs. size	0.39980704	**0.0001982**
SLA–WP TLP	FSS	Metabolic pace vs. stress tolerance	0.38126557	**0.0013375**
SSD–WP TLP	None	Cost of investment (same axis of variation)	−0.41608018	**0.0017527**
WP TLP–SM	None	Cost of investment (same axis of variation)	−0.29099734	**0.0083996**
LDMC–LA	UAT	Cost of investment vs. size	−0.33676208	**0.0097420**
SLA–SM	GSPFF + LHS	Metabolic pace vs. cost of investment	−0.25711896	**0.0138795**
LDMC–WP TLP	None	Cost of investment (same axis of variation)	−0.37639778	**0.0152858**
Height–LA	GSPFF	Whole plant size vs. organ size	0.20908175	0.0644240
SLA–SSD	FSS + GSPFF	Metabolic pace vs. cost of investment	−0.21713147	0.0709887
WP TLP–LA	None	Stress tolerance vs. size	0.21266199	0.0998743
Height–SM	GSPFF	Whole plant size vs. cost of investment	0.14245089	0.1595604
Height–SLA	LHS + GSPFF	Metabolic pace vs. size	−0.13527971	0.2115529
SSD–SM	LHS + GSPFF	Cost of investment (same axis of variation)	0.0755523	0.5403090
Height–SSD	GSPFF	Cost of investment vs. size	−0.06293563	0.6074325
Height–WP TLP	None	Cost of investment vs. size	0.04655247	0.6798381
Height–LDMC	None	Cost of investment vs. size	−0.05720905	0.6811466
LDMC–SM	None	Cost of investment (same axis of variation)	0.05425447	0.6912651
SLA–LA	UAT + GSPFF	Metabolic pace vs. size	−0.03696893	0.7369425

FIGURE 2 | Summary of relationships between functional traits and their Pearson correlation coefficient.

The strength and significance of these trait relationships are summarised in **Figure 2**, which distinguishes the case study genus, *Magnolia*, from the species that are more commonly used in northern European urban forestry. **Figure 2** suggests that it is possible to make generalisations about *Magnolia* but not necessarily in ways that support heuristic or cultural assumptions (Watkins et al., 2020): for example, in relation to the other species in this study, the genus tends to have relatively heavy seeds, low density woody tissue, and relatively low resistance to cavity embolism but on the other hand, it has other leaf traits that are comparable to many species that are already used in urban forestry, suggesting that whilst some species in the genus may be more susceptible to stresses such as drought, they may also possess traits that allow them to establish quickly in the right conditions. Further, the range of trait values found in genus *Magnolia* appears to support biogeographical assessment of the wide range of environmental niches that the genus is distributed across (**Table 2**).
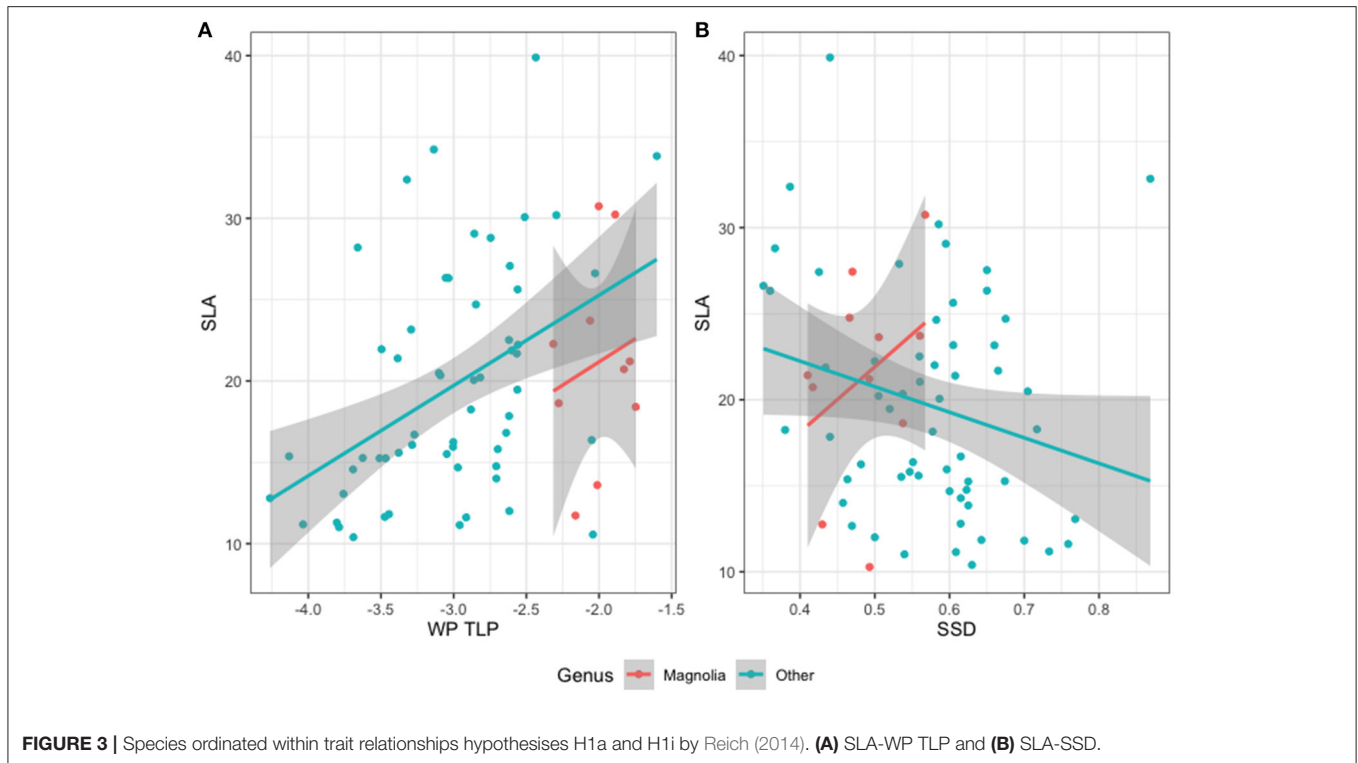
Fast Slow Spectrum
This study evaluated two of the hypotheses within the Fast Slow Spectrum, assessing the balance of resources within a single organ (Reich's Hypothesis 1a) and the coordination of resources between organs (Hypothesis 1i). SLA plays an important role in Reich's hypotheses and the wide range of values for SLA found in *Magnolia* suggests that using relatively plastic traits (such as SLA) in a paired study presents issues at this scale as it is possible for non-representative data to distort findings. Whilst the relationship between traits within a single organ (H1a, **Figure 3A**) may be significant, this relationship is weak and especially so in the case of genus *Magnolia*. We found a weak and non-significant relationship between SLA and SSD, showing that whilst Magnolia traits support Reich's hypothesis (H1i) that being "fast" for one trait requires being fast for others, this does not hold for the other species within this study, as shown in **Figure 3B**.

