UNIVERSITY OF LEEDS

Identifying Biodiversity Controls on Stability of Forest Ecosystems and Their Services

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Intellectual Property and Publication Statements

The candidate confirms that the work submitted is his own, except where work which has formed part of jointly authored publications has been included. The contribution of the candidate and the other authors to this work has been explicitly indicated below. The candidate confirms that appropriate credit has been given within the thesis where reference has been made to the work of others.

Chapter Two

Background climate conditions regulated the photosynthetic response of Amazon forests to the 2015/2016 El Niño-Southern Oscillation event. September 2022. Max Fancourt, Guy Ziv, Klaas Folkert Boersma, Julia Tavares, Yunxia Wang & David Galbraith.

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Assertion of moral rights

MFancourt

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Abstract

The high and multifaceted value of forests globally provides a strong motivation to better understand how they respond to perturbation, and the key variables that moderate this response. However, forest-stability research lacks a unified framework for defining and quantifying stability, and has historically focused on smaller spatial scales, resulting in considerable uncertainty about the variables that moderate climate-forest stability at landscape scales. Our results highlight the importance of understanding forest stability when seeking to explain landscape scale variation in forest response to climate perturbation. In all case studies when investigating climate perturbation, the magnitude of the perturbation alone was insufficient to explain productivity patterns. Therefore, any examination of productivity response to perturbation without considering variance in stability will be missing a crucial component. The methods presented in this thesis demonstrate that it is possible to quantify and describe spatial patterns in stability of forests to climate perturbations at landscape scales, and to understand the mechanisms behind the variation in stability that we observe. Investigation of which variables were important revealed that for both tropical and temperate forests, the background climate that a forest has experienced was the single most important group of explanatory variables, except when functional traits were directly included in models (which were then most important). Background climate, we argue, ultimately acts as a measure of the selective pressure acting on the community, and thus is informative of the community composition in terms of species and functional traits present. The finding that functional traits are important in understanding the response of forest ecosystems joins a growing body of literature highlighting the power of a functional trait approach in understanding variation in productivity responses, and offers a mechanistic understanding of the processes underlying stability, and giving us valuable insights into how these forests may respond to ongoing climate change.

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Acronyms

AGB Above Ground Biomass

AGWP Above Ground Woody Productivity

AICc Aikaike Information Criteria Corrected

ALE Accumulated Local Effect

DBH Diameter at Breast Height

DGVM Dynamic Global Vegetation Models

ENSO El Nino-Southern Oscillation

GPP Gross Primary Productivity

IPBES Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services

LMA Leaf Mass per Area

MCWD Maximum Cumulative Water Deficit

MGST Mean Growing Season Temperature

MSGSP Mean Sum of Growing Season Precipitation

NCP Nature's Contributions to People

NDVI Normalised Difference Vegetation Index

NPP Net Primary Productivity

PET Potential Evapotranspiration

PFT Plant Functional Types

SCDB National Forest Estate Subcompartments

SIF	Solar Induced Fluorescence
UK	United Kingdom
VI	Vegetation Index
VIF	Variance Inflation Factors

Chapter One

Introduction and Literature Review

1.1 Seeing the forest through the trees

Viewed from space the vibrant living green of the Earth's forests is arguably one of its most striking features. Globally they cover nearly a third of the Earth's surface[1] and provide a multitude of services[2] benefiting all life on Earth. Forests are critical to the survival of humanity, providing services including climate, nutrient and water regulation, provision of both timber, and non-timber products, they sequester vast amounts of atmospheric carbon helping to combat climate change and are home to a wide range of biodiversity[2].

Forests can be loosely defined as areas containing woody vegetation[3]. However, beyond this, a range of forest definitions exist reflecting the diversity in form and function of forests globally. Forests have been defined as economically important sources of timber [3], as ecosystems composed of trees with myriad forms of biodiversity [4], as a home for indigenous people[5], as repositories for carbon storage[6], as natures contributions peoples [7]. In addition to conceptual definitions, operational definitions of forests (used to measure and quantify the amount, or quality of forest in an area) can also vary significantly depending on the data available for measurement. From survey data, one may delineate forests using variables such as tree density, canopy cover, and tree height. By comparison, if remotely sensed data is being used, forests may instead be defined using information from passive and active remote sensing systems to create proxies of forest biomass, phenology, canopy cover, canopy and forest structure, and reflectance signatures. Finally, for socioecological forest definitions, economic studies may have to be conducted to evaluate the economic value of the services that the areas provide to determine if the areas meet the definition of a forest, and what type of forest it is[8].

Forests definitions have historically focused on defining forest, and forest health in terms of timber production[3]. It is only in the past fifty years that definitions looking more holistically at forests have been developed. The definition of a forest and forest health can have significant impacts on both predictions of global forested area, and forest status [9]. Historically, forests assessments at the global scale were motivated by concerns of timber shortages, and so forests were defined as being "land covered with woody growth of economic importance"[3], and primarily focused on the capacity of these areas to yield timber. It was only in the 1990s [10] that other aspects of forest such as biodiversity and species loss were considered to be important in understanding forest status. The UN Food and Agriculture Organisation Global Forest Resource Assessment 2020, the United Nations Framework Convention on Climate Change and many other international processes and institutions define "forest" primarily in terms of land use and the potential for forest to be in an area (definitions shown in Table 1.1).

Table 1.1: Definitions used by the UNFAO, UNFCC and UNESCO for Delineating Forest Areas

Organisation	Definition
UN Food and Agriculture Organisation Global Forest Resource Assessment 2000	Lands of more than 0.5 ha with a tree canopy of more than 10%, which are not primarily used under agricultural or urban land uses[11]
The United Nations Convention on Climate Change (UNFCCC)	A minimum area of land of 0.05–1.0 ha with tree crown cover (or equivalent stocking level) of more than 10–30
UNESCO	Closed forest: trees = 5 m with crowns interlocking. Woodland: trees = 5 m tall with crowns not usually touching but with canopy cover = 40%

This focus on land use and the potential of trees to exist in an area can result in areas being classified as forests even if currently treeless. Conversely, agricultural and urban areas with tree cover may be considered as land uses other than forest. Even within this paradigm of forest definitions, significant variation exists. Comparing various national reporting thresholds, Lund (2002)[8] showed (Table 1.2) that the thresholds used to delineate forested areas varied considerably, requiring significant work to harmonise in order to arrive at estimates of global forest coverage.

Table 1.2: Comparing highest and lowest thresholds used to define what a forest is, from FAO national reporting adapted from Lund et al. 2002[8], considerable variation in the threshold can be seen to exist between in definition, which in turn will significant impact is defined as being forest

Threshold	Lowest/Highest	Value	Countries
Area	Lowest	0.01ha	Belgium, Northern Marian Islands
	Highest	100ha	Malawi, Papua New Guinea
Crown Cover	Lowest	1%	Iran
	Highest	80%	Malawi, Zimbabwe
Tree Height	Lowest	1.3m	Estonia
	Highest	15m	Zimbabwe
Strip Width	Lowest	9m	Belgium
	Highest	60m	Philippines

In summary, forest definitions should be context dependent and should relate to, the system you are studying, the tools you are using to do so, and the purpose of your study. As this thesis studies a range of forest types, each chapter of this thesis makes use of a contextually appropriate, albeit harmonised, definition of forest appropriate for the specific research question.

Inherently linked to the definition being used to define what a forest is, the definition of forest health, or status of a forest also varies widely. At the level of the individual health is relatively simple to define as the absence of damage and disease, and that the individual continues to grow[12]. However as the unit of measurement increases from individual trees, to stands, entire forests, landscapes and ultimately at a global scale forest health becomes increasingly difficult to define. In addition to definitions varying at scale, definitions can also vary based on perception of forest value. More utilitarian definitions of forest health tend to focus on forest productivity, the volume of timber produced, and the material benefits that forest supply to local communities as way to monitor their health, while more ecosystem centric definitions tend to focus on community composition, metacommunity dynamics, soils and other such indicators[13].

Combining scale, and the utilitarian/ecosystem centric perspectives it is therefore easy to see how a great number of definitions of forest health can exist. Table 1.3 adapted from Trumbore et al (2015)[12] summarises a number of the most common definitions of forest health.

Table 1.3: Showing a range of different measures of forest health, over a range of different units of measurements, and from both utiltarian and ecosystem-centric perspective Adapted from Trumbore et al (2015)[12]

Utilitarian Indicators			
Disease Damage Growth	Wood yield Pest infestation Leaf area	Water quality Wood supply Aesthetics	Carbon storage Energy fluxes Element fluxes
Ecosystem Indicators			
Dead wood Disease resistance Genetic variability	Habitat quality Community structure Soil fertility	Seral diversity Connectivity Patchiness	Persistence Invasion Extinction
Assessment tools			
Inventory cruise Inventory plots	Inventory plots High resolution remote sensing	Inventory plots Remote sensing	Remote sensing Monitoring networks
Tree	**Forest**	**Landscape**	**Global**

Forests are not static systems, spatially or temporally, and even considering all of the above metrics, across all of these scales will ultimately fail to accurately capture forest health if the inherent spatial and temporal variance in forest ecosystems isn't accounted for[12]. Death of a forest patch can occur due to a stress or perturbation, and may affect both healthy and unhealthy trees equally e.g. windfall, fire, or may target unhealthy trees disproportionately e.g. drought stress. While this forest patch itself might be considered unhealthy, can facilitate a whole suite of essential ecological process such as regeneration, nutrient cycling, or habitat creation at broader spatial scales[12, 14] . A healthy forest therefore might be considered one that is comprised of a mosaic of patches, in different successional changes, that promote nutrient dynamics, a diversity of cover types and niches.[15, 16].

1.2 What do the forests of the world look like?

Forests can be found across boreal, temperate, subtropical and tropical climatic domains. In total, they cover 4.06 billion ha (40 million km^2)[17] representing nearly a third of the planet's land surface[1]. The tropical climatic domain has the largest proportion of the world's forests containing around 45 per cent of global forest cover, followed by the boreal, temperate and subtropical domains[1]. If we look at the distribution by countries then it can be seen that over half of the world's forests can be found in just five countries, Russia, Brazil, Canada, the United States of America and China.

Forests vary considerably across these climatic domains to take advantage of the environment they find themselves in, resulting in a myriad of different forest forms globally. These forms include but are not limited to tropical and temperate rainforests, coniferous, deciduous, mangrove, boreal, and montane forests, as well as savanna and tundra. Further adding to this diversity is the impact of natural and human disturbance which creates mosaics of different aged forests, secondary regrowth forest areas which were deforested and have recovering tree stocks, plantations, and managed forested areas.

1.3 Global Forest Status

Globally forests are experiencing a wide range of threats, from a multitude of different sources that have changed over time primarily as a consequence of the evolving nature of human development, in 2010 the world had 3.92 Gha of tree cover extending over 30% of total land area [18], as of 2022 we have lost a total of 22.8 Mha of tree cover[18]. We will focus primarily on tropical and temperate forests, as this thesis will focus on forests that fall under these domains.

1.3.1 Tropical Forest Status

Globally tropical forests represent about half of all forested areas ($\backsim$ 20 million km^2)[17]. Climatically they are defined by having year round high levels of rainfall, and stable temperatures[19]. Their status is dominated by unprecedented levels of loss and degradation[20], attributable to the interacting effects of a diverse set of threats. Global primary tropical forest loss over the period 2011-2021 averaged 3.8 million ha per year [18] (for comparison the total amount of woodland in March 2022 in the entirety of the United Kingdom (UK) was estimated to be 3.24 million ha[21]), with the highest loss in recorded history of 6.13 million ha occurring in 2016[18]. Over the 10 year period 2011-2021 this totals over 42 million ha of primary tropical being lost[22]. The rate of loss varies amongst countries containing tropical forest. Between 2010 and 2020 tropical forests in Africa have experienced the highest annual rate of net forest loss in, at 3.9 million ha, followed by South America, at 2.6 million ha[23].

To date approximately half of all potential tropical closed-canopy forest has already been removed[20], this dramatic loss has largely been driven by the processes of conversion into non-forest systems and further compounded by degradation of existing forests[24]. The conversion of primary forest into non-forest systems for agricultural purposes[25] has resulted in an estimated 100 million ha of tropical forests being converted between 1980 and 2012 commonly for soybean sand oil palm production[25, 26], the creation of cattle ranches[27], and for mining activities[28].

Forest degradation can occur in a range of circumstances, with and without deforestation subsequently occurring, for example, in the forest fragments that remain following deforestation [29], in areas made accessible through selective logging, or in forested areas which are located close to human settlements. The magnitude of area exposed to degradation is significant, in the Brazilian Amazon alone as a result of deforestation 20,000 km of new forest edge is created each year[30], and the area of forest in fragments of 100 km^2 or within 1 km of the nearest forest edge is greater than the area deforested[31].

1.3.2 Temperate Forest Status

Temperate forests are forested areas found in the temperate zones between 25° and 50° latitude, between the boreal and tropical zones[32]. They account for 10 million km^2 of global forested area[17]. The predominant climate of these forest regions is characterised by distinct cyclic, seasonal changes involving periods of growth and dormancy[33]. Temperate forests are often categorised into broadleaf (hardwood) dominated, conifer (softwood) dominated, or mixed forests highlighting their importance in timber production. These forests, more so perhaps than any other forested biome[33] are characterised by the extent to which human actions have shaped them, and the length of time over which this has been happening.

The extent to which human actions have shaped the current day distribution of temperate forests is demonstrated when looking at the distribution of old-growth temperate forests in the Eastern United States. Today it is estimated that less than 1% of the original forests cover remains today as old-growth forests[34] highlighting the widescale deforestation, as well as the subsequent regrowth that has occurred. In Europe, widespread anthropogenic alteration and the resulting ecological legacies can be traced back over 2000 years to the Roman occupation of central France[35]. Older still is the impact left on temperate forests of China, where evidence of extensive forest alteration dates back some 6000 years ago and indicates such a degree of disturbance that the roles of climate and anthropogenic disturbance are essentially confounded in understanding long-term patterns of change in vegetation[36].

When considering the balance between forest loss and gain, temperate forest systems are the only forested biome between 2000 and 2020 that demonstrated a net gain in forest cover[18]. However, this balance is potentially shifting with temperate forest in both Europe and Asia recording substantially lower rates of net gain in 2010–2020 compared to 2000–2010, and temperate forests in Oceania demonstrating net losses of forest area in the decades 1990–2000 and 2000–2010 [23].

Temperate forests have so far displayed a remarkable ability to recover following deforestation and degradation, with large swaths of forest that have been felled in recent centuries continuing to regrow vigorously, absorbing significant proportions of anthropogenic carbon dioxide emissions[37]. While historically the major threat to temperate forests has been anthropogenic deforestation, and land use change, there is increasing evidence the greatest threat facing temperate forests is increasing rising global temperatures which are contributing to increasingly severe droughts, and increased average temperatures[38]. These "hotter droughts"[39] have been shown to be the main driver of temperate forest morality over the past few decades[39].

Hotter droughts affect trees directly by increasing the atmosphere's evaporative demand for water[40], increasing tree water stress, which induces detrimental physiological effects on trees directly[41], and indirectly by reducing the amount of snow that falls and which as a source to replenish soil moisture[42]. In addition to these direct mechanisms, hotter droughts can indirectly make trees more vulnerable by increasing the frequency of novel insect and pathogen outbreaks[43].

In addition to driving mortality, hotter droughts are also interacting with a number of other stressors to alter fire regimes[44]. This is resulting in an increase in the frequency of uncharacteristically severe and large fires, and longer fire seasons in temperate forests globally[45].

1.4 The Importance of Temperate and Tropical Forests

Describing forest value and importance is difficult and is as much a political and philosophical exercise as it is a scientific one. The value of forests depends very much on the paradigm being employed to value them, and there are good arguments that say that given the critical role that forests play in sustaining life, they are by definition invaluable, and so any valuation can only serve to underestimate their true worth[2].

One of the most commonly used frameworks through which to view forest ecosystems more holistically is the “ecosystem services” framework. First proposed in the 1970’s[46] and subsequently becoming mainstreamed following its incorporation into the Millennium Ecosystem Assessment [2]. Under this paradigm forests are viewed as a collection of services that arise from the functioning of the ecosystem. Value is attributed to these services by the contribution that each of these services makes towards human well-being and linking these services to markets to achieve a financial valuation.

However, while partly successful in communicating the value of ecosystems to decision makers, a number of key criticisms of the ecosystem services paradigm exist. Many of these criticisms[47] focus on the fact that during the conceptualisation of the ecosystem services framework, and when it is applied to value an ecosystem, the information and paradigms used are dominated by knowledge from the natural sciences and economics. As the research and policies based on this framework have developed, they have tended to focus more narrowly on natural sciences and economics, and those services which are more easily amendable to valuation by these fields[7]. Over time this has resulted in a failure of the paradigm to communicate the full value of ecosystems to decision makers and to meaningfully engage perspectives from the social sciences, or those of local practitioners, including indigenous peoples, who have significant knowledge, insights and tools to understand the intricacies of human-nature relationships[48].

