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Global variation and drivers of crown architecture in canopy-dominant trees – an airborne laser scanning perspective

MATHILDA AMBER DIGBY

A dissertation submitted to the University of Bristol in accordance with the requirements for award of the degree of Master of Science by Research in the Faculty of Life Sciences.

School of Biological Sciences – October 2023

Abstract

Forests play a vital role in sequestering CO_2 from the atmosphere and storing it as wood, and the 3D structure of these ecosystems provides crucial habitat for biodiversity. Canopy-dominant trees contribute disproportionally to forest carbon sequestration and storage, as well as shaping the 3D structure of these ecosystems. However, the factors that drive variation in the size and shape of the crowns of canopy-dominant trees across different forest ecosystems remain poorly understood. Traditionally, ecologists have relied on field data to measure and model variation in tree size and shape using allometric functions that predict one attribute (e.g., height, crown diameter or biomass) from other attributes that are easier to measure (e.g., stem diameter). But this presents an inherent challenge for canopy-dominant trees, as they only make up a small proportion of stems in a plot and their crown attributes are challenging to measure accurately from the ground due to occlusion in the canopy. Recent developments in remote sensing, in particular airborne laser scanning (ALS), have transformed our ability to capture information about the size and shape of the crowns of canopy-dominant trees across large spatial scales. And yet, we continue to lack a global assessment of the drivers that underpin the enormous variation in tree crown size and shape we observe in nature.

To address this knowledge gap, we used ALS to directly measure tree height, crown area, crown shape and height-to-crown scaling relationships of canopy-dominant trees from above. Specifically, we compiled co-located ALS and RGB imagery at 25 sites spanning all major forest types and used these to manually delineate the crowns of >30,000 canopy-dominant trees. Using this unique dataset, we explored how crown area–tree height scaling relationships and crown symmetry vary within and between forest types in relation to climate, disturbance, topography, and local competitive environment. We found climatic variables to be the key driver of broad-scale differences in crown architecture across forest types, and local factors such as competition and disturbances were important in explaining the variation of crown symmetry among individual trees. Interestingly we found topographic variables to have little to no effect on crown architecture in a global context. Crucially, we also show that the crown architecture of canopy-dominant trees is poorly predicted using existing allometric databases compiled from field data, as they are systematically biased towards smaller trees. Our study takes a key step towards better representing the spectrum of crown architectures that characterise the world's canopy-dominant trees, with important implications for integrating forest monitoring programs with remote sensing and forest models.

This thesis is structured into three chapters:

- **Chapter 1** reviews existing literature on drivers of tree crown architecture and the challenges we have faced previously with measuring and quantifying tree metrics, namely for canopy-dominant trees. This chapter also delves into the capabilities of new technological advancements in this field of research, particularly ALS, and how these are being used better to understand global variations in the architecture of canopy-dominant trees.
- **Chapter 2** leverages a global dataset of forests surveyed using ALS to assess how crown area–tree height scaling relationships and crown symmetry vary within and between forest types in relation to climate, disturbance, competition, and topography.
- **Chapter 3** reviews the study's results and methods in comparison to past research and looks forward to future opportunities.

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I'd like to thank my supervisor Tommaso Jucker for his undivided support throughout my project and his Friday meetings that always leave me feeling encouraged and excited for what's to come next. I'd like to thank Fabian Fischer for working closely with me on this project, providing me with this wonderful dataset, and teaching me everything I know about efficient and tidy code. A big thank you to BCAI for supporting and funding my MRes through the Emily Smyth studentship, enabling me to put my all into this project. I'd like to thank Selva Lab for inviting me to the team with warm hearts and laughs. And of course, a big thank you to my wonderful friends and family who have tirelessly told me to believe in myself and put my feelings of imposter syndrome back in the box where it belongs!

Author’s Declaration

I declare that the work in this dissertation was carried out in accordance with the requirements of the University's *Regulations and Code of Practice for Research Degree Programmes* and that it has not been submitted for any other academic award. Except where indicated by specific reference in the text, the work is the candidate's own work. Work done in collaboration with, or with the assistance of, others, is indicated as such. Any views expressed in the dissertation are those of the author.

SIGNED: .....[redacted]................ DATE: 01-01-2024

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List of Abbreviations

ACD	Above-ground Carbon Density
AI	Aridity Index
ALS	Aerial Laser Scanning
BCI	Barro Colorado Island
CA	Crown Area
CAR	Crown Aspect Ratio
CE	Crown Eccentricity
CHM	Canopy Height Model
DBH	Diameter at Breast Height
DEM	Digital Elevation Model
DSM	Digital Surface Model
DTM	Digital Terrain Model
ET	Evapotranspiration
F	Fire
H	Height
LiDAR	Light Detection and Ranging
MAP	Mean Annual Precipitation
MASL	Meters Above Sea Level
MAT	Mean Annual Temperature
MCH	Mean Surrounding Canopy Height
MST	Metabolic Scaling Theory
MWS	Maximum hourly Wind Speed
NEON	National Ecological Observatory Network,
QSM	Quantitative Structural Model
RGB	Red, Green, Blue (orthophoto)
TCH	Total Canopy Height
TLS	Terrestrial Laser Scanning
TPI	Topographic Position Index
TWI	Topographic Wetness Index
UAV	Unmanned Aerial Vehicle

1. Chapter 1: General Introduction

1.1. The importance of understanding tree architecture

Forests cover 31% of the Earth's surface, providing an enormous range of ecosystem services and are the primary terrestrial sink for carbon dioxide, playing a vital role in mitigating the effects of climate change (FAO and UNEP, 2020). To understand the contribution that forests play in global carbon cycling, we must understand the drivers of differences in biomass accumulation and variation in crown architecture, which here we define broadly as encompassing all aspects relating to crown size and shape, including tree height. This architectural variation arises from an interplay of mechanical constraints and physical stressors (Niklas, 1994), that a tree experiences throughout its lifetime, as well as some genetic structural characteristics that have evolved. Trees have developed mechanisms to best exploit resources while preserving surrounding conditions for survival. Including preserving soil moisture, reducing surface temperature, and maintaining microclimates (Zellweger et al., 2020). Large trees also play a key role in shaping the structure of the forest canopy, therefore making them essential for providing habitat for biodiversity and regulating microclimate in the forest understory (Lindenmayer et al., 2022). This contributes to forest structural dynamics, nutrient cycling, and subsequent carbon sequestration (Hardiman et al., 2013).

The shape and size of trees vary greatly across environmental, disturbance, competitive and topographic gradients. An English Oak (*Quercus robur*) growing within a forest will exhibit a long straight stem with a tightly packed gnarly branched crown. Compare this with an English Oak growing in an open field, with little surrounding canopy competition, and you'll find a large dome-shaped canopy, with numerous branching levels reaching right down to the ground. A conifer growing on a steep rocky slope exposed to high wind velocity will likely be deformed and short in stature. Or a redwood growing in an alluvial part of the Humboldt National Park will display great structural height while desert trees struggle to reach any height. Trees growing in a savanna habitat will be shorter than those of the same stem girth growing in a forest habitat (Shenkin et al., 2020). Understanding the processes that influence architectural differences of trees globally, better helps us perform biomass assessments, produce realistic forest models, and improve remote sensing applications for forest ecology (Jucker et al., 2017; McNeil et al., 2023).

Until recently our ability to measure the structural characteristics of trees has been limited to ground-based measurements of tree height, and crown dimensions, using tools such as tape measures, clinometers, and laser range finders. These methods are time consuming and result in small sample sizes, from which allometric models have been built (Duncanson, Rourke and Dubayah, 2015). Allometric models provide a way to estimate tree volume using easily measurable parameters (Malakini et al., 2020). Inherently, the crowns of canopy-dominant trees are hard to measure, obscured by the trees below. As a result, there is a bias towards the study of smaller trees or building equations that only include height and stem measurements. Not including crown measurements in allometric models is detrimental to the accuracy of these assessments. Canopy-dominant trees contribute disproportionally to above ground carbon (Bastin et al., 2015) with the largest 1% of trees contributing to 50% of aboveground live biomass (Lutz et al., 2018). Including tree crown dimensions in allometric models has been found to increase mass estimates by ~ 10% (Goodman, Phillips and Baker, 2014).

Stephenson et al., (2014) found trees with 100cm trunk diameter added three times the amount of aboveground dry mass each year compared to trees half the diameter size (50cm). Even if a forest has high species richness, it cannot sequester large quantities of carbon without large-diameter trees (Lutz et al., 2018). The largest trees have high predictive capabilities of ground-measured properties such as the quadratic mean diameter, the basal area, Lorey's height and community wood density (Bastin et al., 2018). If we are focusing our studies and building models on smaller, more easily measurable trees we will produce unreliable and inaccurate assessments of biomass and carbon. The underlying assumptions of allometric models need to be tested and adapted to include large trees that contribute massively to forest biomass (Calders et al., 2022). The development of top-down aerial data from remote sensing technologies is allowing us to fill in the data gaps to better describe scaling relationships and test the assumptions of allometric models for quantifying biomass and carbon which is essential as we move into an era of carbon offsetting climate mitigation.

1.2. In search of general tree allometric scaling relationships

Due to the shear expanse of global forests and the difficult nature of mapping and measuring individual trees at large scales, there has been an attempt to derive general rules about allometric scaling relationships between different axes of tree size and shape (West, 1997). One example of this is metabolic scaling theory (MST), which hypothesises that organisms fill space with a fractal-like structure to optimize resource utilization and distribution. It is widely used to measure and model tree resource use and biomass allocation (West, Enquist and Brown, 2009). The models are used as a general baseline for hypothesising scaling relationships and predicting scaling relationships of tree dimensions. Using MST alone to predict tree biomass and growth fails to account for crown morphology and the influence of past development, inner structure, and outer morphology on tree growth (Pretzsch, 2021). MST is based on generic branching networks that assume typical growing conditions, overlooking the effect that environmental and evolutionary factors, as well as tree-to-tree competition, might have on influencing observed structures (Patrick Bentley et al., 2013). This theory does not always hold true for trees, as their ability to fill space depends on the availability and location of resources, as well as interactions with their neighbours. We see this as most trees do not exhibit an optimal external branching network. When applied across tree and landscape scales the models exhibit high uncertainty and bias (Vorster et al., 2020). So where is this uncertainty coming from and how can it be accounted for?

There are several reasons why we might expect trees to deviate from the predictions of MST based on the local environmental conditions and competitive environment in which they are growing (McNeil, 2023). However, while global assessments of the accuracy of the predictions of MST have been made, they have been from field-surveyed measurements which tend to be biased to understory trees and frequently lack detail about the canopy dominant trees. The modelling of tree architecture has primarily focused on simple measurements of stem diameters and tree height, often neglecting highly detailed measurements of crown shape and size. A rare example of a study incorporating variation in crown size and shape is Shenkin et al. (2020), which assessed a range of different general and gradient-specific models using field measurements of trees in the tropics. They found that the assumptions of MST were consistently violated by their dataset but found models including more detailed crown measurements and phylogenetic information improved model predictions. Overall, they concluded that MST describes a central tendency of allometric scaling but this is heavily influenced by ecosystem types and environmental variables. Savanna trees were shorter than forest counterparts of the same stem girth, precipitation had no effect on crown depth and crown width decreased with decreasing elevation. In doing so, Shenkin et al. (2020) highlight the variation of tree structure when factoring in environmental gradients of tropical forests in Ghana, Peru and Brazil, but the study still lacks information on other forest types. Jucker et al. (2022) expanded on this analysis using a global dataset of 500,000 field-surveyed trees, to see how well MST predicts a range of scaling exponents in different biomes. On average, they found MST over-predicted the scaling exponent of tree height and crown radius relationships. Both Shenkin et al. (2020) and Jucker et al. (2022) identify important discrepancies found within allometric models about tree-scaling relationships, based on field-surveying methods. These data collection methods can lack information about canopy-dominant trees that contribute greatly to biomass (as stated above; Lutz el al., 2018). Allometric models have tried to pinpoint generalities and have contributed to our understanding of tree growth scaling. However real-world trees depart significantly from theoretical predictions due to factors including climate, competition, disturbance, and topography. Including data on these individuals and incorporating environmental stressors and the effects of neighbouring individuals may answer some of these questions (Lines et al., 2012; Loubota Panzou et al., 2021).