Global Spectrum of Plant Form and Function
The Global Spectrum of Plant Form and Function identifies six traits that "capture the essence of plant form and function" (Díaz et al., 2016). The five soft traits that are used in other theories were measured in this study and of the 10 possible trait combinations, only three were significant ($p < 0.5$): LA-SM, LA-SSD, and SM-SLA. None of these three were strongly correlated ($r < 0.5$ or $r > -0.5$), and strongest correlations were between LA-SSD ($r = -0.46$, **Figure 4C**), and LA-SM ($r = 0.39$).

FIGURE 3 | Species ordinated within trait relationships hypothesises H1a and H1i by Reich (2014). **(A)** SLA-WP TLP and **(B)** SLA-SSD.

Correlations for SSD-H (**Figure 4A**), SLA-SM (**Figure 4B**), and SLA-LA (**Figure 4D**) replicate the findings of **Figure 3B**, where data for *Magnolia* supports the hypothesised trade-offs, whilst the correlation between these traits in other species were in the opposite direction to that which was found in the global study by Diaz et al.

Leaf Height Seed Scheme

The Leaf Height Seed scheme was proposed in response to Grime's CSR theory, with a number of points of difference that allowed for replicable studies that use functional traits in a consistent manner to ordinate species. Crucial differences include the delimited, unconstrained axes in three dimensional space (as opposed to a ternary plot, as shown in **Figure 5**) and using traits to explicitly relate to functional characteristics, with SLA capturing the ability of species to respond to opportunities for rapid growth and H and SM reflecting species ability to respond to the effects of resource-depletion through competition by investing in stature and reproductive traits. In this study, none of the relationships between these three traits were strong: the strongest relationship was also non-significant (SM-SLA: $r = -0.25$, $p = 0.13$), with the other two trait combinations decoupled and not significant (SM-H and SLA-H, $p > 0.05$).
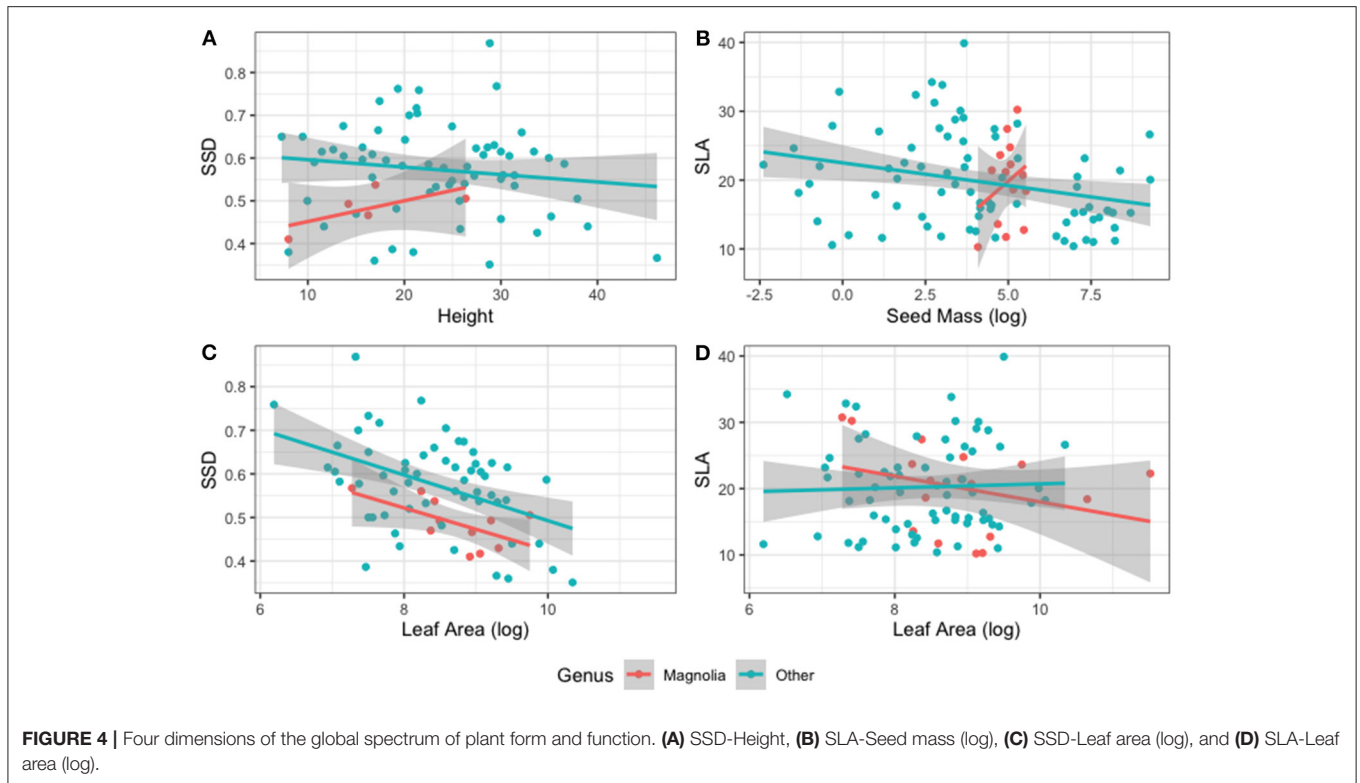
Universal Adaptive Theory

The Universal Adaptive Theory (Grime and Pierce, 2012) is the most advanced iteration of the CSR hypothesis, extending the principles to all forms of life across trophic boundaries, rather than just vascular plants. In Grime's original formulation of

CSR (Grime, 2001), three strategies are identified that allow organisms to respond to stress and disturbance, with organisms displaying each of these three strategies to different extents but always in ways that are constrained, hence the use of the ternary plot with extreme positions of C, S, and R in each corner. In this study, we used the methodology developed by Pierce et al. (2013, 2017) on the basis that it allows for species to be ordinated within CSR space in a manner that is replicable and uses only "soft" traits that can be measured within a single leaf. This study found that two of the three trait combinations were found to be significant (SLA-LDMC and LDMC-LA, $p < 0.05$), with the relationship between SLA-LDMC being the strongest of all trait combinations studied in this research ($r = -0.57$) and most significant ($p = 0.000001$). Within the ternary plot in **Figure 6**, most of the species studied are shown to be stress-tolerant generalists whilst *Magnolia* species tend to be competitive generalists, broadly in line with the conditions found within their natural ranges.