As an effort to address the criticisms of the ecosystem service framework, the Nature’s Contributions to People (NCP) paradigm[49] was developed by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES). Based on the ecosystem service framework nature’s contributions to people are all the contributions, both positive and negative, of living nature (diversity of organisms, ecosystems, and their associated ecological and evolutionary processes) to people’s quality of life[49].

The key differences between the NCP approach and the ecosystem services framework, is that the NCP paradigm focuses on recognising the central and pervasive role that culture plays in defining all links between people and nature[7]. The second key difference is that the NCP approach aims to elevate, emphasise, and operationalise the role of indigenous and local knowledge in understanding nature’s contribution to people[7].

Nature's contributions to peoples are grouped into three broad NCP groups, these being regulating, material and non material contributions[49]. Although these categories bear some resemblance to the ecosystem services broad groups of provisioning, regulating, support and cultural service, a key difference is that culture permeates through and across all three broad NCP groups rather than being confined to an isolated category[7]. In addition, the three broad groups are explicitly framed as overlapping rather than as independent compartments, as within the ecosystem services approach. An example of this is food, food is primarily a material NCP because calories and nutrients are essential for physical sustenance. However, food is full of symbolic meaning well beyond physical survival and indeed, non material and material contributions are often interlinked in most, if not all, cultural contexts[7].

Applying this paradigm to forests we can start to understand the substantial contribution that they make towards people. Material contributions of forests to people for instance include food, firewood, timber, medicine, tradable goods, plant fibres for the production of clothes, and animal fodder. The material contributions provided by forests are used globally, and it is estimated that 1.2 to 1.5 billion people directly rely on tropical forests for food, timber, and medicine[50]. Rural populations located geographically close to forested areas may have an even higher dependence of forest provisioning services. Kalaba et al. 2013[51] for instance found that forest provisioning services in Africa's Miombo woodlands provided 44% of average household income, and that for the poorer households the income from these provisioning services was the largest relative contribution.

Regulating contributions are often global at the scale at which they contribute towards humanity, the value of forest regulating contributions is extremely high and are often considered to be the most valuable set of contributions offered by forests[52]. Examples of forest regulating contributions include flood regulation, and the moderation of disturbances[52]. In addition to these forests play a critical in regulating global climate, via water transpiration, cloud formation, and atmospheric circulation[53, 54]. Forests also play an important role in water and carbon cycles, exchanging more water and carbon with the atmosphere than any other biome[53, 54], and storing upwards of 190 billion Mg of carbon above-ground[6].

Studies have shown that forests provide a number of non-material benefits. De Groot et al 2012[52] for instances estimated the contributions from forests in terms of aesthetics, recreation, inspiration for culture and art, spiritual and cognitive experience, to be twice the value of regulating contributions globally across temperate forests, and less than half the value of regulating contributions in tropical forests.

1.5 A Rationale to Study Forests

Forests are globally important, and are being exposed to a variety of interacting stressors which threaten them, and the diverse set of services and benefits that they provide humanity. A strong rationale exists to study these systems to better our understanding of the threats that face them, how they respond to these threats, and to allow us to prioritise conservation efforts.

There is considerable diversity in how forests respond to stress. Some forests when experiencing drought, for instance, show relatively little change, while others for a similar magnitude drought show dramatic responses in productivity, mortality, community composition or ecosystem service provision. Understanding why this difference exists, and how mechanistically it occurs will be one of the key themes of this thesis.

In this next section we will examine the language and methods around how stability is described, quantified, and analysed. Considerable diversity exists in the literature on the topic of stability, and so the following section will synthetize the literature in order to provide a single framework for use in this thesis to help understand what forest stability in the face of change means.

1.6 Forest Stability

The field of ecosystem stability straddles conceptual and applied ecology and is extensively discussed by both. This has resulted over time in a large amount of paradigms, concepts, components, and definitions for understanding what ecosystem stability is. The diversity in approaches and authors has resulted in concepts which overlap, labels and definitions being used to mean different things by different groups, and methodologies which are only applicable to some definitions of stability components.

From reviewing the literature, no definitive consensus exists that unifies the many definitions and paradigms into a single framework. Therefore, for this thesis the literature has been reviewed and a conceptual framework developed based on definitions that are discreet and non-overlapping in scope, quantifiable using the data that are available to us, and consistent with the broader literature on the topic.

Two key paradigms are used in this conceptual framework, the stability landscape[55], and the posing of stability in the format of “stability of what, to what”[56].

1.6.1 The Stability Landscape

The stability landscape is a multidimensional state space that represents all possible state variables (ecosystem descriptors e.g. percentage tree cover) for a particular ecosystem, and the potential energy that is required to move through the landscape[55]. Figure 1.1 shows a hypothetical stability landscape with two alternate stable states that demonstrates a number of the key features of stability landscapes. The stability landscape likens an ecosystem being perturbed to a ball moving through this landscape. When located in one of the wells, the ecosystem tends to move towards the bottom of the well by gravity (a proxy for the processes and mechanisms that an ecosystem that stabilise interactions within a community), when the force of attraction is greater than the force of the stressors on it. When forced by an external force the ball is moved in a certain direction, how far the ball moves depends on the steepness of the terrain it encounters which is defined as ecosystem resistance[57]. Steeper walls of the well mean higher resistance (when moving up them), and in real life represent ecosystems which change little when exposed to a stressor.

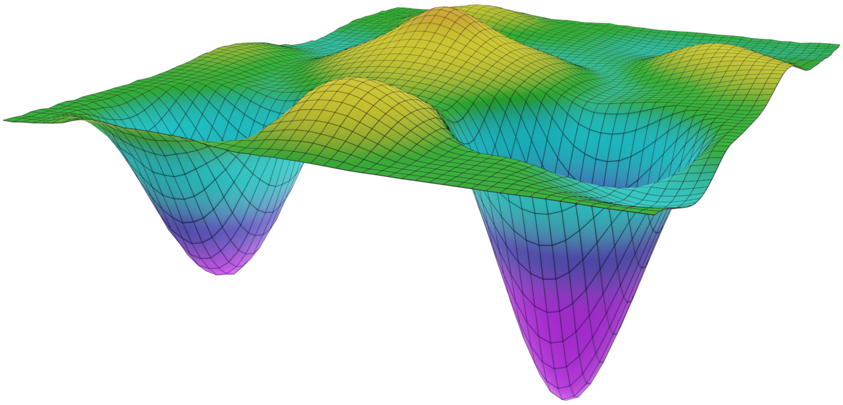

Figure 1.1: A Hypothetical landscape with two basins of attraction separated by a hill which must be overcome if the system is to change to a new basin of attraction

Another commonly defined component is ecosystem resilience[58]. Resilience is the rate, or by some definitions the extent[59], to which an ecosystem recovers to steady state following a perturbation. Within the landscape metaphor this is related to the steepness of the local terrain that the ecosystem finds itself following perturbation. Resilience can be independent of resistance as explained by this metaphor, as moving towards the bottom of the well is aided by gravity, rather than hindered by it, if the ecosystem is moving up the well. This type of stability is commonly referred to in the literature as engineering resilience, however, the literature also uses term “ecological resilience” to refer to another aspect of stability. To prevent confusion between these two elements in this thesis engineering resilience will be termed resilience, and ecological resilience will be termed latitude following the naming convention of Walker et al (2004)[55].

Ecosystem latitude, commonly referred to in the literature as ecological resilience, in this paradigm is the width of the well that each ecosystem is currently in. Higher latitude means a wider well and thus a wider range of state space that if an ecosystem is moved to by external stressor, will still be influenced primarily by the same attractor, and thus will tend to the same state it was before perturbation[60, 55].

How close the ecosystem currently is to the lip of the well is defined as the ecosystems precariousness[55], with a system that is closer to the edge needing less of a push by external stressors to end up in the well of attraction of a different ecosystem state and thus resulting in phase shift or state change, this element is also referred to in the literature as a tipping, or bifurcation point[61].

The landscape itself is not constant over time, and the potential energy required to move through the landscape at any point is only constant if all possible biotic and abiotic features and their relationship with the potential energy required to move through landscape remain constant, which is unlikely to happen for any length of time in reality given that ecosystems are constantly changing, and stressors such as climate change are altering these fundamental relationships.

In summary, the landscape stability paradigm gives us an easy way to conceptualise, delineate and define four components of ecosystem stability, resistance, resilience, latitude, and precariousness. Taking this discussion into consideration, the definitions for each of these components for the purposes of this thesis will be:

- Resistance

  - The ability of an ecosystem to withstand perturbations and remain unchanged.
- Resilience
  - The ability of an ecosystem to return to pre-perturbation levels following a perturbation.
- Latitude
  - The maximum perturbation that the ecosystem can take and still remain as the same ecosystem.
- Precariousness
  - How close is the ecosystem currently to changing to a different system.

1.6.2 Stability of What, to What?

The stability landscape paradigm can provide conceptual definitions of the subcomponents of stability, but not quantifiable metrics that we can use to actually make inferences about the stability of a particular system. In order to do that, we need the specific context of the system[62], and the source of perturbation[56]. Carpenter et al (2001)[56] used the phrase "resilience of what, to what", and this applies more generally to stability as well. By specifically referencing the system and the source of perturbation that we are interested in, we are able to design metrics that provide us information about the stability of the system, and then make wider inferences about properties that in turn influence this stability. To this end, each chapter of these thesis will investigate one of these components of stability, and the variables that influence this stability in relation to a particular source of perturbation.

1.6.3 Press and Pulse Perturbations

Press, and pulse perturbations are different ways in ways an external force may act upon an ecosystem, with the key difference being the temporal span over which they act. Pulse disturbances are discretec usually relatively short lived events, while press disturbances act continuously over a long period of time[63]. In terms of the stability landscape paradigm, pulse events can be considered ones that displace the ecosystem from its current location as a one-off event, while a press event is one that acts to move the ecosystem in certain direction continuously over time.

1.6.4 Quantifying Stability of Forests

A range of different methodologies have been used in the literature to measure stability and its components, this section aims to give an overview of some of the key methodologies used in the literature in order to give context to the methods used in this thesis. The aspect of stability that each of these methodologies measures has been harmonised with the conceptual framework used described previously to describe stability.

Resistance

The most common methodology employed to quantify resistance is through comparing ecosystem descriptors during, or immediately following a pulse perturbation such as a short lived drought, to the baseline value for this descriptor. Although in theory any descriptor of an ecosystem could be used to quantify resistance, overwhelmingly productivity[64, 65, 66, 59] is used to do so. Productivity makes for an ideal metric when investigating ecosystem stability due to it being influenced by both changes in abundance, and condition of the individuals within the ecosystem. A significant change in productivity therefore is a holistic indicator for the status of the ecosystem more generally. Although less common other ecosystem properties used in the literature include canopy water content[67], daily latent energy exchange[68], and ecosystem services[69].

In the baseline method a long-term average for the ecosystem descriptor is calculated and the difference between this and the value of the ecosystem descriptor during, or immediately after a pulse disturbance is calculated, this value is often normalised through the calculation of anomalies, to allow comparison between different areas. Lower differences between baseline and during/after perturbation are inferred to mean high resistance of the trait in question, to the perturbation being measured and vice versa for higher differences.

All the methods for measuring resistance so far have used discrete pulse events to study resistance of the system to that perturbation. By way of contrast Keersmaecker et al. (2015)[70] and Anderegg et al (2018)[68] used a time series approach to infer resistance. Keersmaecker et al. (2015)[70] used a time series of Normalised Difference Vegetation Index (NDVI) anomalies and model this time series as a function of a measure of instantaneous drought, temperature anomalies and the previous time NDVI anomaly in a autoregressive model. Resistance was then inferred from the magnitude of the beta coefficient with more resistant systems have a smaller beta coefficient[70]. Anderegg et al

(2018)[68] used a time series of daily latent energy exchange as a proxy for evapotranspiration, itself a proxy for productivity and modelled this against vapour pressure deficit, and soil moisture. The beta coefficients for each of these terms was then used to infer resistance, again through evaluation of the coefficient magnitude.

Resilience

In the literature resilience is most commonly defined as either the extent[59], or the rate[70] at which ecosystems return to baseline conditions following perturbation. Of the papers reviewed, the most common methodology was to compare an ecosystem metric to pre-perturbation levels some time following the end of a pulse perturbation and calculate the difference[65, 66, 59]. Highly resilient systems were those with a smaller difference, indicating the system had recovered quickly. In some cases rather than setting an arbitrary timescale to measure recover, the amount of time taken for a particular ecosystem descriptor to return to, or close to, pre-perturbation levels was used as the metric for resilience. More resilient systems being those that take a shorter amount of time to return to, or close to pre-perturbation levels[69].

The final class of methodology to measure resilience from the literature were those that used autoregressive models to model time series of ecosystem descriptors before, during and after a pulse perturbation[70, 71]. Keersmaecker et al (2015)[70] for instance modelled NDVI anomaly as a function of drought and temperature anomalies, as well as a past NDVI anomalies, using an ARX model. In this framework, the coefficient of the past NDVI anomalies within the model is a measure of resilience as it represents how similar current NDVI anomalies are to past ones. A large absolute value of this coefficient indicates a slow return to equilibrium with values being similar to past NDVI values for a long length of time, and thus being associated with a low resilience.

Latitude

Latitude is studied relatively rarely compared to resilience[72] due to a combination of confusion in the literature over what the components of stability are, and the relative ease in which other stability metrics can be calculated. Two broad categories of methodology exist to measure latitude, those that attempt to approximate ecological systems with a low dimensional model parameterised so that quantitatively it matches the empirical system and then infer latitude and other stability metrics from this model, and those that estimate latitude directly from the data[72].

In the first method, low dimensional models are used and parameterised to match an empirical study system, this is usually only possible when examining one-dimensional systems[72]. Although in some circumstances it may be possible to approximate potential functions[73]. With an appropriately parameterised model it is then possible to quantify not just latitude, but a ranger of stability metrics including the size of the basin of attraction[74], and precariousness[75]. In the second methodology, where it is not possible to generate such a model, a probabilistic stability landscape can be reconstructed from observations of the system, assuming that when sampling spatially the system we are observing has “visited” most parts of the stability landscape. Hirota et al (2011)[76] used this methodology to estimate latitude by examining how percentage tree cover varied spatially with precipitation. They found that tropical forest, savanna, and tree-less states existed within discrete precipitation thresholds. This allowed them to calculate probability distributions for each of the states, and using these distributions and a space for time substitution they were able to estimate the latitude for each of the tree systems.

Precariousness

Precariousness is more commonly quantified than latitude, but less frequently than resistance and resilience. Examination of the literature showedd that a variety of methods exist to quantify this component of stability. The most commonly employed methodology is the use of various metrics to identify critical slowing down in the functioning of key ecosystem processes. Critical slowing down has its caveats[77], but can be considered to be an indicator of when an ecosystem is approaching a bifurcation between two or more stable states. The theory behind critical slowing down postulates that as an ecosystem approaches the point where it will be attracted to a different stable state within the stability landscape (and thus start to change into a different configuration), the interactions and self-reinforcing processes within the system that have kept maintained it in its current form break down. As a result of this it takes the system longer to recover from any small perturbation that may occur[78].

This critical slowing down can be identified in a number of ways such as detecting increasing amounts of autocorrelation in an ecosystem descriptor[79], or increased variance in the ecosystem descriptor[79]. For example, Dakos et al. (2012)[79] test the hypotheses that as a system gets closer to a critical transition, or the lip of its current basin of attraction, as a result of the breakdown of internal processes, it may lose resilience, and may experience increased variation. Using biomass as a measure of ecosystem state, they test two different variables for detecting ecosystems close to critical transitions, the robustness of variance, and critical slowing down. Robustness of variance hypothesises that close to critical transitions ecosystems become less able to maintain themselves, and so one might expect to see increased variability in ecosystem descriptors as you get closer. Using this experimental setup Dakos et al. (2012)[79] find that this isn't a good indicator of critical transitions, with several transitions occurring without a subsequent increase in variance occurring. However, the degree of auto-correlation was found to be a reliable indicator of a critical transition. With systems close to a critical transition exhibiting increased auto-correlation in ecosystem variables due to a decreased ability to recover. Thus, this study highlights that studying auto-correlation can be used to infer information regarding not only resilience but also proximity to the edge of the basin of attraction, here defined as its precariousness.

A Gap Identified - Measuring Stability

Generally forest stability in the literature has been studied at small spatial scales, with relatively few studies looking at landscape scales. While understanding what drives forest stability locally is certainly important, it is also important to understand landscape scale patterns, to better understand more generally what drives forest stability. Scaling up local findings to landscape scale processes is difficult, and in many cases not reliable as it's likely that the factors moderating stability at a landscape scale are different to those moderating stability at small spatial scales[80]. To this end, it was decided that in this thesis the factors and processes that influence forest stability at landscape scales would be explicitly examined in order to better our understanding of the large scale processes that moderate forest stability.