1.3. Potential drivers of variation in tree crown architecture

For most tree species the key growth strategy is to gain height to exploit available light and outcompete their neighbours (Fransson, Brännström and Franklin, 2020; Sterck and Bongers, 2001). But for a tree to exploit its environment effectively it must deal with constraints such as mechanical stability, mechanical safety, photosynthetic efficiency, water transport, resource allocation and competitive ability (Givnish, 1995). Trees make functional trait trade-offs due to the constraints and limitations of resources, resulting in differences in height, crown size and crown shape (Verbeeck et al., 2019). Crown plasticity (the ability to adapt branching structure in response to surrounding conditions) among these trees is essential for optimising the allocation of energy and resources (Jucker et al., 2015).

Much of the literature addresses the variables that are driving the differences we see in tree allometry. Factors including biogeography, phylogeny, and environmental conditions have been found to influence these differences. For example, disturbance shaping savanna trees to be shorter, compared to their forest counterparts of similar girth and the variation in crown width tends to decrease with decreasing elevation (Shenkin et al., 2020). Examples from other ecosystems, such as Amazonia and Andean sites, demonstrate how warming, drought, and disturbances can alter the composition of tree functions within a community (van der Sande et al., 2023). The adaptations of global forests to their environments can be observed through the distribution of forest types and biomes across temperature and precipitation gradients (Whittaker, 1970) which has been applied to global tree mortality (Hammond et al., 2022). Here we discuss the contrasting literature on the key potential drivers of variation in tree structure including climate, disturbance, competition, and topography.

1.3.1. Climate

Climatic variables play a key role in influencing the structure and growth patterns of trees (Callaway, DeLucia and Schlesinger, 1994). The key known driver of variation in tree allometry is precipitation and water availability. For trees to grow tall they need to overcome gravitational forces and transport water from their roots to their leaves at the top of the canopy, through evapotranspiration. The width of a conduit determines the level of resistance and drag water experiences when moving up towards the leaves. Having wider conduits reduces drag, increasing the flow of water and the height it can reach enabling trees to grow taller. The wider the conduit, the taller the tree. The vessels need to be large, but not so large that they result in embolisms, which occur when low soil water availability and/or high evaporative demand put the vascular system under high negative pressure (Olson et al., 2018). Therefore, tall trees can only be present in regions where water stress is minimal (Givnish et al., 2014). The same applies to the length of branches, controlling widths of crowns. Forest structural complexity describes the distribution of trees and their canopies in three-dimensional space and has been found to increase with increasing annual precipitation, precipitation seasonality, the water balance and soil water holding capacity across biomes (Ehbrecht et al., 2021). Moles et al., (2009) argue regions with wetter periods allow stems to grow tall for a given diameter, with precipitation during the wettest month being a key determinant of tree height. Work by Scheffer et al., (2018) would add the distribution of the tallest trees is sharply limited to regions with mean annual precipitation is above a threshold of 1,500 mm. Tao et al., (2016) agree an increase in water availability facilitates taller trees, but this trend peaks and becomes a limiting factor for tree height in very wet regions, resulting in water logging and permanent cloud cover reducing incoming solar radiation. Precipitation influences crown dimensions, and stem diameter scaling relationship negatively, at the lower end of the rainfall gradient, forest trees developed deeper, and larger crowns compared with savanna trees having flatter crowns (Loubota Panzou et al., 2021). The tallest trees in the world grow in Northern California, Humboldt Redwoods National Park, growing in the large coastal old-growth stands (~100m) compared to the drier inland redwoods being shorter (~80m; Koch et al., 2004). When assessing the influence of precipitation on tree growth, it's important to exercise caution. Precipitation levels are often closely linked to soil aridity, making it a more nuanced factor in tree growth. Soil aridity and water availability are both defined as the difference between annual precipitation and annual potential evapotranspiration. This complexity is further illustrated by Cartereau et al., (2023), who defined warm drylands based on the aridity index (AI) and temperature criteria. Water availability serves as a primary driver of tree growth. impacting it directly and indirectly by enhancing water use efficiency through increased photosynthetic rates and decreased evapotranspiration (Olano et al., 2023). Silva and Souza's (2018) work highlighted the role of aridity imposing limitations on plant growth and biomass accumulation, driving the creation of floristic subregions in the Caatinga, a tropical dry forest ecosystem in northeastern South America. Aridity has also been found to induce notable traits in trees, including increased wood density, leaf area, and adjustments in the allocation of stem area versus leaf area (Anderegg et al., 2020). While not structural traits, these are likely to influence overall tree structure.

Temperature also acts as a limiting factor for tree height. As explained above, to achieve great height, a tree must increase the width of its conduits. Wider vessels are more efficient at moving water and nutrients when filled with water but are vulnerable to dysfunction during frost events (Hacke et al., 2016). During freeze-thaw events, air bubbles in the sap of wider conduits can result in freeze-induced embolisms (Charra-Vaskou et al., 2023, Zanne et al., 2013). Therefore, the maximum height of trees in cold and dry regions is more conservative and shorter, as they can only grow as tall as their maximum conduit diameter (Olson et al., 2018). We see a strong association between the maximum tree height of global forests and water availability; however, height is further limited by temperatures. A tree may be growing in a moist region with no limit to water supply but if it experiences periods of freezing, it will not be able to reach the same height as another in a region of the same water inputs with a warmer climate (Klein, Randin and Körner, 2015). This can be seen with the world's tallest trees being found between 7 and 15 degrees Celsius (Larjavaara, 2013). Lines et al., (2012) found within species, those in warmer climates were taller and found the opposite across species where taller trees were found in colder regions. They also found no relationship between tree height, crown diameter scaling relationships and temperature. Moncrieff et al., (2014) studied savanna trees in both Australia and Africa finding variations in tree height despite have similar climates, they attributed continental-scale variations to be driven by a few taxa in the dataset rather than climate. Temperature was also found to have no effect on tree heights (Tao et al., 2016). Forests experiencing high temperatures and drought events are at risk of mass mortality. A reduction in soil moisture combined with high humidity and air temperatures increases hydraulic demand and increases risk of embolisms (Rowland et al., 2015). The presence of snow has been found to reduce tree height and DBH in temperate trees too (Homma, 1997), and poses a risk of stem breakage from high snow load (Nishimura, 2005). The conical shapes of conifers found in snow-prone regions are better adapted to shedding snow, aided by needle leaves (Chabot and Hicks, 1982), resulting in smaller, steeper-shaped crowns.

1.3.2. Competition

Height growth not only allows a tree to reach for light but also gives it a competitive edge over its surrounding neighbours, shading out other individuals below the canopy. Trees also adapt the shape and size of their crowns, resulting in irregular forms that pack together resourcefully and exploit available light. Highly comparative environments with little limitation on resources such as water and nutrients allow trees to grow in dense stands. As a result, they must adapt to compete for the available light. Crown asymmetry and plasticity stem from the competitive interactions and mechanical pressures among trees (Seidel et al., 2011). Closed canopy forests, which receive limited light, frequently exhibit asymmetric crowns due to competitive pressures (Aakala et al., 2015), resulting in negative impacts on crown metrics including reduced size and irregular crown shapes (Owen, Flynn, and Lines 2021). Lines et al., (2012) found asymmetric competition from taller trees induced more elongated tree architectures, where trees invest more into height growth over crown expansion for increased light capture. They also found trees under competitive pressure to have smaller crowns. Crowding and shading from neighbouring crowns cause increased crown and stem slenderness (MacFarlane and Kane, 2017), as seen with open-grown trees that display shorter stems with flatter crowns compared to forest-grown trees of the same species. This study also showed there to be a negative relationship between crowding and wind resistance, indicating functional trade-offs between height investment and wind resistance investments.

Different tree species have distinct strategies when it comes to allocating resources for growth, even when they are subjected to similar environmental conditions (Van de Peer et al., 2017). Canopy packing increases with the diversity of forests, whereby mixed species forests are better at optimizing space within the canopy (Jucker, Bouriaud and Coomes, 2015) because their structures are more varied. Niche differences among tree species are a key factor in promoting coexistence by fostering self-limitation, a positive interaction among species (Buche et al., 2022). This optimization is often attributed to higher species richness (Kunz et al., 2019) and mixed tree species, with similar branching densities but differing functional traits, exhibit enhanced crown complementarity (Hildebrand et al., 2021). Pitkänen, Bianchi and Kangas (2022) explored the impact of competition on the crown shape and size of Scots pine and Norway spruce. The results showed that both species are impacted by competition but with differences in morphological determinants, sensitivity, and adaptation.

1.3.3. Disturbance

The composition and structure of forests are shaped by a legacy of historical disturbance events caused by the climate (wind, fire and snow), anthropogenic activity (deforestation, fire, agriculture and urbanisation) and herbivory (pests, disease and pathogens). In this study, we focus on the climate related disturbances of wind and fire. While some fire disturbance is the result of human activity, this project doesn't distinguish between the two. Wind and fire have been found to drastically shape the architecture of trees, with wind limiting height and fires promoting height. Here we discuss the literature around the topic of disturbance and tree architecture.

Fire is dependent upon a spectrum of environmental factors, including temperature, wind dynamics, and water availability. Forests that have endured recurring fires often exhibit lower tree density and are frequently surrounded by open grasslands. In a comparative study conducted by Archibald and Bond (2003), the tree architecture of *Acacia karroo* was examined across three distinct forest types: closed-canopy forests, savannas, and arid shrublands. Their research revealed significant variations in branching patterns and allometry among sites. In closed-canopy forests, trees invest primarily in height to outcompete neighbouring trees for sunlight, resulting in dense crowns that shade out their neighbours. Trees in open-grown savannas adopt a vertical growth strategy to escape crown damage from frequent fires but are not as tall as closed-canopy trees. Instead, they grow enough to escape the fire and then invest more into crown expansion. Trees in arid shrublands exhibit lateral growth and often feature more spines as a defence against browsing herbivores. Three habitat types experience different types and severity of disturbance which is reflected in the architecture of the trees that reside there. Moderate severity disturbance events inhibit canopy height growth and increase canopy openness. High-intensity fires have been found to inhibit canopy height growth and density, leading to the development of intricate interior and exterior branching structures (Choi et al., 2023). Many of the adaptations to fire have evolved over generations. However, in the context of an expanding wildfire season driven by climate change, both conifer-dominated and deciduous woodlands in the global north are experiencing heightened fire risks (Burton, 2023). Species within these ecosystems may not be well adapted to cope with the increasing intensity and frequency of fires. If fires propagate in regions where trees do not have the adaptations and will not be resilient to this kind of disturbance.