DISCUSSION

Interpretation of the Ordinations Within Functional Trait Schemes

Whilst the individual trait data reflect or mediate specialised evolutionary adaptions within a specific organ and allow comparisons to be made between species, three key findings can be reported from the review of the different trait-based schemes when applied to urban forestry species selection. Firstly, our hypothesised trade-off between pace of growth

FIGURE 4 | Four dimensions of the global spectrum of plant form and function. **(A)** SSD-Height, **(B)** SLA-Seed mass (log), **(C)** SSD-Leaf area (log), and **(D)** SLA-Leaf area (log).
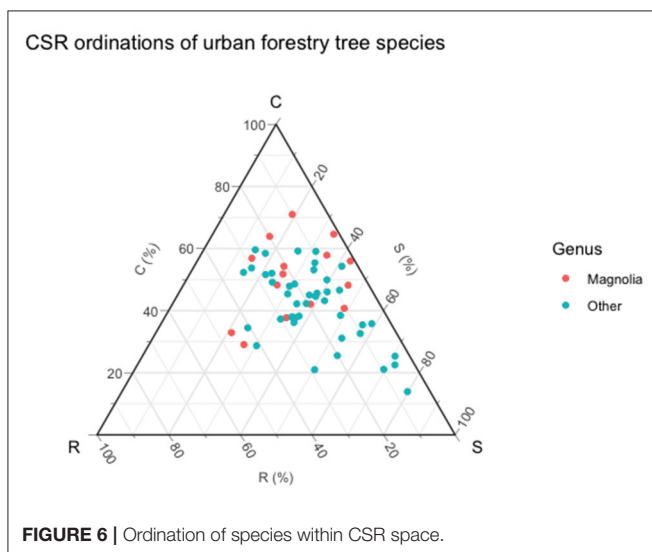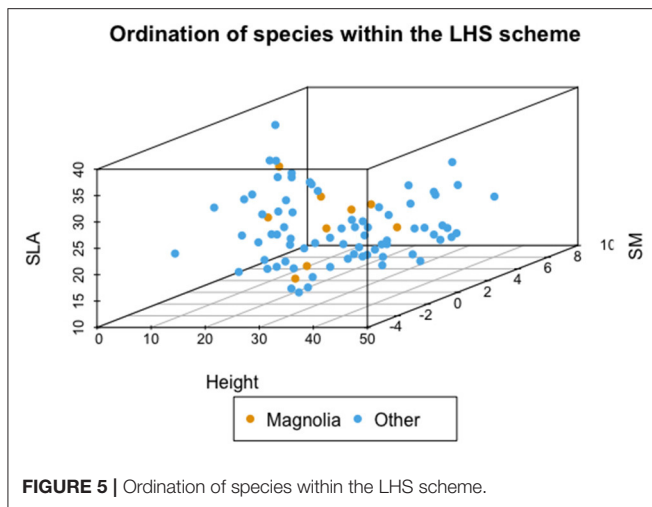
and stress tolerance was identified in some of the schemes in this study, but at the scale of this study, only one of the 21 relationships employed by the theories studied was both strong and significant (LDMC-SLA). Secondly, it is clear that whilst specific characteristics can be inferred from a single trait (Blanuša et al., 2020), a single trait alone cannot be used to guide specification of trees within urban forests, not only because traits need to be understood in the context of other traits and whole-plant functioning (Violle, 2007) but also because urban forests are highly heterogenous stress environments, with sites placing specific constraints on an organism that affect fitness. For this reason, the case for finding an effective suite of traits to measure or a scheme that explains the coordination of these traits is strengthened.

Thirdly, it appears that some trait schemes are more suited to some purposes than others, suggesting that alongside the mantra of "the right tree for the right place," urban foresters need to use the right scheme for the right scale. The Fast-Slow Spectrum and Global Spectrum of Plant Form and Functioning are compelling hypotheses that are well-supported at macro-ecological scales but it is not clear to what extent these are confounded by abiotic influences on plant form at a local scale. The results of this study show that the trait relationships that these schemes are based upon are not sufficiently precise for urban foresters engaging in species selection. In this review, we can see that only 10 trait combinations are statistically significant and that of these, the C-S axis of the UAT is able to explain the most meaningful degree of variation.