1.6.5 What Controls Stability?

When studying ecological systems, we are often interested not just in quantifying an ecosystems stability and how it is changing over time, but to also understand what processes, and variables influence this stability. This next section will focus on summarising the literature on this topic, and to identify gaps that this thesis will aim to contribute to filling. Although this thesis will ultimately focus on stability in forests, this section will examine stability more widely across a variety of ecosystem types and settings.

The role that ecosystem complexity plays in moderating ecosystem stability, is a topic widely and extensively discussed in the literature. Early work to develop this paradigm was based on observations that population density patterns within cultivated land with simplified terrestrial communities tended to exhibit more violent population density fluctuations than more diverse communities as a result of drivers of change such as invasive species which regularly, and significantly impact cultivated human systems, but which are only rarely observed in natural diverse systems[81, 82, 83].

Seminal work by Tilmand & Downing (1994)[84] contributed to this discussion by demonstrating in an experimental setting that primary productivity in more diverse grassland communities was more resistant to, and recovers more fully from, a drought compared to less diverse plots[84]. However, subsequent experimental tests[85, 86, 87, 66] have produced both confirmatory and contradictory results to this work. A review by Isbell et al (2015)[65] of 46 different experiments came to the conclusion that higher biodiversity increased ecosystem resistance to a broad range of climate perturbations including, wet or dry, moderate or extreme, and brief or prolonged events[65]. However, this effect was restricted to just the resistance of the system, as a year after the climate event, ecosystem productivity in both low and high diversity systems had often fully recovered or overshoot baseline productivity[65].

A wide range of mechanisms have been proposed in the literature to explain the underlying processes and interactions that results in the observed relationship between diversity and stability. These explanations generally fall into three broad groups[88] these being, asynchrony of species intrinsic responses to perturbation, differences in the speed at which species respond to perturbations, and a reduction in the strength of competition[88].

Asynchrony of species intrinsic responses to perturbation may arise as the more species in the ecosystem, the more likely it is that there is a species that may respond favourably to any perturbation that occurs, ultimately yielding more stable aggregate ecosystem properties[89] being associated with higher diversity. Variance in the speed at which species respond to perturbation, whereby diversity in the rate at which species respond to perturbation means that the ecosystem aggregate for the ecosystem function in question tends to be more buffered over time, as the ones that initially do badly, recover quicker and maintain the average as the ones that take longer to respond are then effected[90].

Asynchrony in species identity and responses to perturbation is more generally referred to in the literature as the “insurance hypothesis”. The insurance hypothesis postulates that higher biodiversity insures ecosystems against declines in their functioning because many species provide greater guarantee that some will maintain functioning even if others fail[91]. Studies examining disturbance in forests and grasslands have found that asynchrony across species[92], much more than species diversity alone, was the main driver of variation in stability across sites.

Several studies have taken identified specific species and ecosystem composition more generally as also being important when seeking to understand variance in stability at an ecosystem level to climate events. For instance, tree size distribution, stand density and species composition were all found to be important in explaining variation in productivity in mixed fir-spruce forests in Germany, when exposed to moderate droughts[93]. In these cases fir species were found to be significantly more resistant than spruce species and larger trees were more resilient than smaller ones (although under severe drought they did the worst). It makes sense given adaptive evolution that the presence or absence of certain species will impact on stability of the system. What is less certain is how these species interact with each other, and how these species will respond to a changing climate.

There is a growing consensus, that it may be functional diversity, or the value and range of species traits, rather than the number or composition of species, which most strongly determines ecosystem functioning and stability[94].

The study of how functional diversity influences stability is a relatively new area of research comprising significantly less literature than that of species richness. Anderegg et al. (2018)[68], investigated how functional diversity influenced ecosystem resilience during drought. They found that resistance is controlled in part by the hydraulic diversity of the plots, with sites with higher diversity in hydraulic traits being better able to buffer their hydraulic fluxes when experiencing a drought. In this case, functional traits were better able to explain observed variation in response offer compared to species diversity alone. Experimental studies by Chillo, Anand, and Ojeda (2011)[95] and Hallett, Stein, and Suding (2017)[96] both found in their experimental manipulation of functional diversity within arid rangelands, and grasslands respectively that functional diversity was key to understanding resilience patterns for productivity. Functional diversity has been shown to be important in supporting not just productivity but a range of ecological functions in the face of perturbation. Valencia et al., 2015[97] for instance, found that the ability of an ecosystem to sustain multiple functions in the face of increasing aridity and shrub encroachment was positively related to a communities functional diversity and community-weighted mean trait value.

The extent to which diversity either in terms of species, or functional trait diversity controls the stability of ecosystems is the focus of debate (Species traits and species diversity affect community stability in a multiple stressor framework). However, it is generally accepted that the loss of a single species, or functional group can have a significant impact on ecosystem functions[98]. How large the impact that the loss of any particular species or functional group may have depends in part on the degree of redundancy present in the ecosystem, with ecosystems with a higher level of redundancy in theory being better able to recover from the loss of any particular species or functional group[99].

Fonseca et al (2001)[100] examined functional redundancy from a theoretical standing and concluded that the probability of whole functional groups going extinct from a community increases with the number of recognised functional groups (functional richness), but decreases with species richness and functional evenness. They applied this framework to a South American plant community which suggested that as assuming local extinction is random, 75% of the species could be lost before the disappearance of the first functional group occurred. Current extinction risk however is not phylogenetically random[101], and so this result must be interpreted with caution.

Looking specifically at a tropical forest setting, Zhang and Zang (2021)[99], examined redundancy of ecological processes, and vulnerability per se in Chinese tropical forests. Their results indicated that species-rich tropical forest types tended to have more functional redundancy than species-poor ones, suggesting that richer communities would be less sensitive to species loss. However, when examining the evenness of how ecosystem processes were spread across species, they found that combinations of processes were packed into just a few functional entities (combinations of ecosystem system functions/processes provides[102]) rather than being more evenly spread amongst species. This meant that many ecosystem service processes relied on a small number, or even a single species, making the ecosystem as a whole vulnerable to the potential loss of even a small number of species. This ultimately, they concluded meant that functional redundancy due to high species richness did not outweigh the vulnerability of ecological processes more generally in the tropical forests they examined.

The relationship between redundancy and ecosystem stability while theoretically sound, is complicated in reality. For example, the relationship between plant community resilience to an intense fire was tested experimentally in a semiarid shrubland setting by Lipoma et al (2016)[103]. In this case variation in redundancy in terms of species, and functional group was found to have no significant explanatory power in explaining the observed variation in ecosystem resilience to the fire, and instead the resource use strategies, and the presence of regeneration traits appeared to best explain the observed response to the fire.

Looking more broadly, a recent metaanalysis[104] looked across a wide range of ecosystem types, and biomes to understand redundancy more generally. They found across all biomes, and ecosystem types that a positive relationship exists between functional diversity and stability, indicating that systems with higher functional diversity tended to be more stable when undergoing perturbation, this relationship was strongest for studies in which redundancy was measured as species richness within a functional group.

In addition to the role that functional diversity plays in moderating forest stability to climate perturbation, recent work has shown that functional traits themselves can be powerful explanatory variables. Functional traits are particularly powerful when used as explanatory variables as they able to not only explain variation in stability to perturbation, but also provide insights into the mechanism that underpins the stability through their physiological nature.

Tree size for instance has been found to explain drought induced mortality with larger trees generally be more at risk than smaller ones [105], the physiological explanation for this has been suggested to be that taller trees have to lift water to a greater height against the effects of gravity and path length-associated resistance, and therefore face greater hydraulic challenges [105], therefore when experiencing drought with associated increases leaf-to-air vapour pressure deficits larger trees have a higher risk of hydraulic cavitation and subsequent damage[105].

In addition to tree height, Greenwood et al (2017)[106] found that tree species with denser wood and lower specific leaf area, accounting for variance in drought strength and other confounding variables showed lower mortality responses to drought. Wood density has been found at a global scale to negatively correlate with mortality[107], with greater wood density being associated with higher mechanical strength[108] which may confer enhanced xylem resistance to embolism[109].

Other functional traits that have been found in the literature to be potentially important in understanding forest response to climate perturbation include, leaf traits and anatomy[110], leaf chemistry[111], and life strategy[112].

Beyond mortality, hydraulic traits that describe the ability of trees to prevent embolism of xylem vessels, and the proximity with which they operate to critical embolism thresholds (hydraulic safety margins) have been found by Tavares et al. (2023)[113] to the only significant explanatory variable of observed decadal-scale changes in forest biomass. Old-growth forests with wide hydraulic safety margins were found to be gaining more biomass than forests with smaller hydraulic safety margins. Tavares et al. postulate that that this may be associated with a growth–mortality trade-off whereby trees in forests consisting of fast-growing species take greater hydraulic risks and face greater mortality risk[113].

Functional traits have also been shown in the literature to be important in understanding how forests may respond to climate change. Trugman et al. (2020) for instance found evidence for shifts in community composition toward communities with more drought-tolerant traits driven by tree mortality[114]. Tavares et al. (2023)[113] also found a climate change signature with areas of Amazonia that were experiencing more pronounced climatic change, are losing biomass, suggesting that species in these regions may be operating beyond their hydraulic safety limits. Continued climate change is likely to further reduce hydraulic safety margins in the Amazon, with strong implications for the Amazon carbon sink[113].

A Gap Identified – Disentangling climate, biodiversity influences on moderating response

Reviewing the literature highlighted that the variation in response to perturbation is a culmination of many different interacting variables including, the magnitude of the perturbation, climate effects, as well as community, functional trait, and biodiversity composition. However, the independent effect, and the relative importance, of these different groups of variables was often not formally quantified, making interpretation of what actually explains the variation in stability difficult to understand and extrapolate to larger scales. To this end it was decided that in developing specific research questions for this thesis, methods would specifically be designed in order to disentangle the relative impact of these various groups of explanatory variables.

A Gap Identified – At Landscape Scales What Variables Moderate Long-Term Productivity and Short Term Response to Perturbation

This literature review has highlighted that at a landscape scale considerable uncertainty exists in understanding what moderates forest productivity, both in terms of the long term patterns, as well as in response to short term perturbations. To contribute towards filling gap in knowledge, this thesis has focused on understanding not just how stability varies spatially, but also what variables explain this spatial variation.

1.7 The Data Required to Investigate Forest Stability

To investigate forest stability and understand the observed variation in forest response to perturbation a number of different datasets are required. These datasets together need to describe forest response to perturbation, the magnitude, duration and characteristics of any perturbation that occurs, as well as forest biophysical and any other variables that may help explain the observed variance in forests response when we look over time or space.

Ground surveys are often considered the gold standard in terms of the quality of data that they can provide, and the more direct link that they have with the target variable of interest. However, they come with the limitation that they are time consuming, expensive and limited in terms of their temporal and spatial coverage. A further major limitation when looking at forest response to perturbation is the limited number of ground surveys that can be realistically conducted, across the required gradient of forest types following a major perturbation. This ultimately reduces the ability to generalise widely from ground surveyed datasets when examining such perturbations. Satellite remote sensing offers a solution to this by allowing larger spatial extents, to be monitored at much finer temporal resolutions than could reasonably be achieved by ground surveys, but with the caveat that forests responses are not directly being measured, but instead inferred from spectral signatures and patterns.

A range of different satellites, and satellite products exist, and so the following section will give a brief overview of some of the most common satellites sensors, and products used to study forest stability, along with an assessment of their major advantages and disadvantages, only satellites which are active as of 2022 will be covered.

1.7.1 Passive Remote Sensing Sources

Passive remote sensing is the study of light from the Sun after it has been reflected off Earth surface features such as forest, bare ground, water, etc. The light incident on such Earth surface features has its characteristics changed through interaction with the feature. Some frequencies are absorbed to varying degrees, while others are not, resulting in different features having unique spectral signatures [115]. This reflected light is then detected by a remote sensing platform, and the spectral reflectance intensities are examined to infer properties about the Earth surface features viewed. For instance, a healthy forest may strongly absorb red and blue to power photosynthesis, but when damaged by drought, more strongly reflects these colours as the chlorophyll that normally absorbs are less able to do so due to drought induced damage. Therefore, by examining the change in amount of red and blue light reflected for that forest over time, one is able to infer information regarding the level of photosynthetic activity and how drought effects those forests.

Table 1.4). compares a number of satellites commonly used in the literature in the study of forest stability. They vary significantly in terms of their temporal, and spatial resolution as well as the number of spectral bands they provide. There is no satellite which can demonstrated as being quantifiable the best, and the best satellite to use usually depends on what the research question is. Sentinel 2 for instance, offers the highest spatial resolution at 20m, but only has data available since 2017 which makes it less suitable for analyses which require enough data to calculate background averages. MODIS has a longer time series available, and a better temporal resolution, making it better in cloudy locations as cloud free imagery is more likely to be captured, but has a spatial resolution 250m which may be too coarse for many studies. Landsat arguably offers the best compromise, consisting of a series of missions that have been running since 1982 providing a long time series for analysis, a high spatial resolution, but a lower temporal resolution, and fewer bands for analysis, additional processing is also required to harmonise the data collected from different sensor systems in the series due to minor changes in bands collected.

Table 1.4: Comparing the characteristics of a number of the most commonly used passively sensing satellites

Name	Spatial/Temporal Resolution	Bands (band coverage)	Data Coverage
Sentinel 2[116]	20m/ 5 days	13	2017 - ongoing
MODIS[117]	250 – 1000m/ 2 days	36	2000 - ongoing
Landsat 4,5,7,8[118]	30 – 100m/ 8 days	11	1982 – ongoing (harmonisation of data from Landsat 4,5,7,8 required)
GOME 2[119]	40 x 80km/ 3 days	15 (atmospheric composition)	2007 - ongoing
OCO 2[120]	1.29 x 2.25km/ 16 days	3 (atmospheric composition)	2014 - ongoing

Data from sentinel 2, MODIS and the Landsat series are used in a variety of ways to monitor forest extent and status, one of the most common ways is to calculate indices by combining information from multiple spectral bands. Normalised Difference Vegetation Index (NDVI) is one such example, and has been found to provide information relating to forest extent (An assessment of commonly employed satellite-based remote sensors for mapping mangrove species in Mexico using an NDVI-based classification scheme), deforestation and forest vitality[121], vegetation classification[122], and canopy water content[123] to give just a few examples.

In addition to tracking forest status, some studies have sought to model functional traits including leaf chemical traits[124], and photosynthetic traits such as leaf area index[125, 126] although it should be noted that this difficult as the relationship between spectral reflectance values and functional traits are highly context dependent and may not be directly transferable between regions[127].

GOME2 and OCO2 have been included in this table, as even though they were primarily designed to monitor atmospheric composition it has recently been reported that it is possible to measure Solar Induced Fluorescence, a proxy of photosynthesis, and in turn make inferences about Gross Primary Productivity (GPP) from the data collected by these satellites ([128]).

1.7.2 Active Remote Sensing Sources

Active remote sensing systems in contrast to passive systems actively transmit electromagnetic radiation at the Earths surface, and then record the portion of this energy that returns to the satellite. A number of different types of active remote sensing exist including radar, Lidar, laser altimetry, sounding and backscatter[129], and have a wide range of applications in the study of forests, and forest status. One of the major advantages of active remote sensing systems is that they typically use longer wavelengths, and these longer wavelengths are less affected by cloud cover and other such climatic interference. Also, because they are not dependent on light from the Sun, and therefore can make measurements at night.

Active remote sensing differs primarily from passive remote sensing in the type of information that it can provide. The range of wavelengths used is typically much longer than that sensed in passive systems, these longer wavelengths tend to penetrate forest canopy cover to varying amounts and interact with the below canopy environment by being partially absorbed, backscattered and reflected off the ground and tree trunks. Active systems are therefore able to provide information on the structural composition of different parts of the subcanopy, while passive systems provide information on the canopy itself. As the wavelength of electromagnetic radiation can be controlled in this type of remote sensing, different components of forests can be targeted. Longer wavelengths for instance are better able to penetrate forest canopy and so their use provides information on the sub canopy structure, density and composition. One of the most common applications of active remote sensing is biomass estimations. Synthetic Aperture Radar (SAR), LiDAR, and optical imagery for instance were utilised by Shao et al (2017)[130] to provide information on canopy and below canopy structure in order to improve above ground biomass estimations compared to optical estimations of the same areas. The ability of active remote sensing methods to return information on the below canopy composition allows the impact of insect disturbance to examined[131], impacts which optical sensors may only detect at a much later date due to tree mortality.

A number of studies have used active remote sensing to monitor forest status and to identify deforestation, delineate forest area, and to detect deforestation events[132] taking advantage of the higher temporal coverage that active remote sensing can offer because of reduced interference from cloud cover. The ability to penetrate atmospheric effects has provided very useful in the study and tracking the progression of wildfires whose smoke can blind passive remote sensing[133].

The disadvantages of active remote sensing sources, is that they often require significantly greater investment in terms of equipment, processing of the data, and interpretation relative to passive systems data. Topography for instance can have a significant impact on reflectance values[134], and so topographic effects often have to first be accounted for before analysis. Other known limitations include, difficulties in making temporal composites to fill gaps[134], relatively limited area coverage, and the lack of a global level coherent datasets for many actively sensed products[134].