Wind turbulence puts pressure on the branches of trees. To withstand this force, trees have adapted mechanisms that allow them to sway, resulting in variations in tree architecture (Yang et al., 2021). The high ratio of stem length to diameter reduces oscillation frequency, amplifying the motions of slender trees, and putting them at risk of breakage (Sellier and Fourcaud, 2009). Open-grown trees have been found to have high path-fractions (described as the ratio of the mean to maximum trunk-to-twig path length) resulting in wide, large crowns, making them more resilient to the effects of wind (Jackson et al., 2019). The two examples demonstrate how the structure of trees influences their ability to withstand disturbance; trees growing in forest stands can form slender structures, competing for light with their neighbours, compared to open-grown trees forming stout structures that have higher sway frequencies and are more stable. The concept of a critical wind threshold for trees offers a potential explanation for variations in tree height across different forest types that share similar mean annual precipitation inputs, (Malhi et al., 2018). Comparing Bornean trees with an average height of 45 meters to Amazonian trees averaging 30 meters, the absence of cyclone wind regimes in Borneo may account for this disparity (Jackson et al., 2020). Thigmomorphogenesis is the process of trees sensing mechanical stimulation from surrounding factors that put them at risk of damage, resulting in them changing their growth patterns. High wind velocities result in trees opting for radial growth (increasing in girth) to be sturdier and less prone to wind damage (Bonnesoeur et al., 2016). Gorgens et al., (2021) found low wind speeds to be the key predictor of the presence of 'giant' trees in the Brazilian Amazon (above 70m) and that windier regions supported shorter trees in response to damage. Windthrow events occur when high windspeed events uproot and break standing trees and have been found to reduce biomass accumulation in tropical forests as well as increase tree mortality post-wind events (Magnabosco Marra et al., 2018). Patchy forests require higher wind speeds for fires to rapidly propagate over greater distances, shaping the structure of forests at landscape scales, and influencing tree size and age distribution (Begović et al., 2022).

1.3.4. Topography and soil nutrients

Local topography is a key predictor of the differences we see in tree architecture and forest structure. It influences features including nutrient accumulation, water availability, disturbance rates and incoming solar radiation. Topographic features include terrain, slope and curvature, all of which create microclimates and variations in growing conditions that explain the heterogeneity of forest structure. Slope affects the physio-chemical properties of soil (Liu et al., 2020). The soils at higher slope positions are shallow, have little moisture retention, have deep groundwater levels and are more exposed to solar radiation, higher evapotranspiration and strong winds compared to foot slope positions that are cooler, more humid, with lower solar radiation and evapotranspiration and deeper soils that can accumulate surface runoff. Total canopy height (TCH) has been found to peak in alluvial valleys with total height decreasing with increasing slope, and above-ground carbon density (ACD) is highest in flat terrains (Jucker et al., 2018). This is the result of more complex soil structure, and nutrient and water accumulation that occurs in valleys compared to ridges. Mid-elevation trees were found to be more uniform and densely compact because of limited water availability and nutrients. The differences in TCH and ACD would indicate differences in tree architecture. This is also seen where differences in stand structure and biomass allocation between slope positions can be attributed to the limitation of nutrients in the upper slope zones (Werner and Homeier, 2015). Wei et al., (2018) found maximum tree height decreased with elevation, and that maximum tree height was found to be taller in riparian zones. Forest productivity was marginally influenced by temperature and water vapor density and so they attributed differences in height to soil moisture. Madhumali et al., (2023) assessed the effects of geographical aspects and topography on canopy openness, concluding canopy size decreases with altitude, indicating slope and aspect influence tree crown area and architecture.

Topography not only affects temperature, precipitation, and other climatic variables but also facilitates other types of disturbances, such as landslides (Freund et al., 2021). The disturbances, in turn, can have cascading effects on the composition and architecture of forests. Variations in soil type and topography play a crucial role in influencing disturbance rates and can have a significant impact on mean canopy height. These factors often interact in complex ways to shape the structure of forest ecosystems where disturbances are more commonly observed in local depressions and on steeper slopes (Cushman et al., 2022). However, the right aspects and slopes can also provide shelter for trees from wind with steep slopes creating barriers, facilitating the tallest trees (Shenkin et al., 2019).

1.4. Technological advancements in measuring tree size and shape

Creating models to predict tree metrics has been essential in forest ecology and monitoring as it provides a way to assess ecosystem functions without having to be destructive, enabling local, small-scale assessments of trees from manual measurements (Aber, 1979). It does however have its downfalls in accuracy and lacks spatial scale that's often needed when studying ecosystem scale processes and making global tree metric comparisons. Technological methods for measuring forest structure are developing quickly and providing opportunities to test structural theories with increased quantities of data and detail (Jackson et al., 2019; Malhi et al., 2018).

1.4.1. Satellite and aerial imagery for forest assessments

The invention of satellites and UAV imagery enabled habitat and ecosystem assessments to be made at global scales. RGB can be used to identify the expansion of urban areas, deforestation, and the loss of valuable habitat, as well as individual tree crown measurements and estimations of above ground biomass (Baccini et al., 2008; Boulila et al., 2021; Wagner et al., 2023; Weinstein et al., 2019). Automatic individual tree-crown delineations packages have been developed for satellite and UAV imagery (Freudenberg, Magdon and Nölke, 2022), however, this process struggles to delineate small trees from satellite images due to low resolutoion and struggles to delineate large trees from aerial images which results in oversegmentation. Tucker et al., (2023) used artificial intelligence to measure tree crown area from satellite imagery along the Great Green Wall, Africa finding that carbon density models were overestimating carbon stocks. Photogrammetry has been used to create digital surface models of canopies. From this, point clouds can be extracted and used to delineate tree crowns for metrics such as tree height and crown size. Photogrammetry lacks the ability to produce terrain models because it does not collect ground point data, making height estimates from this data inaccurate unlike more recent laser technology that can penetrate the canopy and gather ground data (Alexander et al., 2018). Estimating carbon using satellite and aerial image data and tree allometry allows us to make large-scale assessments from fewer measurements, saving time and resources but it lacks detail about architecture and allometric scaling relationships.

1.4.2. From two dimensions to three dimensions

The development of LiDAR remote sensing accelerated our ability to study tree and forest structure. Assessments of forests no longer had to be made from assumptions gathered from flat two-dimensional images. LiDAR sensors use high-frequency laser pulses to map the surrounding environment in the form of a 'point cloud' – a three-dimensional model of the forest. A LiDAR point cloud can be used to produce a variety of outputs such as digital terrain models (DTM), digital surface models (DSM) and digital elevation models (DEM; Luo, Ma and Zhou, 2017). The DSM is subtracted from the DTM to produce a canopy height model (CHM; Khosravipour et al., 2014; Mielcarek, Stereńczak and Khosravipour, 2018), a 3D representation of the outer surface of the canopy.

LiDAR can be operated both from the ground (TLS, terrestrial laser scanning) and from the air (ALS, airborne laser scanning), each excelling in different areas. TLS is highly detailed. From the ground, this method can capture every inch of a tree from which tree-level assessments can be made about their function and form, metabolism, effects of competition on architecture, and accuracy of allometric models (Disney, 2018). For example, the volume can be predicted using quantitative structural models (QSM; Brede et al., 2019) and multiplied with species-specific wood density values to calculate the biomass content of the tree (Wilkes et al., 2018) and further multiplied by a carbon fraction to estimate stored carbon (Jones and O'Hara, 2018). While TLS provides detailed structural analysis, it is not practical for large-scale data collection, especially due to TLS scanning taking a lot of time and producing enormous quantities of data (Dassot, Constant and Fournier, 2011).

LaRue et al., (2020) assessed the compatibility of using LiDAR for quantifying forest structural diversity, comparing the results of TLS and ALS finding strong agreements between canopy height, openness, internal heterogeneity, and leaf area. This project found that low-resolution, large-footprint ALS systems excel in forest classification by structural diversity at macroecological scales while TLS is required for detailed structural variation within forests. Projects like The National Ecological Observatory Network (NEON; Kampe, 2010) have gathered ALS information from 47 sites around the USA, covering a range of habitat and forest types, with high resolution, regional airborne remote sensing observations as well as ground. This data has been used to assess forest structure for understanding ecological changes in response to disturbance (Choi et al., 2023) as well as creating benchmark datasets for crown detection packages (Weinstein et al., 2021). And now with the development of the GEDI LiDAR satellite, even more possibilities are opening for broad-scale 3D assessments of forests (Dubayah et al., 2020). Coomes et al., (2017) compared tree-based and area-based biomass estimates in the tropics finding area-based estimates to perform better, but state individual tree-based maps are useful for tacking forest dynamics, assessing local resources and producing fine-scale maps of individual trees. ALS is used to map forest carbon stocks and can identify intact forests, deforestation, agriculture, mining and infrastructural development (Asner et al., 2010). Large-scale measurements of forest structure are being performed using ALS and used to calibrate individual-based models (IBM) to predict forest dynamics (Shugart et al., 2015). Forest inventories and ALS can be combined to reconstruct virtual 3D representations of global forests from which packing densities and allometric scaling relationships can be measured (Fischer et al., 2020). ALS has also been used for many forest analyses including using topography to assess species composition (Kopecký, Macek and Wild, 2021), forest and carbon monitoring (Zhao et al., 2018), identifying trait trade-offs made between trees in response to resource availability (McNeil et al., 2023), urban tree classification (Hartling et al., 2019), invasive species classification (Waite et al., 2022) and forest demography studies (Stark et al., 2015). ALS datasets, while not providing the same level of detail as TLS, still increase the accuracy of forest measurements (Popescu, Wynne and Nelson, 2003) and will enable us to examine global variations in tree structure and form, providing a more comprehensive understanding of global tree structure (Calders et al., 2022; Wilkes et al., 2018).

1.5. Research trends and knowledge gaps

We know that tree architecture is controlled by environmental conditions and competition (Lines et al., 2012) and most notably global tree heights are constrained and limited to water availability (Givnish et al., 2014; Jucker et al., 2022; Olson et al., 2018). Yet we lack empirical evidence on the key predictors of crown size and shape. We know that competition influences crown size and plasticity (Condés, Aguirre and del Río, 2020; Loubota Panzou et al., 2021) yet it’s unclear what factors most influence the shape and architecture of the tree's crowns. It’s important that we quantify the plasticity of crown dimensions in relation to competition and surrounding environments to calibrate forest models and ensure overestimations do not have a detrimental impact on our carbon stocks (Calders et al., 2022; Shenkin et al., 2019). The greatest issue we face is that many of our current models are based on small trees, and we lack data about the canopy-dominant trees that we know contribute most to forest biomass (Bastin et al., 2015; Lutz et al., 2018). While many of these studies are comprehensive and contribute greatly to our understanding of forest dynamics, they rarely examine tree properties across the globe with most projects studying 1ha plots per site. Remote sensing technologies, such as airborne laser scanning (ALS) and high-resolution RGB orthophotos, offer an intuitive solution to this challenge, as they allow us to capture the crown dimensions of large numbers of canopy-dominant trees across broad spatial scales. In particular, ALS is perfectly suited to this task as it not only allows for accurate delineation of the crowns of individual trees but also measures their height. Yet no global-scale analysis of how variables influence tree architecture has been performed, especially on canopy-dominant trees.

To address this knowledge gap, we compiled ALS and RGB data from 25 sites across the world and used them to manually delineate the crowns of >28,534 trees (Fig. 1), spanning 8 biomes, including tree height, crown area, crown eccentricity (how spherical is the crown) and crown aspect ratio (how do tree height and crown area scale from a side profile). We then combined this data with information on climate and disturbance data (wind speed and fire frequency) derived from global databases, as well as the local competitive environment and topography derived from the ALS CHMs and DTMs. We used these data to ask three key questions: (1) How closely do scaling relationships between crown area and tree height match the theoretical predictions of metabolic scaling theory (MST)? (2) What are the key drivers of differences in crown area and tree height scaling relationships across global forests? And (3) How do allometric scaling relationships derived from ALS data compare to those from field data?