The Fast-Slow Spectrum is attractive due to its simplicity: the hypothesis that if a plant is fast for one trait, it will by necessity be fast for all, has general support for the integration of hydraulic traits with carbon and nutrient cycling found by Jin et al. (2016) and extends the widely tested Leaf Economic Spectrum (Wright et al., 2004). However, correlation strength between pairs of leaf traits constrains but does not predict whether the traits respond similarly to different drivers of variation (Messier et al., 2017) and in a study of the causes of trait variability, Laughlin (2014) found that leaf and stem traits were the most consistently meaningful, with seed traits and height less consistent. Further, the lack of consistency in findings across the literature in correlations between SSD and other functional traits is counter to the hypothesis that SSD is part of a fast-slow spectrum (Hypotheses 1c, d, i, and j in Reich, 2014) and suggests that we still have much to learn about stem traits and their roles in plant ecology. For this reason, the caution advised by Rosas et al. (2019) when interpreting comparatively simple trait covariation structures that are revealed at global scales should similarly be applied when using the Global Spectrum of Plant Form and Function.

Whereas, the schemes above hypothesise that one or two axes are sufficient to explain a large proportion of variation in plant form, Westoby's LHS scheme uses three, thereby potentially increasing the potential for statistically meaningful results, irrespective of the meaningfulness of the traits themselves. When each possible combination of trait relationships within this scheme is tested separately (i.e., H-SLA, SLA-SM, SM-H) it can be seen that the clustering indicated by this study

FIGURE 5 | Ordination of species within the LHS scheme.

FIGURE 6 | Ordination of species within CSR space.

using traits common to all plants, harnessing the Leaf Economic Spectrum proposed by Wright et al. (2004). Our study suggests that in using the StrateFy calculator proposed by Pierce et al., this scheme presents the best way of representing (if not explaining) variation in plant strategies. There remain substantial aspects that need to be investigated: for example, Liese et al. (2017) found that the Leaf Economic Spectrum is not mirrored below ground, suggesting that the coordinated resource use as predicted by Reich (2014) also needs further testing and refinement. The role of disturbance as a limit to plant growth and its explanation in CSR theory in the context of woody plants is not yet clear: classically, ruderal plants are those that prioritise reproduction and fast growth, and using this scheme, some *Magnolia* species are ordinated in the same location as generalist herbaceous species. There are many viable traits and strategies for responding to disturbance and we need to ask, how many of these (such as fire, soil disturbance, or grazing) are relevant to urban forestry?

Although the schemes tested in this study reveal some dimensions of trait coordination, there remain aspects that are not captured, some of which could be potentially significant as revealed by traits that the genus *Magnolia* specialise in. For example, aside from Seed Mass, none of the schemes explicitly account for the costs and benefits of different reproductive strategies. *Magnolia* species typically do not sexually reproduce until sufficient reserves of non-structural carbohydrates are maintained, as predicted by Grime's competitive strategy, but once this stage is reached, considerable quantities of these reserves are used in floral thermogenesis to facilitate pollination by invertebrates (Wang et al., 2013; Wang and Zhang, 2015). None of the schemes tested in this study, nor any other to our knowledge, offer a way of accounting for the effect processes such as these might have on whole-plant functioning.

Magnolia Traits Suggest Relatively Competitive Strategies

Magnolia species are generally considered to have characteristics that are not particularly well-suited to the harsher environments found in urban forestry, such as moisture stress or reflected heat. The results of the trait-based experiments in this study tend to support this view, with the Leaf Water Potential$_{TLP}$ study suggesting that most of the species in this study have evolved isohydric strategies that allow populations to escape the effects of stress through fast growth and high investment in reproduction (Bartlett et al., 2016). This perception is supported by findings in other traits, such as SSD and SLA, which indicate strategies in *Magnolia* species that prioritise the speed of growth over tolerance of stress through relatively light or cheap investment in tissue. However, each of the studies in this experiment indicated that although these *Magnolia* species are relatively closely related, there was nonetheless a degree of inter-specific variation in trait values, although this feature was more marked in some studies than others, with LA and LDMC showing higher degrees of variation.

The variations in trait values found in this study compared to others within the functional ecology literature raise the question of how much explanatory power each trait presents. In

provides a reasonable picture of plant functioning but is not as precise or accurate as it could be if other traits were used. Nevertheless, the LHS scheme should be interpreted within the context within which it was created, in that it was proposed as an advance on CSR theory in two ways: firstly, it did not rely upon *a priori* categories and secondly, it ordinated species within unconstrained axes, thereby allowing more meaningful comparisons of different plant life forms. Whilst there remain drawbacks to the scheme (such as the impossibility of ordinating non-seed-bearing plants), the ability to use unconstrained axes in three-dimensional space is a powerful conceptual advantage, even if it is difficult to read the graph itself.