1.8 Aims and Research Questions

The primary aim of this thesis was to develop a deeper understanding of the underlying variables and processes that influence variation in forest ecosystem services stability. Upon reviewing the literature, and identifying gaps, this because focused specifically on productivity, and stability of productivity, to climate, and climate perturbations. A particular focus has been put on identifying mechanistic understandings of processes, and to specifically examine the role biodiversity and functional trait diversity play in moderating these relationships.

1.8.1 Overarching Research Questions

The literature review conducted identified a number of gaps in the literature. The following section details the overarching research questions that we developed based on the gaps previously identified in the literature, and how they relate to the specific research questions and case studies that we then created to answer them.

1. **How can we measure forest stability across large spatial extents to understand landscape scale stability?**

The first gap identified in the literature was that forest stability in the literature has generally been studied at small spatial scales, with relatively few studies looking at landscape scales. While understanding what drives forest stability locally is certainly important, it is also important to understand landscape scale patterns, to better understand more generally what drives forest stability as this is the foundation on which local stability will then build on. Scaling up local findings to landscape scale processes is difficult, and in many cases not reliable as it's likely that the factors moderating stability at a landscape scale are different to those moderating stability at small spatial scales[80]. Therefore, there is a need to develop methods to study stability directly at landscape scales.

Measuring stability in the conceptual framework laid out previously requires that we clearly identify, and quantify, both the aspect of an ecosystem, and the perturbation of interest[56]. As we plan to look across a range of different spatial and temporal scales, this will necessitate that we develop a different methodology for each case study dependent on the perturbation being studied, and the data available to describe the status of the ecosystem.

Three different methods will be tested to see to explore how well they are able to quantify landscape scale stability. In the first data chapter we intend to examine productivity, as proxied by remotely sensed solar induced fluorescence, and see how it responded during 2015/16 El Nino-Southern Oscillation (ENSO). This method will be based around calculating anomalies for productivity and climate, and modelling how well the magnitude of the ENSO explains the observed patterns in productivity anomalies.

In the second data chapter, instead of a single perturbation we will instead seek to instead capture average productivity responses to a range of different magnitude perturbations using UK forests as a case study, we aim to achieve this by modelling NDVI for each series over time as a function of climate, and then extracting model parameters to summarise the relationship and examine how it varies spatially.

Finally in the third and final data chapter we will use a pan-Amazon network of forest inventory plots to calculate above ground woody productivity. Using this time series of productivity data we will then calculate long term average, and trends in productivity, as well as examining the percentage change in productivity before and after the 2015/2016 ENSO.

2. **At a landscape scale can we disentangle climate, biodiversity, and functional trait influences on moderating productivity?**

The second gap identified was that reviewing the literature highlighted the independent effect, and the relative importance, of the magnitude of the disturbance itself, climate effects, as well as community, functional trait, and biodiversity composition, were often not formally quantified, making interpretation of what actually explains the variation in stability difficult to understand and extrapolate to larger scales.

To explore the relative importance and independent effect of each of these different groups of variables, we will use auxiliary dataset containing information on long term background climate, soils, species lists, and functional traits datasets in order to see to what extent they can explain the spatial patterns that we see in productivity stability to climate perturbation.

In all chapters this will be done through statistical modelling, and partitioning variance through a variety of methods. In the first and third chapters we will test an all-in-one approach on a remote sensing, and ground collected data set. In both cases the productivity response that we see, or the long term average/trend in productivity we observe will be modelled as a function of magnitude of the perturbation, background climate, functional trait and soils information to allow their relative importance, and the direction of the relationship with productivity response to be quantified.

In the second data chapter we will trial a two stage modelling approach. In this approach, we will first model NDVI over time as a function of temperature and precipitation for each forested pixel. From each model, we then plan to extract the coefficients and variance explained as measures of stability. We will then model stability over space using background climate, forest attributes, soils and other variables using a Random Forest methodology to examine relative importance through perturbation testing, and the plotting of accumulated local effects plots to aid interpretation.

3. **At the landscape scale, what factors are responsible for moderating long-term productivity, and short term response to climate anomalies?**

The final gap identified was that at a landscape scale considerable uncertainty exists in understanding what moderates forest productivity, both in terms of the long term patterns, as well as in response to short term perturbations.

All the three data chapters, will evaluate a range of potential explanatory variables including background climate, community biodiversity and functional trait composition, soil, topographic variables and forest attributes. This final question will therefore be answered by looking across all three cases studies to understand in each case study what the key factors in moderating productivity are, and comparing whether the controls of long term productivity patterns are different to those that control the response to short-term perturbation.

1.8.2 Chapter Outline

Three cases studies have been scoped in order to provide the required information to answer these overarching question. Each case study will form the basis of one of the three analytical data chapters of this thesis, and an overview of each of these chapters is provided below:

1. In the first data chapter I will quantify the response of Amazonian rainforest productivity to the 2015/2016 ENSO event and compare the relative explanatory power of climate, biodiversity proxies and soils variables
2. In the second data chapter I will quantify UK forests sensitivity to drought using climate using a time series approach, and compare the relative explanatory power of biodiversity information on community composition, and soils information.
3. In the third data chapter I will quantify mean productivity, and trend in productivity across Amazon forest using a database of forest plots, and compare the relative explanatory power of functional trait, and climate information.

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Chapter Two

Background climate conditions regulated the photosynthetic response of Amazon forests to the 2015/2016 El Nino Southern Oscillation event

2.1 Abstract

Amazon forests have been subjected to multiple large-scale droughts in recent decades which have increased tree mortality and reduced carbon sequestration. However, the extent to which drought sensitivity varies across Amazonian forests and its key controls remain poorly quantified. Here we sought to understand the response of Amazon forest photosynthetic activity to the 2015-2016 El Nino-Southern Oscillation (ENSO) by evaluating how the magnitude of ENSO-associated climate anomalies, background climate and soil characteristics influenced basin-wide differences in Solar Induced Fluorescence (SIF) anomalies. Our model explains 25% of SIF anomaly variation, and indicates that climate and soil conditions are more important controls than the climatic anomalies experienced. Our results reveal marked sensitivity differences across Amazonia, with North-Western forests being the most sensitive to precipitation anomalies. These differences in sensitivity likely relate to variation in community species composition, and water stress pre-adaption,

and need to be accounted for in climate change impact simulations.

2.2 Introduction

The tropical forests of Amazonia provide extensive ecosystem services both locally and globally[1] including unparalleled biodiversity provision[2, 3], regulation of regional climate[4] and substantial carbon storage[5]. The high and multidimensional nature of their value means that it is critical to better understand their ability to resist stressors and maintain the provision of these services. Extreme climatic anomalies are a major threat to the services provided by Amazon forests. In recent decades, Amazon forests have been exposed to a number of large climatic anomalies including in 2005[6], 2010[7], and 2015/16[8]. These droughts have resulted in losses of aboveground biomass due to widespread tree mortality[9, 7] and decreased Gross Primary Productivity (GPP)[10].

Previous assessments of Amazonian droughts based on forest inventory plots have sought to quantify the impact on the basin-wide carbon sink[11, 7, 12] but have not explicitly addressed the extent to which Amazon forests differ in their response to such climatic anomalies at sub-basin scales. The variance in response may be substantial as plot scale studies of plant hydraulic properties suggest that forest sensitivity to water stress can vary greatly even at a local level[13, 14]. However, scaling up plot based responses to climatic anomalies in order to explore the implications across larger scales in Amazonia is difficult, because of the limited number of sampling sites that can be realistically be measured following an extreme climate anomaly.

Remotely sensed data allows for variation in the sensitivity of forest productivity to climatic anomalies to be more fully explored across space with the caveat that photosynthesis is not directly being measured, but instead inferred from spectral signatures. Remote sensing of SIF is a particularly powerful proxy of forest productivity and has been shown to strongly track GPP at seasonal timescales, including in tropical forests[10, 15]. SIF has been used previously to evaluate the effects of several large climatic anomalies, including the impacts of the 2015/2016 ENSO on tropical forests[16, 10, 17]. Although these studies have highlighted the widespread negative SIF anomalies associated with the ENSO event across Amazonia, they involved no formal pixel-level analysis of SIF anomalies across space.

The response of forest productivity to extreme climatic anomalies is moderated by a wide range of factors which can be broadly classified into three groups: (i) the intensity of the climate anomaly itself, (ii) the background (long-term mean) climatology and (iii) soil characteristics. Forest plot studies have highlighted significant relationships between drought intensity based on precipitation anomalies and biomass losses following large drought events[9, 12]. Temperature anomalies have the potential to amplify these effects[18]. Background climate and soil characteristics can substantially modulate the impacts of anomalous climatic events. Forest sensitivity to water stress may be related to background climate as forests found in drier regions have been shown to be better adapted hydraulically to drought than those found in wetter environments[19]. Mean annual precipitation varies widely across Amazonian forests, as does the seasonality and interannual variability in rainfall, greatly affecting species composition[20] and forest resilience to drought[17]. Soil properties can further strongly modulate responses to drought events[21]. Soil texture exerts a strong control on water holding capacity and hydraulic conductivity[22] while water table depth can greatly influence forest access to water, with forests on deeper water tables expected to be more at risk of water shortage during drought events compared to shallower water table areas[14]. This relative vulnerability of deep water table forests is despite these forests containing more drought-tolerant species[23], and is driven by the ability of shallow water table areas to buffer the negative effects of drought through the groundwater memory effect[23]. While it is clear that each of these variables plays a role in determining Amazon forest response to climate, their relative importance in regulating response to natural climatic anomalies remains unclear.

In this study, we use a multivariate regression framework to explicitly evaluate the relative importance of ENSO associated climate anomalies, soil characteristics and background climate variables as controls of Amazon forest photosynthetic anomalies during the drought associated with the 2015/16 ENSO. The 2015/16 ENSO event was associated with the most extreme drought and period of warming on record[16] and thus offers an ideal case study in terms of the strength of signal to noise ratios. Using this methodology we found that background climate and soil conditions were more important controls on forest photosynthesis responses than the magnitude of the climate anomalies associated with the ENSO in explaining the variance in SIF anomalies. Our results reveal marked differences in sensitivity Amazonian regions response, with North-western Amazonian forests being the most and the South-western forests the least sensitive to precipitation anomalies. These differences in sensitivity likely relate to community species compositional differences across Amazonian forests, which vary greatly in the extent to which they are pre-adapted to water stress, and need to be accounted for in simulations of climate change impacts.

2.3 Results and Discussion

2.3.1 Solar Induced Fluorescence during the 2015/2016 ENSO

To evaluate the impact of the 2015/2016 ENSO on Amazon forest photosynthesis we computed standardised anomalies defined as:

$$StandardisedAnomaly = \frac{X_t - \overline{X}}{\sigma} \tag{2.1}$$

where $\mathrm{X_t}$ represents the mean SIF/climatic value during the October to December 2015 period, $\overline{X}$ represents the mean and σ the standard deviation of the baseline period (October to December) between 2007 and 2014 (excluding 2015). In line with the findings of previous studies[16, 10, 24], retrievals based on SIFTERv2.0 show widespread negative SIF anomalies, across Amazonia. Indeed, 93% of forested pixels in our study domain exhibited negative SIF anomalies during October-December 2015 and mean pixel-level SIF over this time window was 1.03 standard deviations lower than baseline values. Moreover, anomalies during this time period (delineated by the vertical dashed lines in Figure 2.1) are the most negative on record in all Amazonian regions except the Southwestern (SW) Amazon.

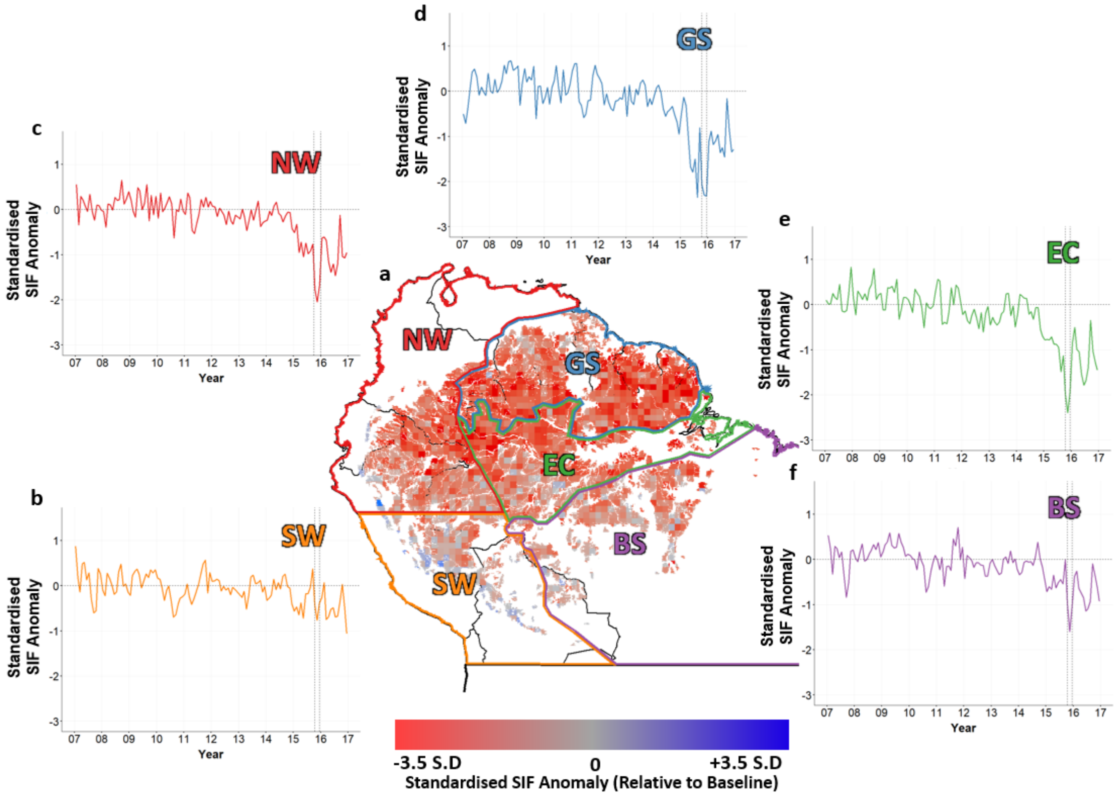

Figure 2.1: **Spatial distribution of Solar Induced Fluorescence Anomaly during the 2015/16 ENSO and temporal trends in SIF anomaly at a regional scale.** **a** Spatial distribution of mean standardised SIF anomaly for October-December 2015. **b–f** Monthly Standardised Solar Induced Fluorescence (SIF) anomalies from January 2007 to December 2017. Results are split by geographical regions established by [25] Vertical dashed lines signify the 2015 Oct-Nov-Dec period used in this study. **b** SW South West, **c** NW North West; **d** GS Guiana Shield, **e** EC East Central, **f** BS Brazilian Shield. Analysis is restricted to natural forests as defined by the Intact Forest data product[26]. See methods for details.

2.3.2 Climate Anomalies during the 2015/2016 ENSO

Surprisingly, we find that ENSO-associated climate anomalies (anomalies in precipitation, temperature and Maximum Cumulative Water Deficit (MCWD)) were very poor predictors of the observed variation in the mean standardised SIF anomaly for Oct-Dec 2015 (hereafter referred to as the standardised SIF anomaly) during the peak of the drought associated with the ENSO. Indeed, a linear model constructed exclusively with variables describing ENSO-associated climate anomalies explained only 2% of the regional variation in SIF anomalies (Table 2.1). This contrasts significantly with our final multivariate linear model, which models SIF anomaly as a function of soil characteristics and background climate variables in addition to ENSO-associated climate anomalies and which accounted for 25% of the variation in SIF anomaly (for full model see Supplementary Table A.1). Given the relatively coarse scale at which this study is being conducted, and the fact that forest-scale ecological responses are typically noisy, the amount of variance explained by our final model is reasonable and comparable with that found in plot scale studies. For instance, the best model of Sullivan et al. (2020)[27] for woody productivity (based on changes in diameter over time), explained 30% of observed variation.

Table 2.1: Proportion of variation explained by groups of predictor variables and the impact of their removal on the explanatory power of the final model.

ENSO-associated climate anomalies	Background climate	Soil characteristics	Adjusted R^2	Drop in R^2 compared to full model	Change in AIC compared to full model
✓	✓	✓	25%	-	-
	✓	✓	24%	1%	+28
✓		✓	14%	11%	+270
✓	✓		19%	6%	+165
✓			2%	23%	+553
	✓		17%	8%	+215
		✓	12%	13%	+319

The relatively low importance of the ENSO-associated climate anomalies is further highlighted by the fact that removal of soil characteristics and background climate variables from this final model resulted in a far greater reduction in explanatory power as observed in change in adjusted R^2, and in the increase in Aikaike Information Criteria Corrected (AICc) than dropping variables denoting ENSO strength (Table 2.1). Of the three groups, the background climate variables were found to be particularly important, as its removal resulted in a substantial lowering of R^2 from 0.25 to 0.14, and an increase in AICc of +270.