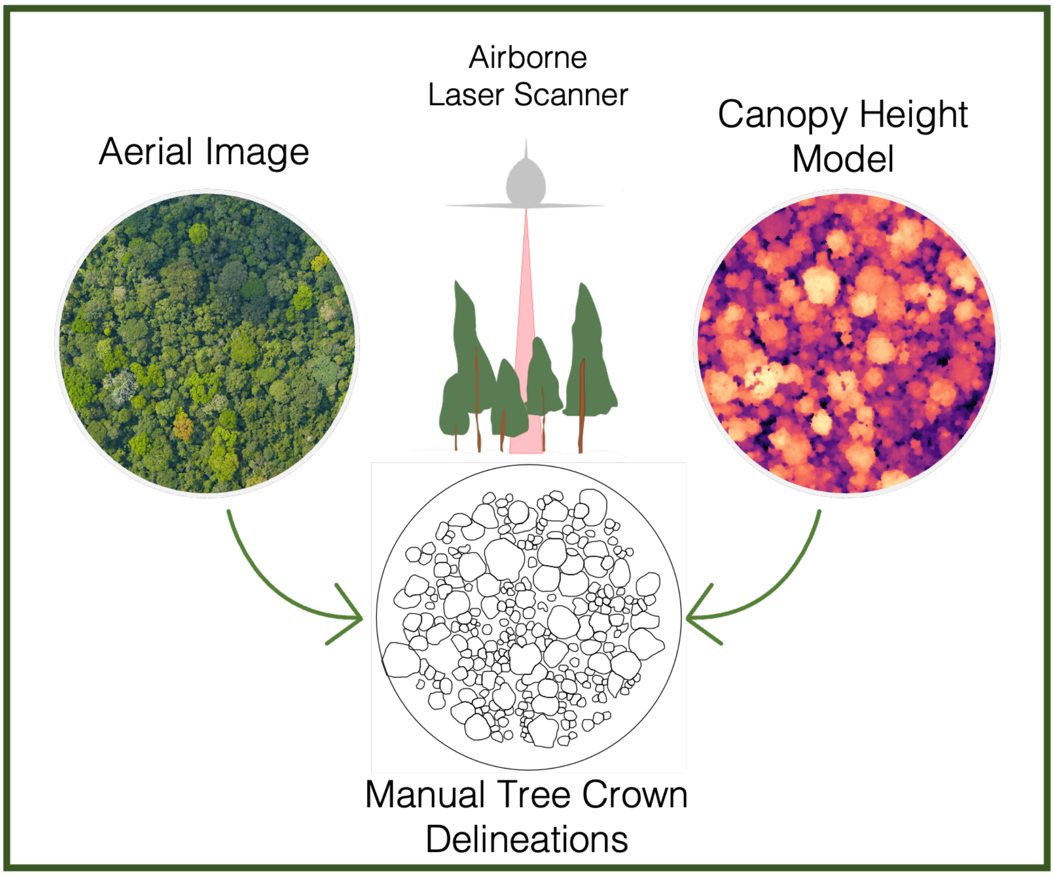

Figure 1: Schematic diagram illustrating the approach used to manually delineate individual trees crowns using a combination of RGB imagery and ALS (airborne laser scanning) derived CHMs (canopy height model).

2. Chapter 2: Methodology and Results

In this chapter, I will explain the methods used to extract and analyse crown metrics from the ALS data. Results and figures will be reported in this chapter and discussed in chapter three.

2.1. Methods

2.1.1. Study sites

To determine how crown allometric scaling relationships vary across different forest types we identified 25 sites where we have access to both ALS data and high-resolution RGB imagery needed to manually delineate individual tree crowns of canopy-emergent trees (Fig. 1). The 25 sites range in mean annual temperature of -4-27°C and in mean annual rainfall from 260-3200 mm yr^{-1}. They cover all continents except Antarctica and include sites that are representative of 8 different biomes (Olson et al., 2001): Tropical Savannas; Tropical Rainforests; Temperate Woodland; Temperate Grassland; Mediterranean Forests; Temperate Conifer Forests; Flooded Savannas; And Boreal Forests (Fig. 2).

2.1.2. Plot selection within study sites

For each of the 25 study sites, we used the ALS point cloud data to generate 1-m resolution canopy height models (CHM) and digital terrain models (DTM) using a standardised processing pipeline in LAStools. From this model, we excluded areas with obvious evidence of disturbance and forest clearing (e.g., large gaps and clearings, roads etc.). We did this using various thresholds. Minimum canopy height was set to 5m, FAO default is 2m, but we deemed this too low as we did not want to include shrubs. Minimum canopy cover was set manually for each site depending on forest type. FAO default is 10% cover, but this is too low for some forest types, especially those in the tropics, therefore we used our intuition based on information we had on forest types. A minimum forest area ensured we weren't looking at too small patches to not be a forest. We set this to 5000 m which is the minimum scale that can be defined as a forest, FAO default of 0.5 ha. We added a 50m buffer along the scan area to remove edge effects. Plus, some other parameters to run the classification. Within each of the 'forest' classifications in the CHMs, we placed 3-4 circular plots (each 5-ha) within which to delineate the individual tree crowns. The position of the plots was selected using the DTM to ensure we covered an elevation gradient within each site. This allowed us to select plots within areas of low human disturbance, range of elevations and containing the forest type we were aiming to study.

2.1.3. Tree crown delineation and crown size measurements

Tree crown delineation was performed manually, as this is currently the most accurate way of delineating individual tree crowns (Aubry-Kientz et al., 2019). For each 5-ha plot, we used a combination of the CHM (primary reference) and RGB imagery (secondary reference) to delineate all visible crowns using QGIS (https://www.qgis.org). Each crown was classified into one of three categories: '*confident*', corresponding to crowns that were clearly discernible in the imagery, '*less confident*', for crowns that we were less sure about the attribution to an individual tree, and '*defoliated*' for ones without leaves that we presumed to be standing dead trees.

For the purposes of our analysis, we focused exclusively on crowns classified as ‘*confident*’ and for each of the crowns we used the CHM to measure the top height of the tree (H, in m; defined as the 99% percentile of the CHM falling within the crown) and the crown polygon to measure its crown area (CA, in m^2). We also used the crown polygon to estimate the crown eccentricity (CE) of each tree, defined as the ratio between the maximum and minimum crown width (calculated as the width and length of the largest rectangle capable of fitting within the crown polygon in any orientation). When crowns are approximately circular $CE \simeq 1$, whereas CE will decrease progressively as one side of the crown becomes greater than the other. Finally, we also calculated the crown aspect ratio (CAR) of each tree as: $\left(\left(\sqrt{\mathrm{CA}/\pi}\right)\times 2\right)/\mathrm{H}$, where CAR = 1 indicates a tree that has a crown that is as wide as the tree is tall, while CAR will become progressively smaller than 1 for trees that are taller than they are wide.

2.1.4. Drivers of variation in crown allometry

To test how crown size and shape are influenced by broad-scale differences in climate and disturbance regimes among sites, as well as local-scale variation in topography and competitive environment, for each manually delineated crown we compiled data on the attributes listed below. All data processing and subsequent analyses were performed in R (R Core Team, 2022). using the following packages: *Terra* (Hijmans R, 2023), *sf* (Pebesma and Bivand 2023), *lme4* (Bates et al., 2019). We tested for collinearity among variables using variance inflation factors (Vif) leading us to remove precipitation, TWI and MASL as these were found to be correlated with other variable we were interested in testing.

Climate

Mean annual precipitation (MAP, in mm yr^{-1}) and mean annual temperature (MAT, in °C) were extracted for each site from the WorldClim2 database (30 arc-second resolution; Fick and Hijmans, 2017). Additionally, we extracted the aridity index (AI) of each site from the Global Aridity Index and Potential Evapotranspiration Database (30 arc-second resolution; Zomer, Xu and Trabucco, 2022). AI is defined as the ratio between a site's MAP and its mean annual evapotranspiration (ET). The higher the AI value, the lower the level of aridity. When MAP is lower than ET, AI<1, and as sites become more humid AI increases progressively. As a general reference, $AI > 0.65$ corresponds to humid sites, AI = 0.2-0.65 corresponds to semi-arid and dry-subhumid sites, while $AI < 0.2$ corresponds to arid sites.

Disturbance

To measure the impact of disturbance events on tree height and crown area fire and wind intensity were extracted for each site. Decadal maximum hourly wind speed (2010-2020) (MWS, in m/s) was extracted for each site from the ERA5 Land database (5-minute resolution, https://www.ecmwf.int/en/era5-land). MODIS-derived burned area fraction (mean of cumulative annual value between 2001-2010) (F, as %) was used to assess the effects of fire on allometry taken from Global Fire Emissions Database (15 minute resolution, Giglio, Randerson and van der Werf, 2013).

Topography

Topographic variables were calculated from the 1-m resolution DTMs generated at each site. From the DTMs, we calculated the terrain slope (in degrees) and topographic position index (TPI) and assigned a value to each tree based on the location of the centroid of its crown. TPI is a method of terrain classification where the curvature of each data point is evaluated against its neighbourhood. A negative TPI indicates a depression or gulley (concaved) and a positive TPI a ridge (convex). For each plot, we use the DTM of the whole site rather than using the DTM for each plot as this would not give a TPI value relative to the whole site.

Competition

To capture the effects of competition on tree crown size and shape, we used the CHMs to measure community structural diversity. A buffer of the largest crown diameter was added to each tree crown in a search area to ensure that the largest tree would be fully included in the surrounding trees' competition analysis. Any surrounding trees that were contained inside the buffer by less than 50% were removed. The mean surrounding canopy height was recorded (MCH) and scaled by dividing it by the max height of the CHM to directly compare the effects across sites with very different canopy heights. This was to understand to what extent is the tree competing successfully, for example, a tree with a low surrounding canopy height is competing well. The percentage of trees taller than 5m was recorded to measure how dense/ open the surrounding forest was.

2.2. Data analysis

2.2.1. Comparing crown area to height scaling relationships with the predictions of metabolic scaling theory (Q1)

MST predicts that a tree's crown radius (CR) should scale isometrically with H (i.e., $CR \propto H^1$), from which we can derive that $CA \propto H^2$ (Jucker et al., 2022; Shenkin et al., 2020). To determine if trees in our dataset approximate this scaling relationship and test how deviations from MST vary among study sites, we modelled CA–H scaling relationships using a power-law function by fitting linear mixed-effects regressions to log–log transformed data and allowing both the intercept and slope coefficients of the regression to vary among study sites:

$$log(CA_{ij}) = \alpha_j + \beta_j \times log(H_{ij})$$

where CA_{ij} and H_{ij} are, respectively, the crown area and height of tree i from site j (factor with 25 levels); α_j is the intercept that varies among the j sites; and β_j is the slope coefficient that varies among the j sites. From the model we extracted the slope coefficient (β_j) for each of the sites and compared it to the theoretical predictions of MST, as well testing how β varies as a function of the aridity of the site.

2.2.2. Drivers of variation in tree crown allometry and shape (Q2)

To test how climate, disturbance, topography and competition influence variation in crown allometry (H and CA) and shape (CE and CAR) among sites, we used linear regressions to model each of the four crown attributes as function of the following predictor variables: (i) tree size (H, or CA in the case of the model for H), (ii) aridity index, (iii) mean annual temperature, (iv) maximum wind speed, (v) burned area, (vi) terrain slope, (vii) TPI, and (viii) relative canopy height of surrounding trees. When modelling variation in H and CA, both were log-transformed to meet the assumptions of normality. Moreover, prior to model fitting all predictor variables were scaled to have a mean of 0 and a standard deviation of 1, so that their model coefficients would be directly comparable. To rule out issues associated with multicollinearity, we calculated the variation inflation factors for each model to confirm they were <2 in all cases.

2.2.3. Comparing crown allometric scaling relationships derived from ALS with field data (Q3)

To test how well the scaling relationship between CA and H obtained from ALS matches to what we typically see in field data, we compared our results with data from the Tallo database (Jucker et al., 2022). Tallo is a collection of around half a million trees for which crown size measurements have been recorded in the field. To match the data to ours, we first restricted Tallo records to those falling within 50 km of our study sites, a distance within which we assume bioclimatic conditions will be similar enough to enable us to compare scaling relationships. This left us with 14 sites with matching ALS (n = 19,445 trees) and Tallo field data (n = 10,935 trees). Using the matched records, we then used mixed-effects models to fit CA–H scaling relationships (as described for Q1 above) and compared the slope coefficient estimates for each of the 14 sites derived from ALS and field data. For trees in the Tallo database, CA was calculated from estimates of crown radius by assuming a circular crown.