It is partly in response to Westoby's LHS scheme that Pierce et al. (2013) developed their methodology for ordinating plants in CSR. Whereas others (Brzeziecki and Kienast, 1994; Hodgson et al., 1999; Cerabolini et al., 2010) used combinations of ordinal and categorical values to ordinate species in CSR, the major advance in this scheme was to find a way of ordinating plants

spite of numerous studies including replications, global studies (Bruelheide et al., 2018; Kissling et al., 2018), and even computer game simulations (Barbe et al., 2020), the degrees to which these traits are individually meaningful pose significant conceptual and practical challenges in their interpretation in urban forestry. For example, in traits which have smaller ranges in variation (such as SSD), it is necessary to ask how and why do these traits vary, to what extent are minor differences significant, and what physiological processes are captured in these traits (Onoda et al., 2017)? In the case of SSD, Magnolias are diffuse-porous species, so early and latewood are likely to be differently influenced by ecological factors (Bergès et al., 2008): SSD expresses a range of physiological processes and in itself reflects a series of trade-offs that an organism needs to make, therefore "blunting" its explanatory power.

Similarly, Messier et al. (2017) found that SLA's sensitivity to multiple drivers of variation has the potential to blur interspecific differences unless their effects are taken into account experimentally or statistically. This study also found that although Leaf Nitrogen Content (LNC) is more difficult to capture, LNC is better suited to detecting community-level responses to large-scale environmental gradients such as climate, whilst LDMC is best suited to detecting plastic responses within individuals to micro-environmental gradients. As a result, the study hypothesised that Leaf Lifespan may potentially be a more useful trait than SLA as (a) it is more meaningful and (b) it is under stronger genetic control.

Toward a Functional Trait Scheme for Urban Forestry

Recognising the heterogeneity of stress created by urban environments, dimensionality in plants is a blessing not a curse as it offers us an opportunity to recognise nuance in the variation of plant traits and strategies, and then apply these theories more precisely to decision making. There does however appear to be a tractable upper limit to the dimensionality of plant traits (Laughlin, 2014), suggesting that a parsimonious trait-based scheme may be within reach for urban foresters- the question this then leads to is, which traits are most effective for this purpose? Numerous studies support the argument that although the trend in functional ecology research has been toward soft traits with large explanatory power, other traits that are more difficult to capture may be more meaningful and reveal more precise trade-offs. Drawing on the orthogonal nature of traits revealed in the Principal Components Analysis carried out by Díaz et al. (2016) and work by Baraloto et al. (2010), in **Figure 7A** we set out a hypothetical relationship between two dimensions of plant functioning and then identify in **Figure 7B** how this scheme might be used to select species in urban forests.

Figure 8 illustrates how this model could work, using the ordinations from the UAT study. Applying this scheme to the species in this study, it is possible to hypothesise that *Magnolia* species are more suited to less stressful environments, being better adapted to sites with higher resource availability. The scheme makes it possible to translate the observed inter-specific differences into practical guidance in ways that are not currently captured by the heuristic literature. Whilst quantitative associations between climate and traits were not part of this study, the traits recorded in this study appear to support hypotheses generated by Jardine et al. (2020) and Watkins et al. (2020): for example, in a study of 5 bottomland species, Nash and Graves (1993) found that *M. virginiana* was well-suited to urban environments with high oxygen and nutrient availability. A wider implication from this scheme is that it appears many of the species currently recommended for urban planting may need to be investigated in greater detail, with comparatively few species appearing to be suitable for planting in stressful, paved environments.

To develop this model for species selection in urban forestry, a number of issues need to be resolved. Firstly, counter to other Plant Functional Type proposals in urban forestry, it is necessary to emphasise the importance of ecological criteria (which describe a tree's ability to survive and grow in a given condition) over design criteria (where ecosystem services such as aesthetic values are prioritised). Secondly, from the perspective of data analysis, the number of axes of variation sufficient for this purpose will need to be established and weighed against their ease of interpretation for practitioners. In separate studies, each with their own advantages and constraints, Jin et al. (2016) developed a two axis Fast-Slow Spectrum model for ten woody plants in China whilst Lavorel et al. (2007) propose four axes of variation. As discussed in this paper, Grime and Westoby use different configurations of three axes, but it is possible to identify three strategies using two axes of variation as shown in 7a and by Grime (2001), who originally used 2 axes to create a ternary arrangement. Alongside these conceptual considerations, quadratic (instead of linear) equations should also be explored to identify trade-off boundaries, and recent progress in understand the changing roles played by traits through time should be harnessed to acknowledge the different impacts of biotic and abiotic stress on maturing and senescing trees.