2.3.3 The Role of Soil Characteristics and Background Climate Variables in Explaining Photosynthetic Response

The importance of soil characteristics and background climate variables on photosynthetic anomalies is further confirmed through evaluation of the standardised regression coefficients of individual predictors in this final model which is summarised visually in Figure 2.2. The sign and magnitude of the standardised regression coefficients in Figure 2.2 describe the relationship between SIF Anomaly and the explanatory variable as part of the overall contribution of all variables towards the model prediction of SIF anomaly, all other variables being held constant. Positive coefficient values, for instance, indicate a positive relationship between explanatory variables and SIF Anomaly. Hence, a unit increase in the explanatory variable will contribute a positive amount to the SIF anomaly model prediction, all other variables being held constant. Applying this logic to our explanatory variables allows understanding of which traits contribute positively and negatively to SIF anomalies.

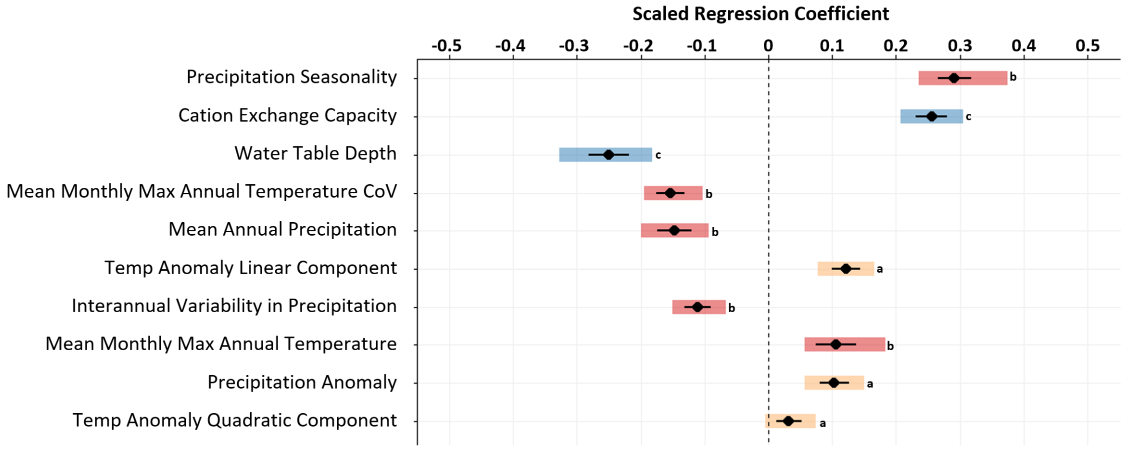

Figure 2.2: **Scaled and centred regression coefficients for all variables found in the final model.**
Variables have been ranked by absolute magnitude of regression coefficient. Wings are standard errors and bars represent the 95% confidence intervals estimated via a bootstrapping analysis. Bars are coloured and numbered according to variable group: 1) yellow indicating ENSO associated climate anomalies variables, 2) red denotes background climate variables and 3) blue represents soil characteristics.

The five most important variables in the final model, ranked in order of descending importance based on the magnitudes of the standardised regression coefficients were: 1) rainfall seasonality, 2) cation exchange capacity, 3) water table depth, 4) variation in monthly max temperature and 5) mean annual precipitation. Precipitation anomaly during the peak of the drought emerged as only the ninth most important explanatory variable. Overall, our results suggest that forests found in regions with high rainfall seasonality, high soil fertility, lower water table depth, and which have a higher monthly variation in max temperature and lower mean annual precipitation are more resistant to the drought associated with the ENSO than wetter, more aseasonal forests and forests on lower fertility soils and deeper water tables. However, we do not find evidence that forests exposed to higher interannual rainfall variability were more resistant to the drought, as has been inferred in previous studies based on examination of tree cover distributions[17] nor do we find a significant role of soil texture in mediating photosynthetic response to this drought. (The spatial distribution of all predictor variables are shown in Supplementary Figure A.3).

The overarching importance of background climate, water table depth and soil fertility relative to ENSO associated climate anomalies helps to explain the weak spatial structure in

SIF anomalies observed (Figure 2.1), despite substantial spatial variation in the ENSO associated climatic anomalies (Supplementary Figure A.1). Amazonian forests vary greatly in background climate[28], soils[29] and water table depth[30] and these system properties translate into considerable differences across forests in sensitivity to this drought. Using SIF anomaly and climate anomaly data, we calculated sensitivity (defined as standardised SIF anomaly/climate anomaly) of Amazon forest photosynthesis to precipitation and temperature anomalies at the pixel level (Figure 2.3). Using this approach, we identified marked variation in sensitivity to climate in forests in different biogeographical regions. Northwestern (NW) Amazonia is the wettest and least seasonal region in Amazonia in terms of rainfall and temperature seasonality (Supplementary Figure A.3 for spatial variation) although variation in temperature seasonality is generally low across the entire study domain. Forests in the NW region were found to be the most sensitive to precipitation reduction being twice as sensitive as the Amazon-wide mean, and more than twelve times as sensitive as the least sensitive BS region. On the other hand, the forests of the Brazilian Shield (BS) which are the driest and most seasonal in the Basin were found to be least sensitive to precipitation reduction and were five times less sensitive than the Amazon-wide mean. The Guiana Shield (GS) region, simulated by many climate models to be the region most likely to be affected by future rainfall reduction[31] was found to be the third most sensitive to rainfall change during this drought after NW and EC Amazonia. Whereas there is clear evidence of different sensitivity to precipitation across Amazonian regions, differences in sensitivity to temperature are less obvious (Figure 2.3), and might reflect the fact that spatial variation in temperature across Amazonia is much less marked than the spatial variation in precipitation.

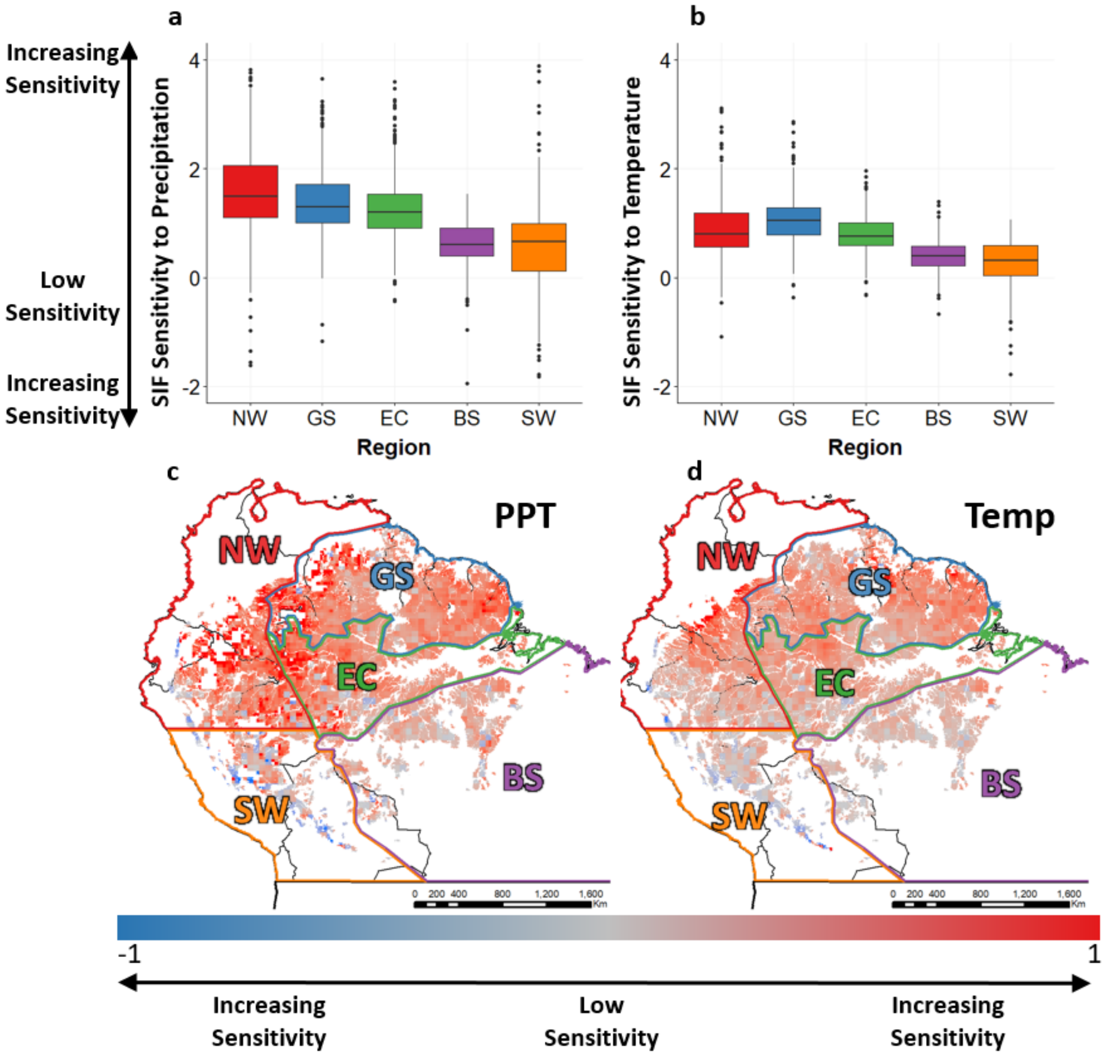

Figure 2.3: **Spatial Distribution and Regional Averages of SIF Sensitivity to Temperature and Precipitation Anomalies**
a-b: Show precipitation (**a**) and temperature (**b**) regionally averaged sensitives. SIF Sensitivity is calculated as Log10(Standardised SIF Anomaly /Standardised PPT Anomaly) and Log_{10}(Standardised SIF Anomaly / Standardised Temp Anomaly) respectively. Box plot centre line, top, and bottom line represent the median, 75th and 25th percentile respectively. Upper and lower whiskers represent the largest and smallest value within 1.5 times the interquartile range above and below the 75th/25th percentile respectively. Results are split by geographical regions established by Feldpausch et al. (2011)[25]

2.3.4 The Role of Community Species Composition in Determining Variance in Response

The effects of background climate, water table depth and soils on forest resistance to this drought, and droughts more generally, are ultimately mediated via tree species composition. Seasonal water stress has been found to exert a fundamental control on the biogeographical distributions of Amazonian tree species, with many species being restricted in range to the wetter regions of the Amazon[20]. Over more local scales, variation in water table depth can also strongly influence community species composition, with near complete species turnover observed in closely occurring forest plots on shallow water tables compared to those on deeper water tables[32]. Such large differences in floristic composition along water availability axes are likely associated with differences in community-level drought tolerance. It has been shown for example that species occurrence along hydrotopographic gradients in Central Amazonia is underpinned by differences in embolism resistance[33], as species occurring on water-limited plateau areas are considerably more embolism-resistant than those occurring in valley areas with more access to water[33]. Community-level differences in hydraulic traits have been found to explain why a more seasonal Amazon forest experiencing a strong drought anomaly during the 2015/16 ENSO presented a similar canopy conductance response to a less seasonal forest experiencing a weaker climatic anomaly[13]. Our results raise the prospect that such a compensatory mechanism may have been in operation at a Basin-wide scale during the drought associated with the 2015/16 ENSO as forests that experienced less severe climatic anomalies but are less adapted to water stress experienced similar reductions in photosynthesis to forests that experienced more severe climatic anomalies but are more adapted to seasonal drought.

The positive relationship between cation exchange capacity and SIF anomaly may reflect differences in life history strategies of species along fertility gradients. Amazon forests on fertile soils are generally more dynamic and more productive than those found on infertile soils[29]. The functional attributes of tree species occurring on fertile soils, such as low Leaf Mass per Area (LMA) and high foliar N and P content [34] are indicative of species with acquisitive (high resource acquisition rates and high growth that tend to do better in high resource habitats[35]) rather than conservative life histories (geared towards high resource conservation, high stress tolerance and high survival which tend to be more successful in lower resource habitats[35]) and thus prioritising growth over survival. Forest communities consisting largely of acquisitive species would be more likely to maintain photosynthesis rates high under drought, despite increased risk of hydraulic cavitation, than communities consisting of more conservative species[36, 37]. Although the interaction between nutrient availability and drought impact has been largely unstudied in tropical forests, our results are consistent with analyses on temperate systems which found that more fertile soils enhanced resistance of tree growth to drought[38].

Our finding that Amazon forest response to ENSO associated climatic anomalies is controlled more by the sensitivity of the forests and less by the intensity of the event has important implications. It suggests that insights derived from well-studied sites in Central and Eastern Amazonia e.g. Barros et al. 2019[13], and Rowland et al. 2015[39], may not be readily generalizable to other regions of the Amazon, which may be more sensitive (e.g. NW Amazonia) or less sensitive (e.g. SW Amazonia) to reduced rainfall. Our results also highlight the pitfalls of assuming a universal sensitivity of Amazonian forests to drought in ecosystem models. Most widely employed global vegetation models incorporate a very limited functional diversity across Amazonian forests[40], restricting confidence in future projections of climate change over the region. Indeed, most of the Dynamic Global Vegetation Models (DGVM) included in the TRENDY project (e.g. Friedlingstein et al. 2020[41]) and which are used to inform our best estimates of the global carbon budget assume that Amazon forests are represented by 1-2 discrete Plant Functional Types (PFT). For example, in the LPJ model[42] and the ORCHIDEE model[43] Amazon forest vegetation is described by a tropical evergreen PFT and a tropical deciduous PFT, while other vegetation models have an even more limited description of functional diversity (e.g. Galbraith et al. 2010[44]). Such architectural restrictions mean that spatial variation in forest biomass storage and dynamics is poorly captured by many DGVM[45] and limit ability to capture variation in forest sensitivity to drought. However, there have been notable recent attempts to improve the description of functional diversity in DGVM which replace prescribed trait values with more flexible trait values shaped by climate and competition (e.g. Thonicke et al. 2020[46]). Such approaches present promising avenues for better representation of variation in forest sensitivity to climate in global models.

While our study documents spatial patterns and large-scale controls on forest sensitivity to drought in Amazonia, it does not allow for determination of the specific mechanisms which underpin these differences. These may include variation across forests in ability to withstand negative xylem tensions under drought or below-ground rooting properties. Elucidating these mechanisms is of high importance to enable more informed predictions of the impact of climate on this critically important biome, but is not yet possible due to the lack of Amazon basin scale databases of relevant plant traits. Thus while our study identifies patterns of varying climatic sensitivity across Amazon forests and the overarching controls of climate and soils, an understanding of the specific mechanisms will only be possible with new basin-wide products of plant functional properties.

2.4 Methods

2.4.1 Study Area

This study focuses on forested areas with minimal human impacts within Amazonia. Amazonia was delineated using the geographical boundaries described by Feldpausch et al. (2011)[25] which is based on a combination of climate, hydrology, flora, fauna and biogeography criteria. These regions vary markedly in forest composition and dynamics and have been used extensively to evaluate how forest structure and function vary across different biogeographical regions[25, 47, 45]. We restrict our analysis to Amazonian forests defined using the Intact Forest data product which maps unbroken expanses of natural ecosystems within the zone of current forest extent, having a minimum tree cover of 20%, and with no remotely detected signs of human activity[26]. Savanna ecosystems as identified using the WWF Ecoregions[48] were excluded from the analysis to restrict our study to forest areas. As a final step, any forested pixels that experienced a fire in 2015 were identified using the MOD14A2 8-day fire product[49] and removed.

2.4.2 Overarching Approach

We modelled 2015/16 ENSO associated anomalies in photosynthetic activity over Amazonia as a function of variables representing the ENSO associated climate anomalies, soil characteristics, and background climatology. The relative importance of each of these groups of variables and of the individual variables within these groups was then explored using multivariate regression analysis with final model selection based on AICc and model stability analysis. The full model and explanation of variables is provided in the supplementary information (Supplementary Table A.6).

2.4.3 Solar Induced Fluorescence Data

Photosynthetic activity was proxied using SIF retrieved at 09:30 hrs local time using the SIFTERv2 algorithm[50]. The SIFTER v2 algorithm retrieves SIF from GOME-2A reflectance spectra in the 734-758nm window, by examining the filling in of Fraunhofer lines relative to the depth of the Fraunhofer lines observed over the non-vegetated reference region of the Sahara, while accounting for the influence of the surface albedo and atmospheric transmission[50]. The algorithm improves on previous versions of the SIFTER algorithm used by previous studies[10] by explicitly attempting to correct for sensor degradation effects post-2013 (Supplementary Figure A.5) and by using narrower spectral windows that avoid oxygen absorption and are less sensitive to water vapour. The SIFTERv2 product corrects for sensor degradation through analysis of changes in reflectance over the sites where reflectance is known to be stable[50]. Data from this analysis was used to calculate degradation correction spectra for all seasons post July 2014, and these correction spectra were subsequently applied prior to the spectral retrieval to stabilise the observed declines. The corrected product removes any large-scale SIF trends over our study period (up to the end of 2016) and also reveals a rebound in SIF values in 2017 (Figure 2.1). We note, however, that caution should be applied when using the product beyond the timeframe of this study as post-2017 SIF values appear to be associated with lower seasonal maxima and minima than values up to that point (Supplementary Figure A.5).