2.3. Results

2.3.1. Database overview

After classifying our delineations into confidence bands, 28,534 ‘confident’ trees remained in our dataset for the analysis. On average, sites contained 1100 ‘confident’ trees however there was considerable variation between sites, ranging from 308 trees in Australia’s Great Western Woodlands to 2866 at Bonanza Creek in Alaska. The tallest tree in the dataset was found in the Humboldt Redwoods National Park of Northern California and had a height of 106 m and a crown area of 301 m^2. By contrast, the tree with the largest crown size in our dataset was found at Barro Colorado Island in Panama and had a crown area of 1096 m^2 and a height of 53 m.

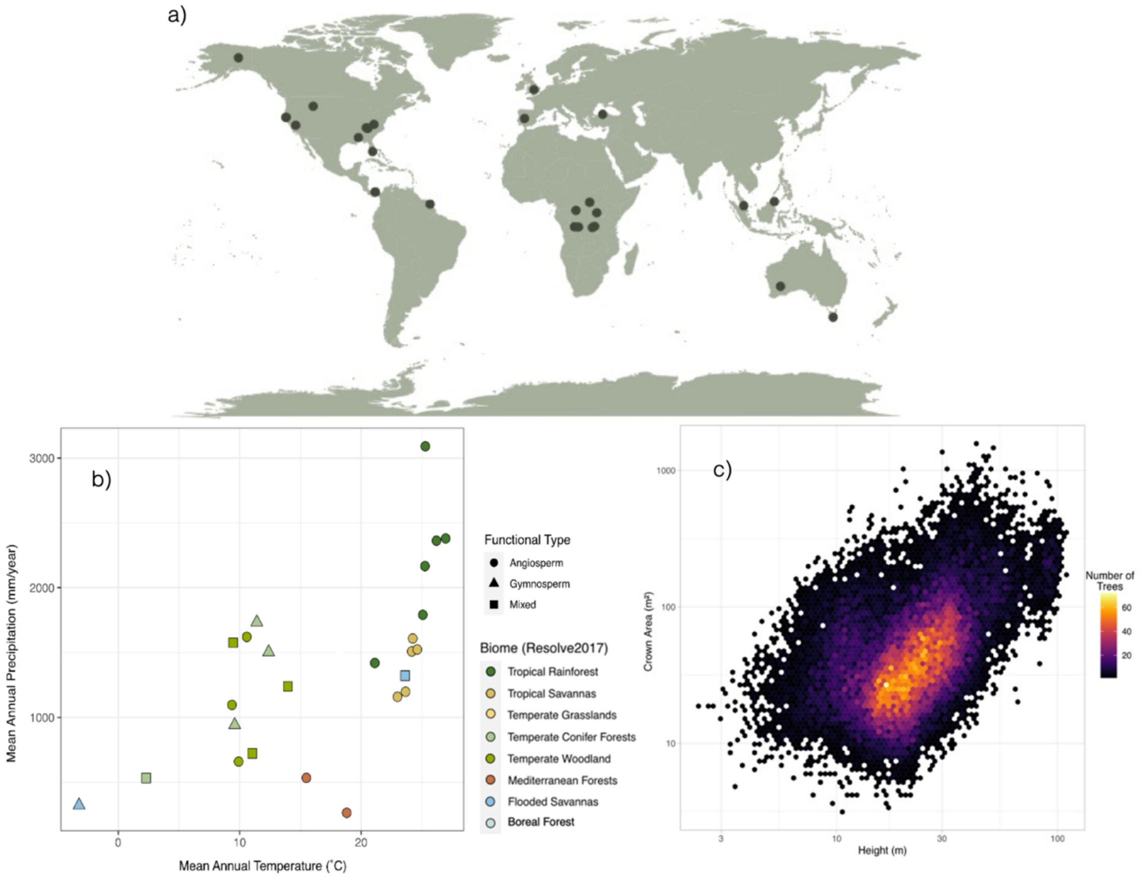

Figure 2: Overview of the crown allometric data compiled for this study. (a) World map with study sites. (b) Allometric scaling relationship between crown area and tree height for the 28,534 trees for which we were able to confidently delineate crowns in the imagery. (c) Variation in climate among the 25 study sites, as captured by their mean annual temperature and rainfall.

2.3.2. Comparing crown area to height scaling relationships with theoretical predictions (Q1)

We found the $CA{:}H$ scaling relationship of trees across all sites to be substantially lower than MST predictions, with an overall slope estimate of 1.15 [0.96–1.34 95% CI] compared to MST theoretical exponent of 2. Our model's total explanatory power was substantial ($R^2 = 0.72$). When looking at functional types for each site it's clear to see differences in slope exponent, with angiosperms higher than gymnosperms (1.21 vs 0.87). The lowest scaling exponent was found in DRC (tropical savanna, 0.32) and Alaska (tundra, 0.33) compared to BCI (tropical rainforest, 2.23) and Tasmania (temperate broadleaf forest, 1.95). We found a significant positive correlation coefficient of 0.5 [0.13 - 0.74 95% CI] between the $CA{:}H$ scaling coefficients and the aridity index ($p = 0.01$). Overall, when plotted across an aridity index gradient we find that trees growing in environments with high water availability (less arid) have higher scaling coefficients compared to those growing in more arid regions (Fig. 3).

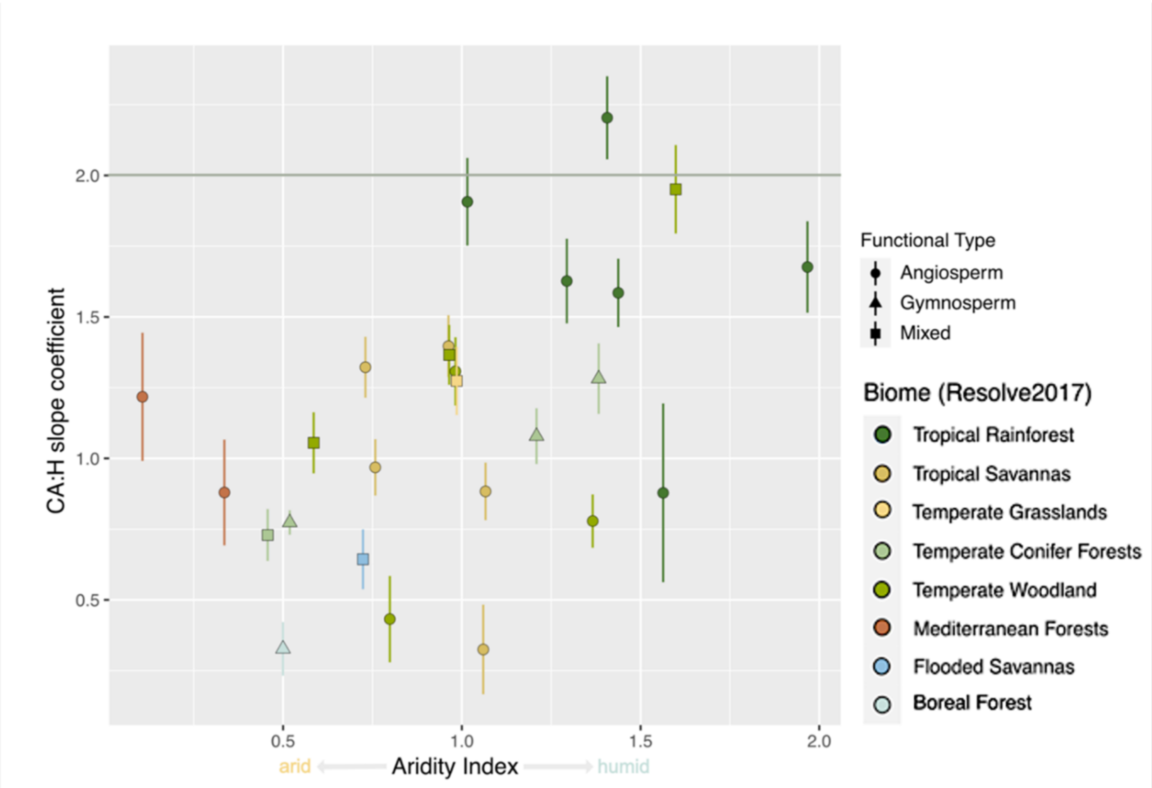

Figure 3: Crown area-tree height (CA:H) slope coefficients for each of the 25 study sites, characterised according to their aridity index. Slope coefficients were extracted from a linear mixed model and error bars correspond to 95% confidence intervals. Across all sites, the overall CA:H slope coefficient was 1. 15 [0.96-1.34 95% CI], significantly lower than the value of 2 predicted by metabolic scaling theory (horizontal grey line).

2.3.3. Drivers of variation in tree crown allometry and shape (Q2)

Tree height

All variables were found to be significant predictors of tree height (Fig. 4a) and overall, the linear regression model explained 65% of the variation in height across all trees. After accounting for the effects of CA, the key predictor of H was the AI (β = 0.35, 95% CI [0.40, 0.42], p < .001), confirming that the tallest trees were found in regions with the highest available water to plants. Trees in fire-prone regions were more likely to be shorter than those growing in regions that experienced little to no fire disturbance (β = -0.28, 95% CI -0.29, -0.27], p < .001). We also found a strong effect of surrounding competition on height (β = 0.25, 95%, CI [0.24, 0.25], p < .001), trees growing in highly competitive environments invest more into height gains. MAT was found to have a negative effect on H (β = -0.26, 95% CI -0.27, -0.25], p < .001), hotter regions have shorter trees. Disturbance variables were found to significantly reduce H. MWS is found to reduce H (β = -0.13, 95% CI [-0.14, -0.12], p < .001), and the tallest trees are found in regions with low MWS. Local topographic variables were found to be significant however, in relation to other coefficients they did not have a large predictive power (TPI, β = -0.008, 95% CI [-0.02, -0.001], p = 0.015; Slope, β = 0.01, 95% CI [3.76e-03, 0.02], p = 0.004). We find local topography only plays a minor role in explaining the variation in H relative to broader scale differences in climate and disturbance, and to the localised effects of competition.

Crown area

Most variables were found to be significant predictors of CA and the model explained 44% of the variation in CA between trees (Fig. 4b). The key predictor of CA (after H) was the MAT (β = 0.46, 95% CI [0.44, 0.47], p < .001), and aridity (β= -0.15, 95% CI [-0.16, -0.14], p < .001), indicating that trees growing in warmer, more humid regions expand their crowns larger than those in cold and arid regions. Surrounding competition was a significant predictor of CA (β = -0.14, 95% CI [-0.15, -0.13], p < .001), demonstrating surrounding competition from neighbours reduces CA. Fire had a positive effect on CA (β = 0.09, 95% CI [0.08,0.10], p < .001), suggesting trees that experience a higher frequency of fires have increased CA. MWS was a significant predictor of CA (β= -0.07, 95% CI [-0.08, -0.05], p < .001), the negative coefficient signifying regions of higher MWS produce trees with smaller crowns. Topographical variables were found to have little to no effect on CA. TPI was significant but had weak predictive power (β = 0.009, 95% CI [4.85e-04, 0.02], p = 0.037), and slope had no significant effect (p = 0.28), again showing that local topography plays a minor role in explaining variation in crown area.

Crown eccentricity

All climate, competition and disturbance variables were found to be significant predictors of CE (Fig. 4), however, the model had a weak explanatory power only explaining 2% of the variation. The key predictor of CE was MAT (β = -0.08, 95% CI [-0.01, -0.09], p < .001), indicating that trees growing in colder climates have more regular shaped crowns compared to those in warmer climates that have more irregularly shaped crowns. Trees growing in highly competitive environments had lower CE values (β = -0.06, 95% CI [-0.07, -0.05], p < .001), indicating surrounding competition negatively predicts CE. MWS was found to positively predict CE (β = 0.04, 95% CI [0.03, 0.06], p < .001), showing trees growing in regions of high MWS have more spherical crowns. Fire was also found to be a significant predictor of CE however negative (β = -0.03, 95% CI [-0.05, -0.02], p < .001), showing trees growing in regions with more burned areas had more irregularly shaped crowns. Again, topographic variables were found to be non-significant, slope (p = 0.75) and TPI (p = 0.06) and aridity was found to be non-significant too (p = 0.28).