Thirdly, the potential combinations of traits that could be studied show that further correlative studies are unlikely to yield meaningful advances until clear rationales for selecting traits are established and our understanding of their significances are resolved (López et al., 2021): in the age of big data and powerful statistical software, it is increasingly important to emphasise the importance of hypothesis-driven research (Moles, 2018) and incorporating evolutionary adaptions (McGaughran et al., 2021) if industry guidance is to be generated. A periodic table of traits has long been mooted by ecologists (Salguero-Gómez et al., 2016) but remains a distant prospect in spite of recent efforts. In this spirit, we call for an Urban Forestry Periodic Table of Traits that builds on the emerging standardisation of trait definitions (Garnier et al., 2017) and trait-performance studies (Scheres and Van Der Putten, 2017; Boisvert-Marsh et al., 2020; Sack and Buckley, 2020), and that can be tested by researchers to become the foundation for a model of species selection. The Urban Forestry Periodic Table of Traits would assist specifiers and researchers in knowing which traits or axes of variation are relevant in a given context and how they are integrated (Laughlin, 2014; Barry et al., 2019; Mertens et al., 2021), thereby
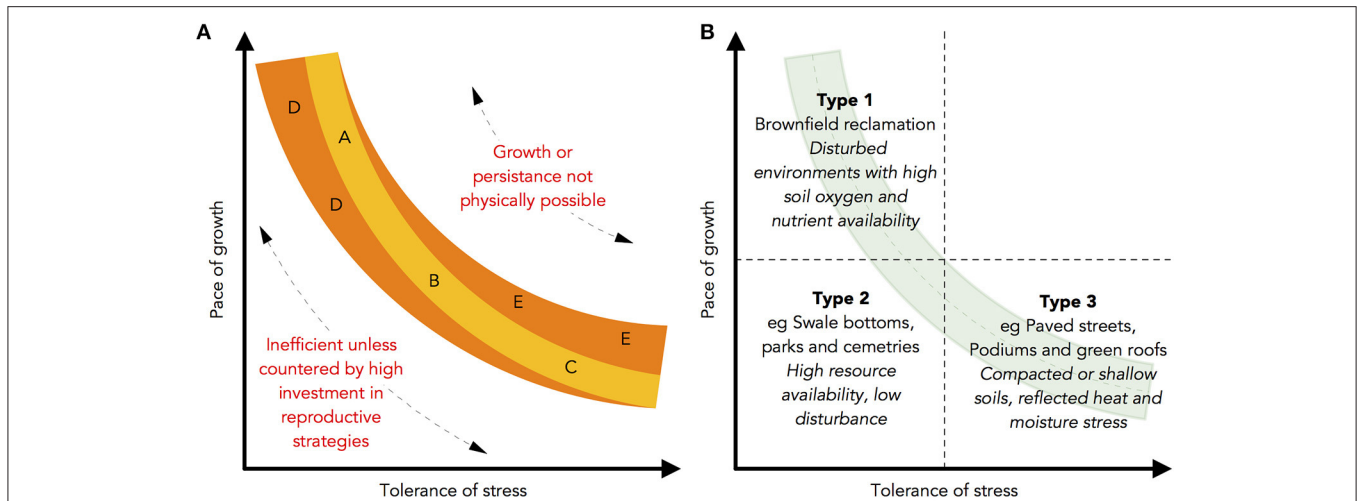
FIGURE 7 | (A,B) Hypothetical trait-based scheme for urban foresters. Building on CSR theory, **(A)** shows the variety of viable plant strategies in a trade-off between fast growth and high tolerance of stress. Positions A and C equate to different extremes of the trade-offs between competitive-stress tolerant strategies, with position B representing a generalist strategy. A greater investment in reproduction and faster growth is required in disturbed environments, resulting in more ruderal strategies (D), whilst in more stressful situations, delayed sexual maturity allows for greater investment in dense structural and photosynthetic tissues (E). Note that unlike other similar graphs, the trait trade-off is fitted by a quadratic rather than linear line of best fit. **(B)** Overlays environments found in urban forests upon this model, resulting in a method for best fitting tree species to urban forestry sites.
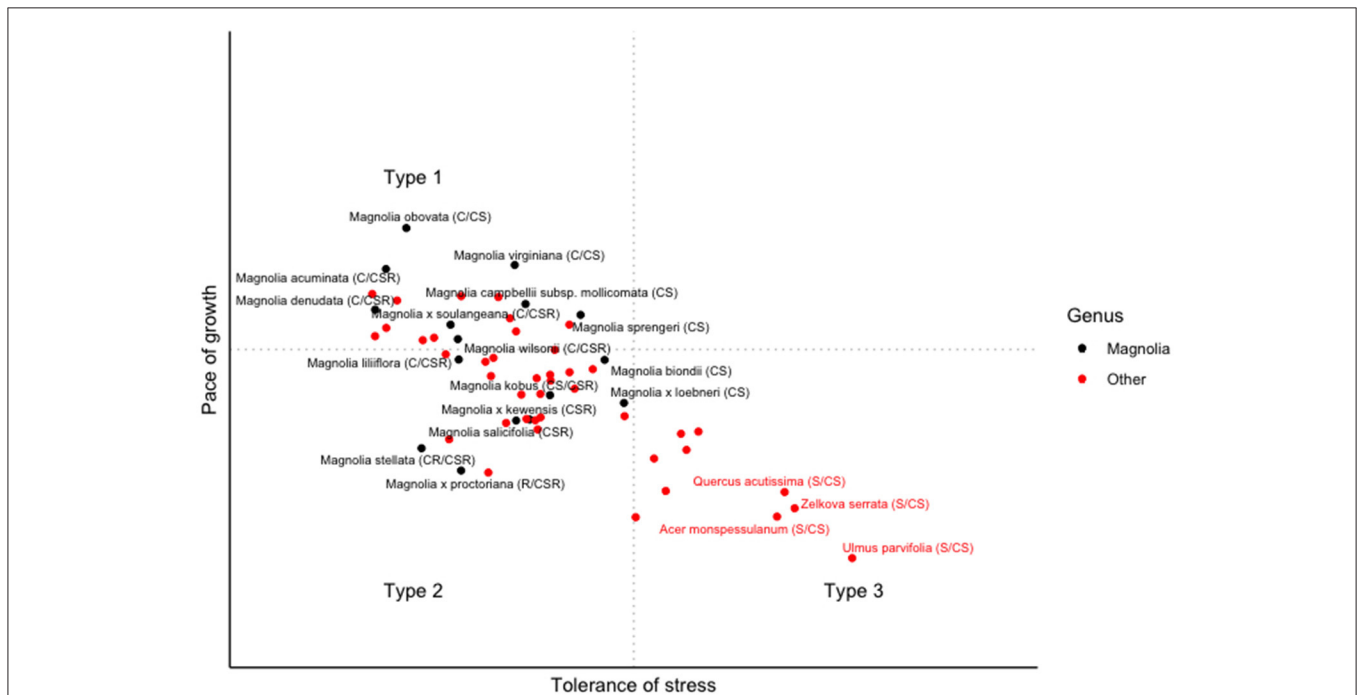