Daily SIF Retrievals from 2007 to 2017 from the SIFTERv2 algorithm[51] were resampled to a monthly mean 0.5°x 0.5°gridded resolution using an inverse distance weighting algorithm implemented using the python library Pyresample[52]. Following the advice set out in the SIFTERv2 Algorithm Theoretical Basis Document[51], pixel-level retrievals with QA values less than 0.6 were excluded from the study to ensure that only high-quality (low cloud fraction, small spectral residual) retrievals were used. QA values are calculated pixel wise from cloud faction and spectral residual, pixels with high cloud faction and high spectral residual will have a small QA value.

The monthly mean gridded data were then used to calculate a standardised SIF anomaly (Equation 2.2):

$$StandardisedAnomaly = \frac{X_t - \overline{X}}{\sigma} \tag{2.2}$$

where $\mathrm{X_t}$ represents the mean SIF/climatic value during the October to December 2015 period, $\overline{X}$ represents the mean and σ the standard deviation of the baseline period (October to December) between 2007 and 2014 (excluding 2015). Information after the ENSO period was not included in the calculation of the baseline as evidence suggests that Amazonian forest dynamics following ENSO have changed significantly[53]. Wigneron et al. 2020[53] for instance show that Above Ground Biomass (AGB) had not recovered by the end of 2017. Thus, we excluded post ENSO years in the calculation of the baseline as a precaution. October to December was chosen as the analysis period as this corresponded to the period of most negative SIF anomalies across all Amazon regions, as shown in previous studies that examined the SIF response to the 2015/2016 ENSO event[54, 10] and shown in Figure 2.1.

The interpretation of changes in SIF as changes in productivity has been used by several studies[10, 55, 24] including this one. However, the relationship is complicated, and the use of SIF as a proxy in this manner comes with a number sources of uncertainty and assumptions that must be taken into consideration when interpreting the results. Porcer-Castell et al. (2021)[56], summarised the key uncertainties surrounding interpreting SIF as productivity and we recommend the reader to read their work for a comprehensive summary. However, the key uncertainties relevant to this study include[56]: 1. A lack of understanding how alternative energy sinks e.g. photorespiration may help sustain electron transport during stress conditions when carbon assimilation and thus productivity is impaired resulting in a potential decoupling of SIF and productivity. 2. Uncertainty due to variation in species and leaf biochemistry, canopy architecture and the presence of non-photosynthetic material 3. Uncertainty arising from the integration of SIF controls across space and time that may strengthen or disrupt the SIF-GPP relationship. While it is important to acknowledge these uncertainties when interpreting the results, we remain confident in our findings, as many studies[57, 58, 59, 60] examining SIF-GPP relationships to date find strong agreement in-terms of variance explained, between SIF and GPP when using data collected from flux-towers, ground measured SIF, and remote sensing SIF products at spatio-temporal scales both finer and coarser than used in this study.

2.4.4 Climate Anomalies Associated with the ENSO

ENSO associated climate anomalies were calculated as anomalies in mean monthly temperature, precipitation and MCWD using Equation 2.2 where in this case $\mathrm{X_t}$ represents the mean temperature, precipitation or MCWD value during the October to December 2015 period, $\overline{X}$ represents the mean, and σ the standard deviation of the baseline period (October to December) between 2007 and 2014 (excluding 2015). Temperature data was retrieved from ERA5 monthly aggregates[61], and precipitation data from TRMM 3B43 monthly precipitation product[62]. MCWD was computed monthly as the difference between precipitation and Potential Evapotranspiration (PET)[63] (i.e. vegetation is assumed to experience stress when PET is greater than precipitation), with deficits accumulated over all months where precipitation was inferior to PET and being reset to zero when precipitation exceeded PET. The evapotranspiration threshold was explored using two different methods, the first being a constant threshold set at 100 mm a month for this analysis, based on mean water fluxes from tower networks and remote sensing products[64] and in line with many other studies on Amazon forests[11]. However, we acknowledge that evapotranspiration can vary substantially across different Amazonian forest as studies have found that some regions have a monthly evapotranspiration closer to 150mm[65]. Thus, we also explored the implications of computing MCWD using other absolute thresholds. The conclusions of our analysis did not change for a range of evapotranspiration thresholds (Supplementary Figure A.2). The second method we tested, was using a satellite (MODIS) derived Potential Evapotranspiration[49] product. This product allowed us to calculate estimates of PET at a monthly timescale. Each month's PET average was subtracted from that month's rainfall to calculate the water deficit. This was then accumulated over time to calculate MCWD resetting to zero if rainfall exceeded PET as before. This methodology arguably allows for a more realistic variation and estimation of PET than a simple threshold applied across all Amazonian forests. The results shown in this paper are based on this methodology.

Where required, climatic data were temporally and spatially resampled to match the resolution of the SIF data to ensure consistency of scale. After processing and applying quality filters, standardised anomalies were calculated for each ENSO associated climate anomalies using Equation 2.2.

2.4.5 Soil Properties

Percentage sand and cation exchange capacity for different horizons from 0 to 30 cm depth were extracted from the SoilGrids dataset at a 1 km resolution[66]. These were averaged over the entire 30 cm depth and resampled to match the SIF dataset spatial dimensions. Water table depth was retrieved from the water table depth map produced by Fan et al. (2013)[30], based on a data-model fusion approach. As with all other data layers, this product was spatially resampled to the resolution of the SIF data.

Soils grids is produced through the interpolation from ground collected data accounting for a range of environmental covariates using machine learning algorithms. The quality of this product at any particular point therefore relies on number of points in the region, the distance from those points, and the scale of the analyses. The spatial coverage of the Amazon is good[66], especially when considering that this study is at a scale of 0.5°x 0.5°with over 8,000 soil profiles distributed across the study area. If this study was looking at finer scales, then issues of data validity may be of much higher concern, however at this scale it means that each of our pixels is covered by a good number of points, and thus is likely to be representative of the regional gradients in soil characteristics.

The Water table depth product used published by Fan et al. (2013)[30] interpolates globally from 1,603,781 observations of water table collected from government archives and published literature using a ground water model forced by present-day climate, terrain and sea level[30]. Observation density over the Amazon, is relatively low compared to other regions and this should be taken into account when interpreting water table depth. However, while water table depth at finer scales may differ from reality due to low data density, at the scale we are using, the data available should be sufficient to provide regional trends allowing us to test its importance. The Fan et al. product has been used extensively to evaluate the impacts of water availability on vegetation structure and function (e.g. Costa et al. 2022)[67].

2.4.6 Background Climate Variables

Background climate variables considered included mean annual precipitation and temperature, the interannual variability in mean annual precipitation and temperature and the seasonality of monthly precipitation and temperature. These variables were calculated using data from all years prior, and after ENSO, but excluding data from during the event itself (2015/16 data excluded). Temperature data was obtained from ERA5 and precipitation from TRMM 3B42, the same data used for the computation of ENSO associated climate anomalies. The interannual variability was assessed by computing the coefficient of variation (CoV) across all years (except 2015), while the seasonality of precipitation was expressed as a seasonality index[68] using Equation 2.3:

$$\overline{SI} = \frac{1}{R}\sum_{n=1}^{12}\left|\overline{X_n} - \frac{\overline{R}}{12}\right| \tag{2.3}$$

where $\overline{X_n}$ is the mean precipitation of month n, and $\overline{R}$ is the mean annual precipitation. Seasonality in temperature was calculated as the average annual coefficient of variation of temperature. All data processing was performed using Google Earth Engine[69].

2.4.7 Statistical Analysis

Explanatory variables were split into three overarching groups representing ENSO associated climate anomalies, (temperature, precipitation, and CWD anomalies), soil characteristics (percentage sand, cation exchange capacity and water table depth) and background climatology (mean annual precipitation/temperature, interannual variability in precipitation/temperature and seasonality of precipitation/temperature). We considered both linear and quadratic terms for temperature anomaly to better represent its non-linear relationship with productivity, whereas all other variables were included as linear terms only. The full model and predictor variable description is provided in Supplementary Table A.6. Model fit was assessed using standard model diagnostics in R, including calculating of model R^2, QQ plots, leverage plots, plots for heteroscedasticity and a plot of fitted vs observed values (Supplementary Figure A.4).

Variable selection for the final model was undertaken using a backwards elimination algorithm based on AICc. During a single step variables are removed one at a time from the model and the change in AIC calculated. The variable which resulted in the greatest decrease in AICc was then eliminated. This process was repeated until the elimination of any variable results in a decrease in AICc of less than 2 producing the final model for interpretation. To remove confounding effects due to correlation between variables, Variance Inflation Factors (VIF) were calculated for all variables before backward elimination was conducted and all variables with VIF greater than 10, indicating likely multicollinearity, were removed. K-fold cross validation was performed (k=10) to check for overfitting. Root mean squared error of the final selected model was calculated as 0.862, and the average k-fold validation was 0.866, the similarity indicating that the selected model does not exhibit significant overfitting.

Model stability was investigated using a bootstrapping approach[70] to quantify the extent to which our final model was stable to mild to moderate perturbation, and thus to what extent we can rely on the final model for inference. The underlying dataset was bootstrapped (n=1000), and backward elimination used to produce a final model as outlined previously. Mean, standard deviation and 2.5/97.5 quantiles were then calculated from the bootstrapped population. Variables for which the 95 quantiles crossed zero were excluded from analysis as the direction of their relationship with SIF anomaly could not be reliably inferred.

Variable importance was assessed at two levels: 1) at a group level by calculating the change in final model R^2 when either ENSO associated climate anomalies, soils or background climatology groups were eliminated and 2) at the level of the individual variable through direct comparison of scaled regression coefficients in the final model.

All statistical analysis was conducted using R version 4.0.0. Data visualisation was performed in R using the ggplot2 package[71] and QGIS[72].

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Chapter Three

Contrasting Sensitivity of UK Forests to Drought Explained by Climate and Community Composition

3.1 Abstract

Rising temperatures are predicted to have a variety of effects on temperate forests including increasing mortality, and boosting productivity. The net balance of these different impacts are likely to vary between regions moderated by spatial patterns in temperate forest climate sensitivity. As a case study we investigate the climate sensitivity of temperate forests in the United Kingdom (UK). Normalised difference vegetation index (NDVI) anomalies were used to proxy productivity over time as a function of temperature and precipitation anomalies at a pixel level. Extracting the standardised coefficients (climate sensitivity) and variance explained (climate coupling) for each of these pixel level models we then used a Random Forest framework to explore how background climate, soil, topographic and forest attribute variables are able to explain spatial variation in climate coupling and sensitivity. Our results show that historic productivity anomalies were best predicted by temperature anomaly at a pixel level. Forests in the north-west, west and south-east were found to respond in fundamentally different ways to climate extremes. Forests in the north-west and west of the UK when experiencing drought have historically tended

to increase productivity, while those in the south-east when experiencing drought have tended to decrease productivity. We compared the relative importance of background climate, soil characteristics and forest attributes in explaining the observed variation in climate sensitivity using a random forest framework. The final model explained 72% of the observed variation in temperature sensitivity, and highlighted the importance of background climate, and forest attributes in explaining NDVI-temperature sensitivity, likely explained by variation in community composition.

3.2 Introduction

Temperate forests are forested areas found in the temperate zones between 25°and 50°latitude, between the boreal and tropical zones[1]. They account for nearly 10 million km^2 of global forested area[2] and are characterised by distinct cyclic, seasonal changes in climate, involving periods of growth and dormancy[3]. These forests, more so perhaps than any other forested biome[3] have been defined by the extent to which human have shaped and utilised them[4]. While historically the major threat to temperate forests has been anthropogenic deforestation, and land use change[3], there is increasing evidence that rising global temperatures are likely to be the greatest driver of temperate forest change in the future[5, 6]. Rising temperatures are predicted to have a variety of effects on temperate forests including increasing mortality[5] though increasingly severe droughts[6], as well as boosting productivity through higher average temperatures[7] with the net balance of these effects likely varying between regions.

The sensitivity of temperate forests to temperature, and climate more generally, has been found to be influenced by a wide range of variables including background climate[8], soil texture[9], species composition and forest structure[10]. Although the individual contribution of these variables have been investigated, the relative importance of these variables in moderating productivity responses is an area requiring further study, as high uncertainty exists[11, 12]. It is important to understand the nature of these response if we are to improve our understanding of how temperate forests may respond to future climate change[2].

In addition to the potential impacts on forest productivity as a result climate change, elevated atmospheric carbon dioxide concentrations may itself directly, or via an interaction with climate effects impact productivity. The fertilising effect of atmospheric carbon dioxide on productivity has been well documented in the literature by free-air and chamber carbon dioxide enrichment experiments[13, 14], and although in the long run forest productivity may well be limited by nutrient availability[15], in temperate forests at least the warmer temperatures and elevated atmospheric carbon dioxide concentrations may well stimulate productivity in the short term although considerable uncertainty exists on the magnitude of these gains[16].

Temperate forests cover a wide area, however they are managed at national, and subnational scales and so need to be understood at these scales for effective management. Reviewing the literature revealed that there are relatively few published national scale assessments of the climate sensitivity of temperate forests, and while larger studies are useful, relationships may differ between regions, and regional breakdowns are rarely provided. Existing national literature, has tended to focus on the response of single sites[17], single[18] or small groups of species[19], probabilistic future projections of forest risk[20, 21] or small scale experimental setups[22]. This lack of information at a national scale means it is difficult for governments and national organisations to make informed decisions on how to prioritise their efforts. Knowledge on how forests may respond to future climatic anomalies may be particularly important as climate projections for many temperate forest regions, are predicting trends towards hotter, drier summers on average[7], with an increased chance of significant climatic anomalies[7].

To address the question of what moderates the sensitivity of temperate forests we use the temperate forests of the UK as a case study. The UK temperate forests cover approximately 13%[23] of the UKs total land area, and provide a range of valuable ecosystem services. A valuation conducted by Forest Research[24] estimated the total annual value of woodland in 2020, to be £8.9 billion a year. Of this, provision of timber and wood fuel accounted for just £372.9 million, with the remaining £8.6 billion attributable to carbon storage[25], biodiversity provision[26], and recreational services[27], with 795.8 million recreation visits to UK woodlands in 2020 alone.

The high value of UK forest highlights the critical need to better understand their inherent sensitivity to climate, their ability to resist stressors, and their capacity to maintain the provision of these services. The UK experiences major climatic anomalies on average once every ten years[28]. These anomalies usually manifest as extended periods of drier, or hotter conditions[29], and in the UK have historically take the form of relatively short summer heatwaves[29] or multiyear groundwater droughts[29], with significant climatic events in recent history occurring in 1975/1976[30], 1995[31], 2003[32], 2010-2012[33] and 2018/2019[29]. These climatic anomalies can have a wide range of impacts on forested areas including loss of aboveground biomass due to tree mortality[34], decreased gross primary productivity[35], and increased occurrence of wildfires[36].

Forest productivity has been proxied in this study using the NDVI MOD13Q1.061 Terra Vegetation Indices 16-Day Global 250m product[37] averaged to a monthly timescale. We use NDVI as it is a vegetation index commonly used in forestry research and provides information on vegetation greenness[38] which has been found to be a strong predictor of tree productivity[39]. Canopy damage or discoloration due to dehydration, high temperature stress, insect damage or other stressors results plants absorbing less visible light and/or absorbing more infrared light resulting in detectable decreases in NDVI[38] thus allowing inferences regarding drought impact on productivity.

The sensitivity of forest productivity to climate anomalies is moderated by a wide range of variables that can broadly be classified into i) the intensity of the climatic anomaly, ii) the background (long-term mean) climatology iii) soils and topography and iv) the identity of the community present. Studies of temperate forests have highlighted the sensitivity of forests productivity[40] and mortality to precipitation and temperature anomalies[41, 42]. Forest sensitivity to water stress may be related to background climate as forests found in drier regions have been shown to be better adapted hydraulically to drought than those found in wetter environments[8]. Soil type and topography[43] have been shown to be important with forests in areas with high soil bulk density and low soil available water capacity being particularly vulnerable to droughts[43]. Finally, variation both within[44] and between[45] species has been shown to influence forest climate sensitivity, with certain species being more or less sensitive to climate than others[45].

Here we investigate the sensitivity of forest productivity to temperature and precipitation anomalies over a 19 year period of time. We use statistical modelling to help us understand what variables control the observed spatial patterns of productivity sensitivity. Our main research questions are therefore, what, if any spatial patterns exist in forest productivity sensitivity to temperature and precipitation anomalies, and what are the key variables that control the observed patterns in sensitivity.