Crown aspect ratio

Most variables were found to be significant predictors of CAR with the model explaining 47% of variation in CAR. The strongest predictor of CAR was MAT, (β = 0.38, 95% CI [0.36, 0.39], p < .001), indicating tree crowns in warmer climates tend to invest more in crown area expansion relative to tree height growth. Trees in more arid regions were found to invest more into tree height growth compared to crown area expansion (β = -0.22, 95% CI [-0.23, -0.21], p < .001). Increased surrounding competition negatively affects CAR (β = -0.22, 95% CI [-0.23, -0.21], p < .001), indicating trees invest in vertical growth over lateral crown expansion in response to competition for light. Trees growing in regions prone to fire invest more into height than crown area (β = 0.20, 95% CI 0.19, 0.21], p = 0.004).

Trees on steeper slopes tended to have smaller *CAR* (β = -0.01, 95% CI [-0.02, -0.01], p < .001), while *TPI* was found to not be a significant predictor of *CAR* (p = 0.07), along with wind speed (p = 0.92).

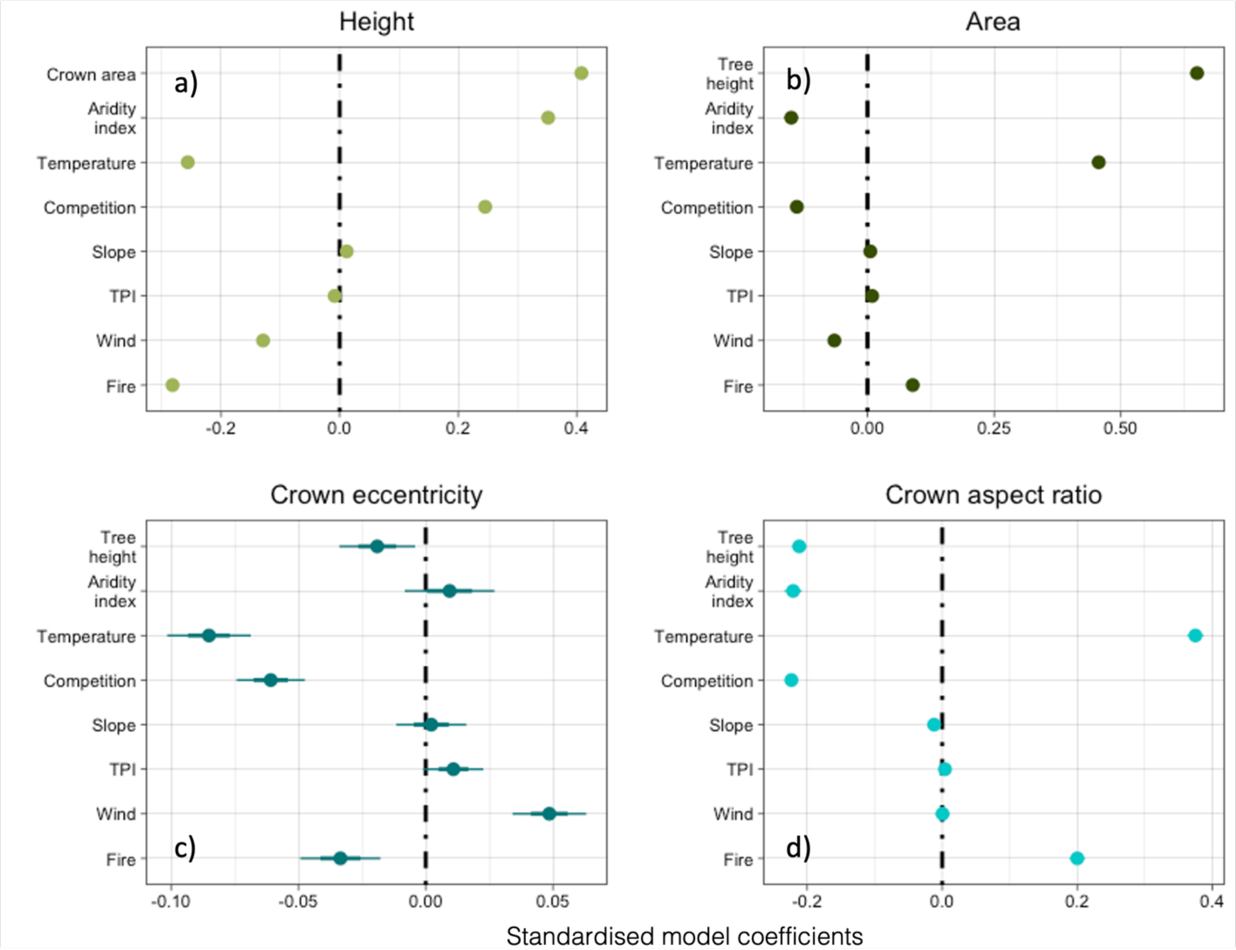

Figure 4: Coefficient plots showing the effects of tree size, climate, disturbance, competition, and topography on (a) tree height, (b) crown area, (c) crown eccentricity and (d) crown aspect ratio. Model coefficients were extracted from a multiple regression linear model and were standardised by scaling each predictor variable to have a mean of 0 and a standard deviation of 1. Error bars show both the 95% (think lines) and 99% (thin lines) confidence intervals.

2.3.4. Comparison of slope coefficients between ALS allometry and Tallo database. (Q3)

The ALS allometric measurements were then compared with field measurements from the Tallo database. Overall, it appears that the two datasets are in agreement with one another when looking at how crown area and tree height scale (Fig. 5a), and as expected the ALS data captured a much bigger proportion of large, canopy dominant trees compared to field data obtained from the Tallo database (mean tree height = 24.5 m vs 14 m; mean crown area = 63.2 m^2 vs 46.4 m^2). However, the *CA:H* slope coefficients estimated for the 14 study sites for which we had matching ALS and field data indicate that on the whole slope estimates are systematically higher in the field data (black circle in Fig. 5b; overall ALS slope = 1.12 ± 0.27 ; overall Tallo slope = 1.42 ± 0.27). Moreover, while for 8 of the 14 sites we found good agreement between the ALS and field data (Fig. 6), in general the *CA:H* slope estimates derived from the two datasets were only weakly positively correlated with one another (Pearson's correlation coefficient = 0.39, p = 0.167; Fig. 5b).

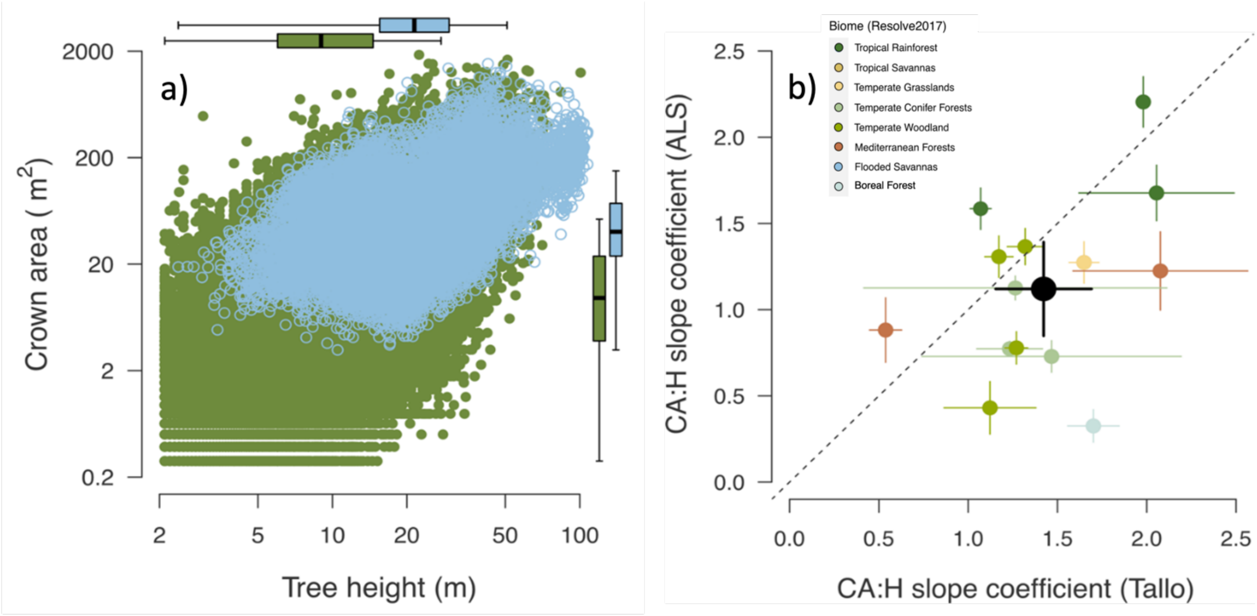

Figure 5: Panel (a) shows the comparison of estimates of tree height and crown area derived from ALS (blue) and field data from the Tallo database (green). Box plots summarise the range of values for both datasets. Panel (b) shows the crown area-tree height (CA:H) slope coefficients derived from 14 sites for which both ALS and field data were available, as well as the overall slope coefficient estimated across all sites pooled together (black circle). Slope coefficients were extracted from a linear mixed model and error bars correspond to 95% confidence intervals.