FIGURE 8 | Preliminary ordination of species according to hypothesised urban forestry environments, with Magnolia species UAT ordinations shown in brackets.

allowing urban foresters to select the right traits for the right place and make informed decisions about the performance of a taxon given certain trait combinations. For example, traits relating to reproduction are of high importance to ecologists but are rarely considered by urban foresters except in the context of

the trade-offs that these traits constrain on other traits relating to persistence, stature or growth rate. Similarly, traits such as SSD or WP TLP may be appropriate for assessing suitability to paved sites, for example, where moisture stress is a limiting factor on growth, whilst Leaf N may be more appropriate to consider when

designing species mixes so that the role of competition can be factored into a specification.

CONCLUSION

This study considers the potential of applying ecological trait-based schemes to urban forestry practise and found that whilst there is no single trait that is sufficient for selecting taxa in an urban environment, it may be that combinations of traits hold promise for future development. We used a case study genus (*Magnolia* L.) and other species used in urban forestry in northern Europe, drawing on experimental research and data derived from global trait databases. We found that *Magnolia* species tend to prioritise speed of growth over stress tolerance and using a novel scheme, suggest that it is possible to identify inter-specific differences within the genus that make them suitable to sites with high resource provision rather than harsh environments such as paved streets. Using this scheme, we hypothesise that many species currently used (or recommended for use) in urban forestry in northern Europe are more suited to resource-rich sites and that further nuance is needed in industry guidance. It appears that most of the schemes discussed in the ecological literature may be too blunt for the purposes of urban forestry specification as selecting the right combination of traits is a significant challenge, with only one axis of variation in this study showed a strong and significant relationship between the two traits. As such, a periodic table of traits that recognises the demands and scales specific to urban forestry would be a significant development and provide a framework for practitioners to select the right tree for the right place based on the right traits.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

HW and JH: research design. HW, AH, and HS: data collection. HW, AH, HS, RC, and JH: data analysis and manuscript drafting. All authors contributed to the article and approved the submitted version.

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