3.3 Methods

3.3.1 Study area and period

This study focuses on the subset of UK forested area covered by the National Forest Estate Subcompartments (SCDB) 2019[46]. We restrict our analysis to mature forests that have remained forested throughout the study period (2000 to 2020) by removing forests identified as experiencing forest loss using the Hansen Global Forest Change v1.9[47] data product. Forests planted after 1980 were removed, as examination of NDVI trends in forests planted after this date showed strong growth patterns which confounded analysis of climate sensitivity (See Supplementary Figure B.5 for analysis).

3.3.2 Overarching Approach

For each individual pixel (250 x 250m) in the study domain, NDVI between 2000 and 2019 was modelled in a linear regression framework as a function of temperature and precipitation anomalies at a monthly time scale. Highly sensitive or coupled forest systems are assumed here to be those that respond more strongly to climate fluctuations[48], characteristics which would be captured by the regression. NDVI was modelled using climate data from the same month as the month NDVI was collected. Climate data from the same month was chosen as comparison of modelling NDVI with the same month, the previous month, and the average of the two previous months climate data revealed that the highest average model R^2 across the study area was achieved when modelling NDVI using climate data from the same month. For each pixel, the variance explained by the model (climate coupling), and the standardised coefficients (climate sensitivity) for temperature, and precipitation were calculated as part of the linear regression. A Random Forest regression was then used to explain the observed spatial distribution of climate coupling and sensitivities using forest attributes, background climate and soils data as explanatory variables.

3.3.3 Normalised Difference Vegetation Index Data

A range of remote sensing products were considered as proxies for forest productivity, including solar induced fluorescence (SIF) retrieved from GOME-2, and OCO-2, and a range of vegetation indices from Sentinel 2, and MODIS. GOME-2 SIF was deemed to have a resolution too coarse (80 x 40 km per pixel) for the scale of the UK, where most forests are smaller than this. OCO-2 SIF had a much better resolution of 1.29 x 2.25km, but was only able to provide partial coverage of the UK due to its orbital path. Sentinel-2 data had a suitable spatial resolution of 10x10m, but only has data available from 2017 which is an sufficient length of time to permit a more generally representative analysis of forest productivity dynamics.

NDVI is a vegetation index commonly used in forestry research and provides information on vegetation greeness[38] calculated using Equation 3.1.

$$NDVI = \frac{NearInfrared - Red}{NearInfrared + Red} \tag{3.1}$$

NDVI data was retrieved from the MOD13Q1.061 Terra Vegetation Indices 16-Day Global 250m product[37] and restricted to forested areas as defined by the National Forest Estate Subcompartments (SCDB) 2019[46]. Using the provided quality assurance layer, NDVI retrievals were selected if the Vegetation Index (VI) quality was flagged as ‘good’, or ‘produced but check QA’, the VI usefulness was 10 or less, and was not flagged as containing mixed clouds. This process resulted in the removal of low quality data, and thus different amounts of data are available for each pixel, depending on how much data was removed. NDVI was resampled to a monthly interval by grouping values by month and averaging. Finally NDVI data was restricted just to the growing season of each year, defined here as May through to September to ensure that we were looking at climate fluctuations during growth periods, and limiting the impact of seasonal cycles of greening.

3.3.4 Climate Data for NDVI Modelling

NDVI was modelled using precipitation and temperature anomaly data. Precipitation data was retrieved from the CEH-GEAR dataset[49] between 2000 to 2019 and temperature data was retrieved from the ERA5 reanalysis dataset[50] covering the same 2000 to 2019 time period. Precipitation was extracted from the provided NetCDF files using the python library Pyresample[51] before being ingested into Google Earth Engine[52] for modelling. Climate data was resampled from its native resolution 1km x 1km resolution to match the 250m x 250m resolution of the NDVI data by using nearest neighbour interpolation. Temperature and precipitation anomalies were calculated for each month using equation 3.2,

$$StandardisedAnomaly = \frac{X_t - \overline{X}}{\sigma} \tag{3.2}$$

where X_t represents the mean climatic value for the month t, $\overline{X}$ represents the mean and σ the standard deviation of all occurrences of month t between 2000 and 2019.

Date was included as a variable in the per pixel model to quantify and account for long term trends in productivity which may occur due to climate change, and CO2 fertilisation. CO2 fertilisation was not directly tested as although its effects on productivity can be significant [53], it's effect over the spatial and temporal period investigated here is unlikely to have varied greatly. Date was overall the least important of the three pixel model level variables, and has no clear spatial patterns. By including in the per pixel model however we increase our certainty that the patterns in the other variables we see are not influenced by any long term NDVI trends.

3.3.5 Background Climate Data

Background climate variables Mean Sum of Growing Season Precipitation (MSGSP), and Mean Growing Season Temperature (MGST) were calculated from CEH-GEAR[49] precipitation data, and CHESS-met[54] temperature data respectively, covering the period from 1990 to 2019. Mean growing season variables were calculated by restricting all datasets to the growing season of each year, creating sum or averages for each year covered as appropriate and taking the average of these yearly sums or averages. Seasonality in growing season precipitation (Precipitation Seasonality within Growing Season or Precipitation Seasonality for short) was calculated using the CEH-GEAR precipitation data and expressed as a seasonality index[55] modified to examine seasonality across just the growing season period of May-September Eq 3.3:

$$\overline{SI} = \frac{1}{R}\sum_{n=1}^{5}\left|\overline{X_n} - \frac{\overline{R}}{5}\right| \tag{3.3}$$

where $\overline{X_n}$ is the mean precipitation of month n, and $\overline{R}$ is the mean annual precipitation.

3.3.6 Forest Attributes

Primary planting year, and genus of the primary species, were derived from the SCDB 2019[46]. A Subcompartment is defined as "an area of land that has similar land use, species, habitat composition, age, thinning and harvesting operations and needs to be managed as a single unit"[24]. As multiple species can be present in a subcompartment, the most prevalent species was chosen to represent the subcompartment and the genus of this taken. Forest attributes were provided as a polygon feature layer, to provide a value for each pixel, the centroid of each MODIS NDVI pixel was taken, and this centroid intersected with the forest attribute polygon layer to provide a value.

3.3.7 Soils Data

Clay[56] and sand[57] percentage content (percentage weight) were retrieved from the OpenLandMap, as the average of each of the aforementioned variables in the top 60cm. Although only sand was used in the final analysis due to a high correlation between the two variables (Pearson's correlation of -0.8). Data was resampled from its native resolution to match the 250m x 250m resolution of the NDVI data by using nearest neighbour interpolation.

3.3.8 Topographic Data

The topographic variables, aspect, elevation, and slope were calculated in Google Earth Engine[52] using SRTM Digital Elevation Data Version 4[58]. Data was resampled to 250m using nearest neighbour interpolation to match the spatial resolution of the NDVI data.

3.3.9 Statistical Analysis

Climate coupling and sensitivities were calculated for each pixel (250mx250m) within the study domain by modelling the NDVI time series for that pixel as a function of precipitation, and temperature anomalies as fixed effects, within a generalised linear framework. Date was added as an additional fixed effect to account for any long term trends in NDVI due to carbon fertilisation effects which have been shown to result in long term increases in NDVI[59]. All variables were standardised by subtracting the mean and dividing by the standard deviation prior to modelling to permit direct comparison between pixels of coefficients in the resulting model. Using Google Earth Engine[52] the pixel level model produced a total variance explained (climate coupling) and individual coefficients for precipitation, and temperature anomalies (climate sensitivities) which were used as the basis for the second part of the analysis.

Spatial trends in climate coupling and sensitivity were confirmed by calculating partial correlation coefficients with latitude and longitude, as well as visual inspection of the spatial patterns, and trends between climate coupling and sensitivity were tested using ordinary least squares.

A Random Forest regression framework was used to explain the observed spatial variation in climate coupling and climate sensitivities with explanatory variable split into three overarching groups representing background climatology (Mean Sum of Growing Season Precipitation (MSGSP), Mean Growing Season Temperature (MGST)), soil characteristics (percentage clay) and forest attributes (genus, and primary planting year). Hyper parameter tuning was used to find the optimum number of trees, and the number of variables (mtry) to test at each tree branch and were set at 1000, and 8 respectively. Relative feature importance was tested using the R implementation of the Boruta algorithm[60]. To better understand the workings of the Random Forest model, Accumulated Local Effect (ALE) plots[61] were plotted using the R package IML[61] to demonstrate the modelled relationship between each of the explanatory variables and the dependent variable. Interactions between variables were tested using the R package randomForestSRC[62, 63, 64], no noteworthy interactions were found (see SI B.8 for table of all interactions tested). All statistical analysis was conducted using R version 4.2.2[65]. Data visualisation was performed in R using the ggplot2 package[66] and QGIS version 3.13.3[67].

The presence of spatial autocorrelation was observed in the residuals of the random forest for both climate coupling and climate sensitivity using a range of spatial structures including, 1,2,3 and 4 nearest neighbours, and distance and inverse distance methods from the minimum distance required for all points to have a neighbour up to all pixels being connected to each other. Statistical significance was investigated through a monto carlo permutation approach, and the calculation of Moran's I. Significant spatial autocorrelation was identified in the residuals, a spatial random forest was attempted to account for this spatial variation, but due to the large number of points involved and the limitation on computation power available, it was not possible to complete this model.

Variable importance within the Random Forest model was accessed using two methodologies. First through calculation of Boruta importance score[60]. Boruta importance is a permutation based methodology, after training the Random Forest on the full data set, the algorithm shuffles the data in a single variable and then uses this new dataset, and the trained model to predict for all samples. The mean squared error before and after shuffling is then used to calculate the increase the mean squared error. Higher importance is indicated by a variable for which shuffling its information results in a large increase in mean squared error. This is then repeated for all variables, and increases in mean squared error is rescaled in order to calculate relative importance. The second method utilised was the creation of ALE plots[61], which show visually the relationships between the dependent variable, and explanatory variable. These two methods were used in tandem, as they each identify different components of importance, first the five most important variables as indicated by Bortua score were selected and then this ALE plots were used to refine this list by excluding variables whose ALE value is close to, constant across most of its range.

NDVI, and climate data were standardised before modelling to permit direct comparison in order to assess relative importance within the climate coupling and sensitivity models. Examining the relative importance of sensitivity of NDVI to temperature, and precipitation anomalies (SI B.4) identified temperature anomalies sensitivity as having the highest average relative importance when looking spatially. To this end we decided to focus this study on understanding what drives the observed variation in NDVI-temperature sensitivity.

3.3.10 Data and Code Availability

Please see SI B.4 for information on data availability, and details on how to access all the base datasets used for this analysis, and SI B.7 for the code used in this chapter. Please see SI B.7 for variance inflation factors, and correlation coefficients between all explanatory variables.

3.4 Results

3.4.1 Climate Coupling and Sensitivities

Examining climate coupling across the study domain (Figure 3.1), significant spatial patterning can be observed. With climate coupling generally becoming more positive as latitude increases (partial correlation of $r = -0.27$, $p < 0.05$) and longitude decreases (partial correlation of $r = 0.11$, $p < 0.05$). High climate coupling (defined here as coupling greater than the nationwide average) can be observed in the northwest and west indicating that in these regions forest productivity has historically been more strongly controlled by climate. The mean climate coupling for all pixels was 16%, with a standard deviation of +/-14%.

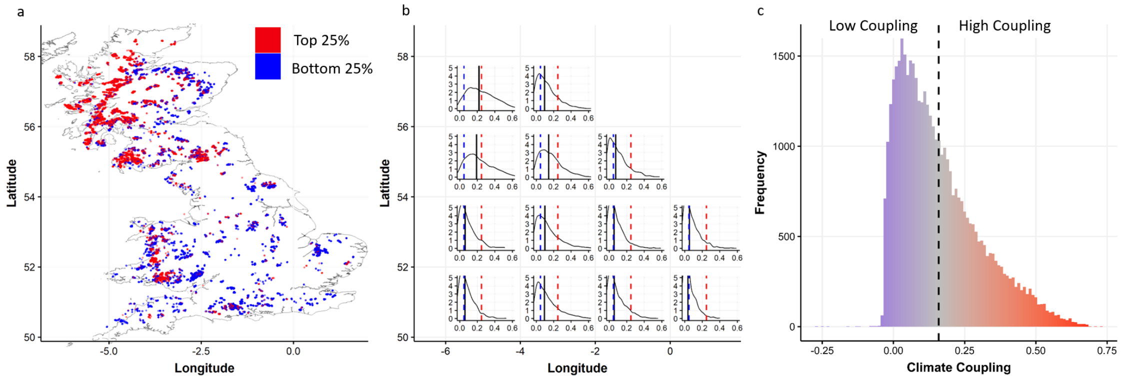

Figure 3.1: **a)** Spatial distribution of classified climate coupling (red top 25% highest climate coupling values), blue (bottom 25% of climate coupling values). **b)** Density distribution for each 2x2 degree square covering the UK, blue dashed line (left) indicates bottom 25% of climate coupling values, red dashed line (right) indicates top 25% of climate coupling values. **c)** Histogram of climate coupling dashed vertical line represents the mean.

While climate coupling provides a measure of how coupled forest productivity in an area is to climate, it tells us little about the direction or magnitude of this relationship which are reflected in the climate sensitivities, or standardised regression coefficients of the pixel level. The relationship between climate coupling and climate sensitivity was tested and a large significant, positive relationship found between coupling and temperature sensitivity ($\beta = 0.43$, $R^2 = 0.52$, $p < 0.05$), and a small but significant relationship between climate coupling and precipitation sensitivity ($\beta = 0.10$, $R^2 = 0.007$, $p < 0.05$). (Please see SI B.4 for maps of relative importance of temperature and precipitation sensitivity).

Figure 3.2 shows the spatial distribution of these coefficients for precipitation and temperature anomalies. Examining the spatial patterns, a strong northwest to southeast gradient can be seen in temperature sensitivity, with temperature sensitivity increasing with increasing latitude (partial correlation of $r = 0.14$, $p < 0.05$) and decreasing with increasing longitude (partial correlation of $r = -0.44$, $p < 0.05$). Precipitation sensitivity by contrast is fairly uniform in its spatial distribution, showing no significant correlation with latitude, and a small positive relationship with longitude (partial correlation of $r = 0.15$, $p < 0.05$). Interpreting these correlations we can say that forested areas in the northwest of the UK and Wales generally exhibit large positive temperature sensitivity. This can be interpreted as meaning that forested areas in the northwest of the UK and Wales when experiencing higher temperatures such as those experienced during a drought exhibit a positive response in forest productivity. In contrast, the southeast demonstrates the opposite pattern with generally large negative temperature sensitivity values. This can be interpreted as that when these areas area are exposed to higher than usual temperatures, these have been historically coupled with lower forest productivity values. Precipitation sensitivity is fairly uniform across the United Kingdom, with the southeast and west of Scotland having a slightly higher frequency of positive forest productivity-precipitation sensitivities.

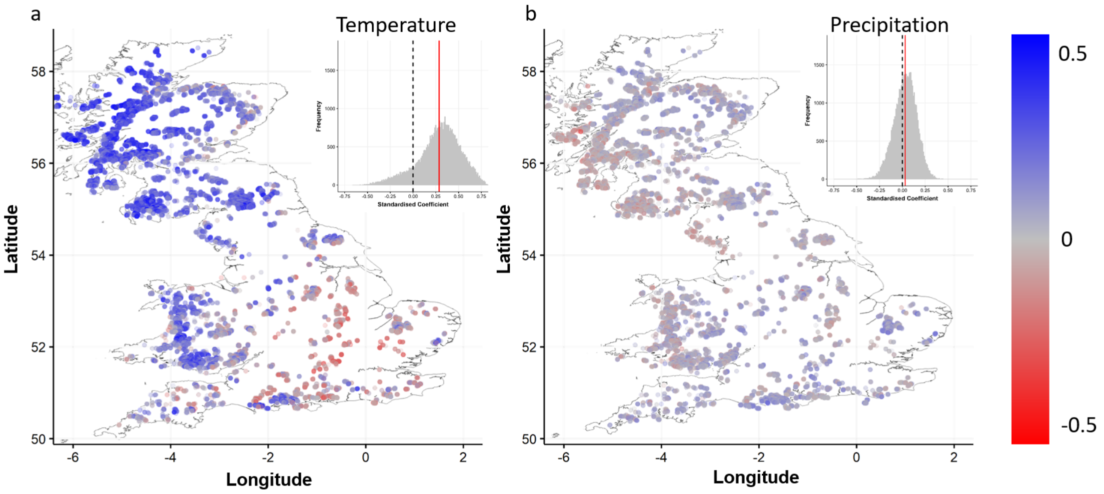

Figure 3.2: Spatial distribution of standardised regression coefficients for **a)** temperature anomalies **b)** precipitation anomalies (standard deviation from mean). Red-solid line represents the mean sensitivity, black-dashed line highlights 0 to be used in comparing to the mean, larger versions of the frequency plots can be found in Supplementary Material B.6

3.4.2 The Role of Climatology, Soil Characteristics and Forest Attributes in Explaining Temperature Sensitivity

Temperature sensitivity was modelled within a Random Forest framework as a function of climatology, soil characteristics, topography and forest attributes. The final model explained 72% of the observed variation in temperature sensitivity. Within this model the top five explanatory variables (ranked by average Boruta score, Figure 3.3 were identified as seasonality of precipitation within the growing season, the primary planting year, the percentage clay content, mean growing season precipitation, and mean growing season temperature.