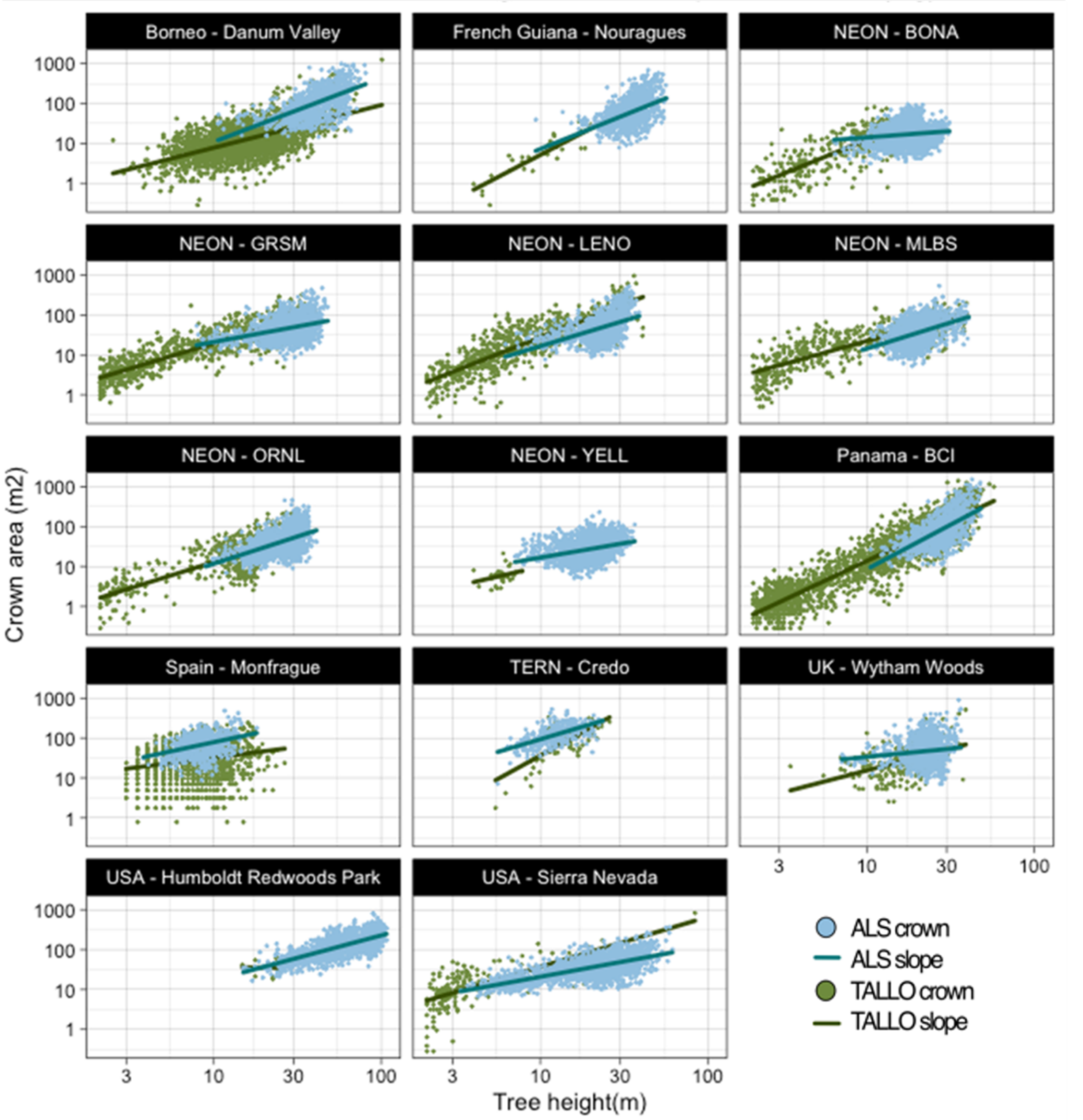

Figure 6: Relationship between crown area and tree height across the 14 study sites for which both ALS (blue) and field data (green) were available. Regression lines show the fit of the linear model fit separately for each dataset for each.

3. Chapter 3: Discussion and future directions

This project has highlighted the usefulness of harnessing airborne laser scanning (ALS, also known as airborne LiDAR) data for assessing structural variation in canopy-dominant trees across the world's forests. Using this novel approach allowed us to characterise the crown shape and size of a large number of canopy-dominant trees that were once inaccessible using ground-surveying techniques. In doing so we were able to test how well the scaling relationships between crown area and tree height ($CA{:}H$) conform to the theoretical predictions of metabolic scaling theory (MST) across a diverse range of biomes. Here I discuss the findings in relation to existing literature and the limitations this project faced. I will also go on to suggest future directions for this research and the contribution this work can make to other studies.

3.1. Key findings and their place in the literature

3.1.1. Tree architecture varies along environmental, disturbance and competition gradients

The tallest trees in our dataset were found in the Humboldt Redwoods National Park, the tallest tree standing at 106 meters tall. This site had a MAP of 1759 mm in line with Scheffer et al., (2018) claim that the tallest trees are sharply limited to regions with mean annual precipitation above a threshold of 1,500 mm. We found the key driver of observed variation in tree height to be aridity, in line with the literature (Lines et al., 2012; Olson et al., 2018). Trees can only grow tall if they can have wide conduits, if there are periods of drought or water stress, trees are at risk of embolism, so arid regions have shorter trees (Givnish et al., 2014; Moles et al., 2009). The next strongest predictor of tree height was temperature which we were expecting to find (Charra-Vaskou et al., 2023; Hacke et al., 2016; Zanne et al., 2013). Even if a region has high water inputs, if the temperatures are too low, freeze events can cause embolisms, thus both cold and dry regions have shorter trees (Klein, Randin and Körner, 2015; Olson et al., 2018). The world's tallest trees would be found between 7-24 degrees which our data agreed with, with the tallest redwoods having MAT of 12 degrees. Surrounding competition was found to be a strong predictor of tree height with increasing surrounding competition promoting tree height growth (Lines et al., 2012; MacFarlane and Kane, 2017). Fire was also a key predictor of height however we found fire to reduce tree height, in contrast to studies attributing the height of savannas to fire (Archibald and Bond 2003). In other areas fire has been found to reduce tree height (Choi et al., 2023), which is an issue with growing wildfire seasons (Burton, 2023). Previously the effects of topography on tree allometry have been assessed at local scales (Jucker et al., 2018; Liu et al., 2020; Wei et al., 2018; Werner and Homeier 2015). Here we have found in a global context, topography doesn't much influence tree allometry. When looking at a tree's position within a landscape on a small scale, its likely differences in architecture will be identifiable, however, when scaled up over different habitats with the addition of other predictors it loses its importance. The effects of topography on architecture may rather be attributed to climatic variables that the topography facilitates indirectly, such as changes in temperature, water accumulation or wind protection/ damage (Liu et al., 2020; Wei et al., 2018).

Temperature is the key predictor of tree crown size; whereby colder regions were predicted to have smaller tree crowns and warmer sites were predicted to have larger crowns. Warmer regions have more available resources so trees can invest their energy into biomass accumulation rather than root expansion in search of those limited resources in cold regions (Reich et al., 2014). They also do not experience freeze-thaw events that are likely to cause embolisms of branches (Lemoine, Granier and Cochard, 1999). Cold regions prone to snow and frost exhibit small, conical shape crowns as a method for shedding accumulated snow to prevent breakage (Chabot and Hicks, 1982), as seen in our data. Increasing aridity is attributed to smaller crowns within species (Lines et el., 2012), again a response to a search for water and nutrients. Like height, long branches in dry regions are at risk of experiencing embolisms during periods of low precipitation and drought as seen in our data with crowns in arid regions being smaller than those in humid regions. Competition was found to reduce crown area as expected. This is a response to crown packing. A tree's photoreceptors will detect surrounding neighbours through a reduced red:far-red light ratio and will activate hormones to position photosynthesising leaves in the upper, better-lit part of the canopy, a method of shade avoidance (Keuskamp, Sasidharan and Pierik, 2010). The change in growth strategy in response to surrounding neighbours. The trees will stop investing in spreading their crowns and instead invest in height, to outcompete their neighbours (Van de Peer et al., 2017), increasing crown slenderness (MacFarlane and Kane, 2017). Pitkänen, Bianchi and Kangas (2022) also found competition to influence the allometry of competing trees where less dominant trees would invest more in height and more dominant trees would invest more into crown area to shade out others around them, indicating that those facing higher levels of competition (less dominant) have smaller crowns. Our data also confirms that wind decreases the size of tree crowns, a response to mechanical damage when crowns sway and crash into one another (Iida et al., 2011). Again, for the crown area, we found local and topographic features to have no significant effect on the crown area going against what was previously thought about the crown area decreasing with increasing altitude (Jucker et al., 2018; Madhumali et al., 2023).

The crown aspect ratio (CAR) describes the height-to-crown area differences. A CAR value close to 1 would indicate trees are able to grow as wide as they are all, and as this number decreases, trees become slenderer with narrow crowns. Our study demonstrated that CAR was most influenced by temperature. Warmer regions had crowns that were large in proportion to their height. This aligned with findings that warm regions, like the tropics, have a lot of resources so trees can invest in crown expansion rather than root elongation (Reich et al., 2014). Large crowns in cold, arid regions would experience more embolisms so trees are more conservative with their growth patterns (Olson et al., 2018), resulting in low CAR values. Competition was found to negatively impact CAR values with highly competitive environments producing taller, slender trees with smaller crowns (MacFarlane and Kane, 2017). The trees in our dataset were those visible from a top-down perspective and represent those competing more effectively. Understory trees and those not able to reach the top of the canopy would not exhibit these same patterns. Rather shade tolerant trees would likely have high CAR values that enable them the capture light that passes through the canopy. Adding species information would be useful in attributing our findings to specific growth behaviours. We expected to see wind have a negative effect on CAR values where regions with higher wind velocities would have narrower trees but instead found no influence of wind on tree slenderness (Jackson et al., 2019; Sellier and Fourcaud, 2009). We found the presence of fire to increase CAR values, indicating trees growing in fire-prone regions would have wide crowns in comparison to their height, unlike Archibald and Bond (2009) who state savanna trees that experience fire exhibit narrow "structural characteristics associated with rapid height gain". Our results may indicate that trees invest in height growth to escape fire initially but are then limited to how tall they can grow due to these systems being dry (Olson et al., 2018). A factor we did not include in this analysis is the influence of herbivores on tree allometry. The presence of herbivores has been found to influence tree height – stem diameter allometry of savanna trees, those exposed to herbivory have a much lower height for a given stem diameter (Moncrieff et al., 2011). Biogeography also plays an important role in the variation we see in CAR values. Moncrieff et al., (2014) observed structural differences between African and Australian savannas, with Australian tree structures having lower CAR values and African savanna trees having high CAR values. The crowns of Fabaceae have been found to be consistently larger than those of the given stem radius of other taxa (Shenkin et al, 2020), signifying the influence of phylogenetic differences in a tree architecture.

Crowns become more asymmetric in warmer sites as they facilitate more species with increased resource availability. An increase in species diversity and richness increases a stand's ability to organise themselves more effectively (Buche et al., 2022; Jucker, Bouriaud and Coomes, 2015; Kunz et al., 2019). The spherical structures we observe in cold regions are to prevent embolisms and branch breakage from snow as explained above (Chabot and Hicks, 1982). It's also likely that colder regions are more likely to be comprised of gymnosperms that grow in circular shapes. Compared to the tropics, comprised mostly of angiosperms that are better adapted to filling available space and having more irregular-shaped crowns. In stands with increased competition trees must fill available space in the canopy if they are to access incoming light (Aakala et al., 2015; Hildebrand et al., 2021; Seidel et al., 2011). Heterogeneous light distributions result in excelled growth of sides of the crowns experiencing high light intensities and little growth on those shaded by others, resulting in asymmetric crowns (Seidel et al., 2011). Trees also detect surrounding neighbours through mechanical stimulation (Pierik and de Wit, 2013) leading to a canopy that exhibits crown shyness, growing crown shapes that complement those of their neighbours (van der Zee, Lau and Shenkin, 2021). We expected to see trees exposed to high wind velocities have more irregular/ lopsided crowns which occur when trees bend away from the direction of the wind to reduce torsion and prevent breakage (Coder, 2021; Hao et al., 2020). However, we found wind to be a predictor of more spherical crowns. Our study sites were selected based on a threshold of forest cover to ensure we included forests and not stand-alone trees, agricultural land or deforested areas. As a result, many of the trees in our study would have a level of protection from their surrounding neighbours and not be open to the wind which would create the extreme end of irregularly shaped crowns (MacFarlane and Kane, 2017). Fire was found to increase the irregularity of tree crowns likely the result of branches and foliage being consumed by fires (Qi et al., 2022), having a lasting impact on architecture. The effects of fire could be due to the fire-prone site in our study were savannas which are also impacted by herbivory. Topography and aridity were not found to be significant. However, it is important to note that the predictive power of these drivers for crown eccentricity was much lower than those of tree height, crown area and CAR.

3.1.2. Using ALS to capture the crown allometry and architecture of canopy-dominant trees

This study was able to capture data on the upper canopy structural characteristics that are commonly missed when assessing tree structure from below the canopy. Our ALS dataset was able to on average capture trees taller than those in the Tallo database (mean tree height = 24.5 m vs 14 m; mean crown area = 63.2 m^2 vs 46.4 m^2). When compared with the Tallo dataset we found that our results estimate the slope exponent of crown area to height to be lower than that of the ground-surveyed data. This could be due to our dataset being more biased toward the canopy dominant trees and Tallo being biased towards the understory, lower canopy. The scaling exponents of the two datasets were not found to be significantly correlated which we expected as they were capturing different ends of the tree height spectrum. NEON sites had better agreement of slopes though, which may indicate the slopes to be closer than the models predict. The 50km buffer may still be the same climatic conditions but the forest type could change making the allometry of trees we used for those comparisons very different compared to NEON sites where TALLO and ALS data were perfectly aligned. This is another good reason for the addition of species classifications that could unpick some of these questions. We also found that the slope exponent varies greatly across biomes and forest types with the MST overestimating most sites, especially those at the dry end of the aridity scale (Jucker et al., 2018).

3.2. Methodological limitations

3.2.1. Data processing and analysis

The delineation of tree crowns was performed manually to increase the accuracy of this process as it incorporated both RGB and CHM to delineate the trees, however, this method took a lot of time and meant that we were only able to include 25 sites. There are automated packages that can perform this task however, they are trained with manually delineated crowns so are inherently less accurate. As these packages develop and become more accurate it would be useful to delineate more tree crowns from more sites and forest types and to run the allometric analyses across all of these (Ball et al., 2023; LeCun, Bengio and Hinton, 2015; Reichstein et al., 2019; Weinstein et al., 2020). The variation in structural characteristics that we see between sites makes using one package to delineate all sites very difficult, with some packages being better for the tropics and others better for temperate regions. With our dataset being global we decided to manually delineate for all sites. Some forest types were more challenging than others. Forest type and functional differences have a big impact on the ease of delineation. For example, Wytham Woods in the UK was one of the hardest to delineate, a mix of densely packed deciduous and conifer species, which likely was delineated less precisely. Deciduous tree crowns in closed canopy forests are flatter than those in conifer forests and so are harder to segment, even for automated packages (Dalponte, Frizzera and Gianelle, 2019). A site that was very easy to delineate was BONA, NEON, a site comprised solely of conifer trees, evenly spread apart. We found conifer sites overall easier to delineate with their spherical crowns, however there tended to be a lot more of them as they have smaller crowns so while the crowns were easy to delineate, they would take a long time. Another factor that aids delineation is the point density (or resolution) of the ALS scan. NEON sites had a high point density, so the CHM produced from these sites were more accurate than those produced from lower point densities. The process of producing CHMs does mitigate the differences in resolution so that the CHMS produced are standardized however, differences between sites would increase the variation of quality.

Our results show environmental, disturbance and competition to be strong predictors of differences in the variation of tree allometry across global forests. The dataset provided nearly 30,000 ‘confident’ trees from 25 sites that we were able to build our models from. We saw evidence of differences in allometry between biomes but to make stronger predictions about these regions it would be useful to include data from more sites. I manually delineated the tree crowns for better accuracy; however, this took up a great portion of the time allocated for this study. While not perfect, automated delineation algorithms applied to ALS and RGB data have improved considerably in recent years, particularly through the use of deep-learning methods (Ball et al., 2023; Weinstein et al., 2021). A method of delineation that combines both CHM and RGB would be good for the sites as we have both datasets. Using automated delineation packages would speed up this process and allow us to significantly increase the volume of available data. It would also be useful to include more regions on the lower end of the temperature scale as our dataset only included one tundra site and no boreal sites.

When comparing the slopes of scaling exponents from ALS and Tallo we found they were not significantly correlated and that field-based measurements generally overestimated the slopes. However, when looking at the plots of the 14 sites we see around 8-9 of them show good agreement in data alignments indicating that they are to some extent, predicting the same spread of data. When searching for Tallo datasets that were from the same area as our ALS datasets, we added a 50km buffer to our ALS sites as a search window. This would explain why the NEON datasets are the sites that have the closest fit for both Tallo and ALS as the sites are precisely aligned. Other sites, while in the search window may be completely different forest types and topography. The closeness of precisely located sites would indicate that the two methods of allometric measurements are more closely aligned than the model suggests. It would be good to perform this study more NEON sites and see how closely the slopes are correlated. If we had field data from the exact plots where we did the segmentation that would likely reduce a lot of the noise (or at least give us more confidence that the differences, we see are not driven by some underlying environmental gradient). The two datasets are also inherently capturing different ends of the $CA{:}H$ spectrum. The field data captures more detail about the below canopy but is less accurate for height measurements, whereas the ALS captures more about the top of the canopy but misses the crown edges obscured by the surrounding canopy (Fig. 5a). To overcome this, I would find the range of measurements that cover both the Tallo and the ALS dataset and use the trees within this range to assess the slopes. However, this would limit the data used in the models as one is from above and the other below. Another option for comparing the two datasets would be to test the model's ability to predict CA and H of trees within a dataset not used to train the model and see which model was better at capturing the scaling exponents.

3.2.2. Variables included in the models

The variables we included in this study were those that the literature deemed as influential in predicting tree architecture. Our initial model included more variables that were removed through tests for covariance - this included mean annual precipitation, TWI and meters above sea level (MASL). We found precipitation to be closely correlated with aridity. We selected aridity deciding this was a better indication of water availability (Cartereau et al., 2023; Olano et al., 2023). The addition of detailed climate records and seasonal variability would allow us to apply our allometry to climate change models. Successive drought events have been found to reduce branch length and tree height growth (Vennetier et al., 2013), and the duration of the wettest month was found to be the strongest predictor of global tree height (Moles et al., 2009). We selected TPI and slope as the most suitable variables to explain topography which both were found to have little to no effect on tree allometry, yet we know from other studies this does have an effect whether direct or indirect (Jucker et al., 2017). We see obvious differences in tree height when we look across a landscape, whereby the tallest trees grow in the valleys and the shorter trees on the slopes. The observed response of tree allometry to topography may not be a response to topography but rather and indirect response to the conditions topographic differences create. Some suggest that tree height declines with altitude, associated with lower temperatures and shortened growing seasons (Coomes and Allen, 2007). However, this has been disputed where temperature inversions were found, this led Wei et al., (2018) to attribute reduction in three heights with increasing elevation to soil moisture. Perhaps the exploration of TWI may have unpicked the patterns or height above the closest drainage (Nobre et al., 2011). The aspect of the slope has been found to influence tree volume and structure, with trees on north-facing slopes being slenderer (Dutcă et al., 2022).

Some other variables I think would have been interesting to explore in the models would have been herbivory, age of stand and soil type. Firstly, we know herbivory plays a crucial role in shaping the architecture of trees (Charles-Dominique et al., 2017; Kurokawa et al., 2022), especially those in savanna habitats (Archibald and Bond 2003). This would also contribute to understanding the effects overgrazing has on tree and forest structure (Arévalo et al., 2021), and be applied to projects where grazers have been removed reduced but also to understand where the presence of grazers is necessary for forest dynamics. The addition of the age of the stand as a variable would have been valuable in pinpointing which variables were the most influential, for example, we know earlier successional stages invest more into height growth compared to older stands that invest more into canopy spread (Lucas-Borja et al., 2016; Matsuo et al., 2021), as well as the age of the stand having an effect on microclimate of the forest (Lindenmayer et al., 2022). Finally, the addition of soil type would have further improved our understanding of how it influences the productivity of forests and how they interact with water and nutrient availability (Shangguan et al., 2017; Zhang et al., 2023).

3.3. Directions for future research

This project was successful at making a global assessment of tree architecture and the drivers that explain this variation. The outputs from this project, both in terms of the raw data and the derived analyses, offer several possible avenues of future research to build on the work presented in this thesis.

3.3.1. Species and functional group classification

Linking this data to species classifications would unlock some of the questions that have been produced through this project, such as, the effects of temperature on tree crowns have been identified within species, not just between species (Line et al., 2012). For some of our sites, we have ground data. It would be interesting to marry up the delineations from this project with the information from the ground. Using tree geolocations would allow us to assess the accuracy of the manual delineations and if confirmed can be used to compare ground assessments with those from above. The NEON datasets are a perfect opportunity to combine RGB images with ALS data to develop species classification packages as each site has both the datasets as well as in-field surveying. It would also help us to explain why ground surveying overestimates scaling exponents. A model for classification of species from hyperspectral imagery was created across 27 of the NEON sites with 77% accuracy for their general model (Marconi et al., 2022). Marconi hopes to expand this model outside of the US NEON sites to produce a general species/ genus/ functional type model for global forests. Our datasets of manually delineated tree crowns, ALS data and RGB imagery may contribute greatly to this. Structural information from ALS has been useful in contributing to species classification. Hyperspectral and multispectral imagery has been used in combination with ALS to classify subalpine coniferous species at some NEON sites (Scholl et al., 2020) and mixed upland forests (Dalponte, Frizzera and Gianelle, 2019). Others are combining the datasets with neural network machine learning to classify species at large scales (Scholl et al., 2021). The addition of species information would help us to identify structures that may be associated with seed dispersal. Malhi et al., (2018) found trees that disperse seeds by wind were tall with small, clustered crowns compared to heavy seed-dispersing trees that couldn't reach the same height but had large, wide crowns they could easily drop large seeds from, the sound-attracting elephants in the forest. The addition of this species information is important if we are to untie structural characteristics across global forests. The importance of species classification is also demonstrated by Moncrieff et al., (2014) who identify the impact of legume structure on influencing tropical allometric models.

3.3.2. Training and validating deep learning tree crown delineation algorithms

More recently, the development of deep learning (LeCun, Bengio and Hinton, 2015; Reichstein et al., 2019) is rapidly improving our ability to delineate tree crowns in an automated workflow. Packages are being written to delineate individual tree crowns from both RGB images and ALS-derived canopy height models. Training the packages requires manually delineated tree crowns, a process that is time-consuming and labour-intensive. Many of the training datasets have also been limited to delineations from single forest types and regions. For example, Detectree2 (Ball et al., 2023) used 3797 manually delineated tree crowns at three sites in Malaysian Borneo and one site in French Guiana, to train a dataset that can delineate from RGB. Brandt et al., (2020) trained deep-learning packages using 89,899 individual trees manually delineated along a north-south gradient to quantify the number of trees in the West African Sahara and Sahel from an NDVI derived from satellite images. Algorithm packages like DeepForest (Weinstein et al., 2020) can delineate tree crowns from CHMs, this one used 10,000 manually delineated crowns to train their algorithm. Our dataset consists of 28,534 'confident' trees and 5,135 'less confident' trees, spanning a range of continents and biomes. Our dataset is also unique because most sites have RGB and CHM. This combination of two datasets can be used to further train and validate the automated delineation packages for a variety of forest types.

3.3.3. Contribution to forest modelling, monitoring, and future climate predictions

The development of models for predicting tree allometries at landscape scales is essential if we are to quantify global biomass. The models are trained from tree height measurements of a sample of trees in a plot and are used to train local allometric models from which the height of multiple trees can be predicted (DeAngelis and Grimm, 2014; Sullivan et al., 2018). Inventories of plant allometry, forest observations and individual-based models are being combined with remote sensing data to improve the accuracy of tree allometry (Fischer et al., 2020) and forest structure assessments (Fischer et al., 2020). The addition of ALS can improve carbon estimations (Hurtt et al., 2004) which have become a common financial scheme for offsetting emissions such as REDD (Reduced Emissions from Deforestation and Degradation; Asner et al., 2010). We have found that allometric models, such as MST, overestimate scaling relationships indicating projects using allometric models to quantify volume are overestimating carbon.

We found climatic variables such as aridity and temperature were the key drivers of tree crown area and height. With global climate change, it's essential we model and monitor the effects of change in climate on trees and forests (Binks et al., 2023; Käber et al., 2023; Marchin et al., 2023; Rodman et al., 2023). Our allometry can be used to perform repeat assessments of grown trees and forest structures. With the NEON dataset, there were CHM available for multiple years. We could use our delineations to assess forest change and also map mortality in response to changing climates. There is also the opportunity to compare how changes in climate affect different forest types over large scales, without having to rely on ground measurements.

3.4. Conclusion

The development of ALS data has opened opportunities to study the shape and size of individual trees at larger scales. It enables us to test previous models' assumptions, improving allometric models and forest dynamics models to better help us predict future responses to changing climates. There is still a need for an improvement of automatic delineation packages, yet this requires a lot of training data. The development of machine learning is speeding this process along and soon we will be able to map large extents of forest quickly and accurately.

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