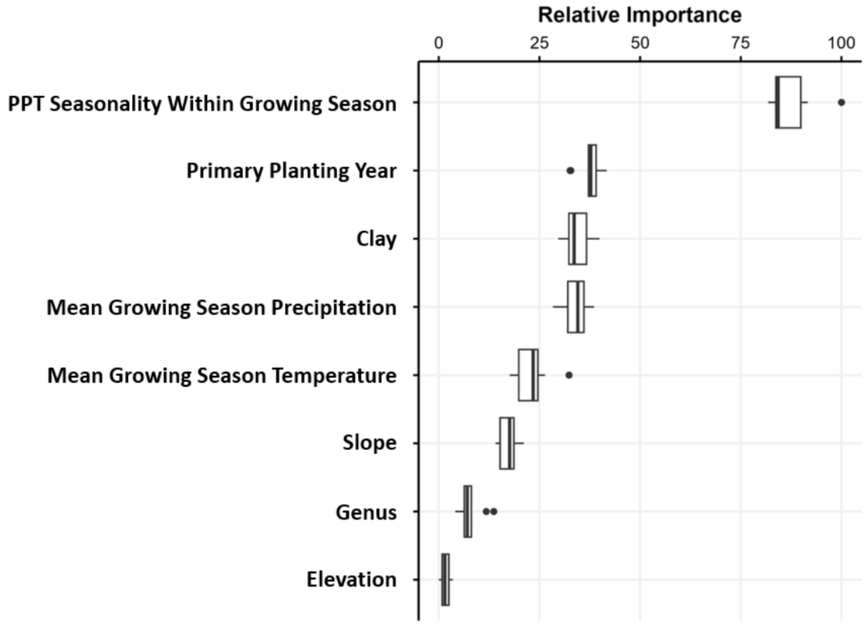

Figure 3.3: Relative importance of explanatory variables within the random forest model. Variables are ranked in decreasing average Boruta score and have been rescaled to fall between 0 and 100. Box and whisker plots, outliers (dots), error lines the minimum and maximum respectively, box, 25th,50th and 75th percentiles.

ALE plots were plotted to understand the shape of the relationship between climatology, soil characteristics and forest variables and temperature sensitivity (Figure 3.4).

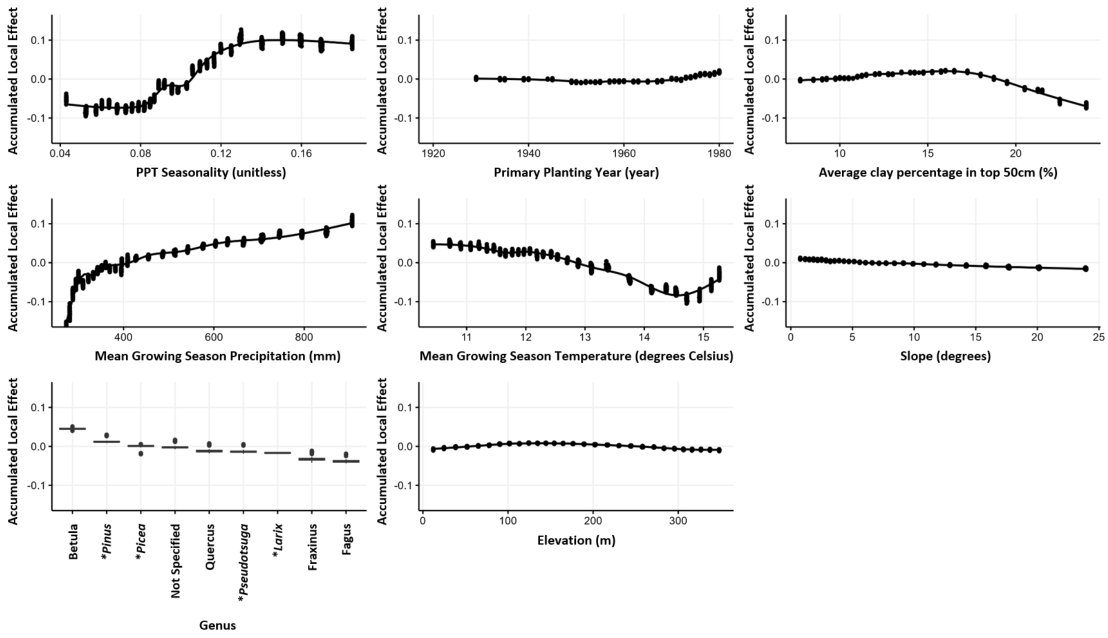

Figure 3.4: Accumulated Local Effect plots for Random Forest explanatory variables. To get a measure of confidence the underlying dataset was bootstrapped with replacement 1000 times with the results for all iterations plotted. Line through points represents the generalised additive modelled trend line. Genera in italics with $*$ represent coniferous genera, normal font without represent broadleaf genera.

While the Boruta score provides a measure of relative importance when the variable is not present in the model, ALE plots provide a measure of the relative contribution each variables makes towards the prediction of the dependent variable. Given that the average temperature sensitivity was just over 0.25, we can see that the relative effect size of each variables varies significantly and gives a different way to understand the relative importance of the variables. As Boruta and ALE plots provide information on a different aspect of variable importance, it is to be expected that they may identify different variables as being the most important. Primary planting year for instance, although flagged as being in the top five explanatory variables by the Boruta score, shows relatively low contribution to the overall prediction in the ALE plots.

The ALE plots for the top five variables as identified by Boruta scores were then examined and the variable removed if their ALE score was close to, or at zero across most of its range indicating that the variable has little changing effect on the models predictions. After applying this criteria we were left with precipitation seasonality within the growing season, mean growing season precipitation, and mean growing season temperature as being the most important in explaining spatial variance in NDVI-temperature sensitivity.

From examining these ALE plots we can see that growing season precipitation seasonality, mean growing season precipitation, and mean growing season temperature, are the most important in terms of their contribution to the prediction of temperature sensitivity, as their contributions relative to the mean temperature sensitivity of 0.25 is quite large.

Taking seasonality of precipitation within the growing season as an example of how to interpret the ALE plots, we can see from the plot that its relationship with temperature sensitivity is non-linear, with low seasonality sites making a negative contribution towards the temperature sensitivity prediction, and highly seasonal sites being associated with positive contributions towards temperature sensitivity. This can be interpreted as sites associated with high rainfall seasonality everything else equal, have more positive relationships between productivity and temperature, and thus when experiencing droughts when it is hotter than average have had higher than average productivity. Conversely, less seasonal forested areas have a negative ALE value, and thus everything else being equal have a negative temperature sensitivity value. These sites when exposed to droughts are associated with a lower productivity values.

In this study we seek to understand the variables that contribute towards making forested areas more or less susceptible to drought, and so it makes sense to split variables based on what values of these variables contribute positively, negatively to the temperature sensitivity. This grouping helps us explain drought response, as when experiencing higher than average temperatures, the former responds with increased productivity, while the latter with decreased productivity. Looking at the values of variables which have historically contributed to positive temperature sensitivity values, they are forested areas that tend to have high seasonality in growing season precipitation, lower mean growing season temperatures, high mean growing season precipitation, and contain Betula genera. These forests we would classify as having a high resistance to short term drought.

Looking at the values of variables which have historically had a negative relationship with temperature we can see that these forests we can see that these forests tend to have low seasonality in growing season precipitation, a high mean growing season temperature, low mean growing season precipitation and contain Fagus or Fraxinus genera. These forests we would classify as having a low resistance to short term drought.

For the equivalent analysis conducted on drought coupling please see SI B.2.

3.5 Discussion

3.5.1 Climate Coupling and Sensitivity Patterns

To understand how resistant UK forests are to climate fluctuations, climate coupling was calculated as the variance explained (model R^2) of the pixel level models. Examining climate coupling across the study domain (Figure 3.1), we find, consistent with previous work[68, 29] high climate coupling can be observed in the northwest and west regions of the UK. This results indicates that productivity in these regions is driven more strongly by short term climate fluctuations compared to other regions. This variation appears to be driven by the relationship between NDVI and temperature sensitivity as we will explain. The variation explained by our models averaged across all pixels was (16% +/- 14%), similar to studies examining climate sensitivity of growth rates in eastern North American temperate forests (climate-precipitation relationship -2.5 to 2.5% explained, climate-temperature 8 to 18% explained)[69] and in the response of Central-West German forests to drought (correlation with drought of 0.18). We therefore consider the variation explained by our model sufficiently large to warrant further investigation given that productivity-climate relationships are inherently noisy by nature, especially at high resolutions, and that we focus on short duration productivity-climate variation and don't consider lag and legacy effects on productivity of multi-year groundwater droughts which can be significant[29].

Our first key finding is that spatial variation in productivity is most strongly driven by spatial variation in temperature anomalies, and that spatial variation in precipitation anomalies plays only a minor role in understanding spatial productivity patterns. This result aligns with the findings of Thom et al 2019[69] who found similarly a sensitivity of growth to temperature but not precipitation change, but contrasts with studies that have looked across larger spatial gradients such as Garbulsky et al 2010[70] who found a significant role for precipitation, but not temperature in explain global gross primary productivity patterns. Our second key finding is that the direction of the productivity-temperature is not consistent across space. A clear pattern can be observed with productivity in the north, and west of the UK having a positive relationship with temperature anomalies, while productivity and temperature anomalies are negatively related in southeast. Our results therefore indicate, that when considering the impact of increasing temperature on temperate forest productivity, it cannot simply be assumed to be positive as is seen at a global scale[71], and instead a more mixed response to higher temperatures is observed[72].

3.5.2 The Role of Climatology, Soil Characteristics and Forest Attributes in Explaining Temperature Sensitivity Patterns

To better understand what drives the observed spatial variation in the temperature-productivity relationships between the north, west, and the south-east a Random Forest model was trained to explain productivity-temperature sensitivity using background climatology, soil characteristics and forest attributes. Modelling highlighted seasonality in growing season precipitation, mean growing season temperatures, and mean growing season precipitation as being the most important explanatory variables. Clay content and genus present were less important but still noteworthy in understanding the observed distribution of thermal sensitivity.

The results of this modelling gives our third key result, as they indicate that background climate variables were the strongest predictors of forest productivity-temperature sensitivity, stronger than either forest attribute data or soils information. Our result is consistent with global scale studies[71], as well as with European Fluxnet[73] based assessments of forest climate-productivity relationships, and our work builds on the literature by allowing us to first demonstrate a similar result in a UK context, and second to then directly compare the relative importance of climate, community identity, and soils information in explaining productivity patterns.

Forests with a lower mean growing season temperature were generally associated with a positive productivity response to higher temperatures (Figure 3.4). This finding is perhaps unsurprising as temperate forests often have mean growing season temperatures (mean growing season temperature found in this study was 13°C +/- 2°C) well below the photosynthetic optimum temperature for the majority of broadleaf (between 23°C and 30°C)[74] and coniferous tree species (between 10°C and 20°C)[74]. Therefore, water and nutrients permitting such forests would be expected to respond positively to higher temperatures[71, 9, 73] associated with drought periods. This hypothesis is supported by our finding that forests that responded positively to increased temperatures were also more likely to have higher mean growing season precipitation thus removing one of the potential limitations. However, this relationship is not constant across the study region, and the ALE values for forested areas with higher mean growing season temperatures are negative (Figure 3.4), indicating that forests with higher mean growing season temperature tended to respond negatively to higher than average temperatures. This could be indicative that because the mean in such forests is higher (mean growing season temperature in the southwest was 15°C +/- 2°C), during periods of higher than average temperatures photosynthetic thermal optima are being breached resulting in decreased productivity. Although the absolute temperatures in temperate regions are often well below levels which are generally considered to impair photosynthesis, studies have shown that plants optimise photosynthetic pathways based on growth temperatures[75, 76], and so relatively high temperatures (even if not absolutely high) may still result in decreased productivity.

Two of the three most important variables identified were linked to precipitation, these being mean growing season precipitation, and the seasonality of precipitation within the growing season. Our results indicate that forests with higher mean growing season precipitation, and higher seasonality of growing season precipitation generally responded positively to higher than average temperatures. A number of mechanisms could facilitate this relationship as high mean rainfall could mean trees have greater water reserves to avoid hydraulic cavitation, and sustain higher levels of productivity during short drought periods. Higher variability of intra-annual precipitation has been shown in a number of temperate forest settings[77] to contribute to greater resistance to drought events though selecting for communities or functional traits[78] better able to cope with fluctuating short term water stress.

Ultimately the relationships that we observe between climate and temperature sensitivity are mediated through variance in community species, and community functional trait composition. To this end genera was included as a variable in our models, and although it was found to less important in explain variation than climate variables we still find a number of genera signals. Consistent with the literature we find that Betula genera[79] exhibit drought tolerance, and were generally associated with forests that responded positively to drought. In contrast Fagus and Fraxinus were generally associated with forest that responded negatively to drought. Our findings that Fagus genera are drought intolerant is consistent with a review[80] of Fagus genera which identified the genera as being particularly drought sensitive, and that UK Fagus populations were the most drought sensitive in Europe[81]. However, our finding that Fraxinus genera were also found to be drought sensitive is a bit more unusual as they are usually considered drought tolerant species[82]. However, the signal we see may be attributable to ash dieback[83] associated mortality compounded with drought.

These results have a number of implications for productivity when considering likely climate change scenarios for the UK. Under a high emissions scenario, all areas of the UK are projected to be warmer, and more so during the summer than the winter[84]. Precipitation during the summer is likely to be reduced significantly (-45% to +5% range across the UK), and increased in the winter (-3% to +39% range across the UK)[84] and changes in the seasonality of extremes in precipitation is likely to increase, with significant increase in rainfall intensity in Autumn[84]. Given the prominent relationship that we have identified between productivity and temperature such a change temperature patterns would likely exacerbate the observed divide in response between the north and southeast, with forests in the southeast experiencing productivity declines more often, and to a great magnitude compared to the north.

In summary we demonstrate for the first time in a UK context the relative importance of background climate, soils and forest attributes in explaining long term sensitivity patterns of forest productivity. Our results indicate that cooler, wetter, forests which experienced higher rainfall seasonality generally responded positively to increased temperature. Conversely hotter, drier forests which experienced lower levels of rainfall seasonality were generally associated with decreased productivity when at higher than average temperatures.

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Chapter Four

Functional trait controls on Amazon forest Productivity: Wood Density Mediates Mean Rates While Leaf Phosphorus Mediates Temporal Trends

4.1 Abstract

Our ability to predict the future evolution of the Amazon sink and its responses to ongoing changes in atmospheric composition and climate relies on a clear understanding of the factors that control productivity and mortality of Amazon forests. A wide range of factors have been found to moderate forest productivity including edapho-climatic factors and intrinsic properties of the trees themselves. Recent work has highlighted that functional traits may be a promising avenue for explaining spatial variation in productivity, and providing mechanistic understanding. Here we use a network of long term forest inventory plots distributed across Amazonia to explore the different ways in which functional traits may mediate stem Above Ground Woody Productivity (AGWP) patterns, considering three distinct modes of AGWP: long-term AGWP, the trend in AGWP over time and in response to a significant climatic anomaly. Our results indicate that nutrient availability and functional traits both play a role in determining long term AGWP patterns, as well as

shorter term responses to climate perturbations. Wood density was found to be important as a control on background AGWP and response to short-term climate perturbations. An apparent trade-off seems to exist with communities with higher wood density having lower growth, and greater resistance to short term climate perturbation. Leaf phosphorous was found to be the only significant predictor of long term trend in AGWP, with more productive forests having greater community-weighted mean leaf phosphorus content. This result may have significant implications for the maintenance of the Amazon forest sink, as it suggests that P availability may ultimately limit forest ability to sequester carbon in its vegetation.

4.2 Introduction

Old-growth forests of the Amazon play a vitally important role in the global carbon cycle, storing an estimated 68 to 80 Pg C in aboveground woody biomass[1], approximately 25% of global aboveground forest carbon[2]. While old-growth forests in the Amazon have acted as a strong global carbon sink over recent decades[3, 4], their ability to maintain this sink appears to be in decline[5]. The Amazon forest vegetation carbon sink fundamentally represents an imbalance between two rates: woody productivity[6] (gains of carbon) and tree mortality[7] (losses of carbon), both of which have increased over time. Our ability to predict the future evolution of the Amazon sink and its responses to ongoing changes in atmospheric composition and climate relies on a clear understanding of the factors that control these core fluxes of carbon into and out of Amazon forests[8].

Forest productivity is controlled by both edapho-climatic factors and intrinsic properties of the trees themselves. At a large-scale, mean productivity rates have been shown to be affected by both climate[6] and soils[9]. The sensitivity of Amazon forest productivity to various aspects of climate including temperature[6], drought[10], and precipitation patterns[11, 12] is well documented. However, less attention has historically been paid to the role of vegetation properties in governing stand-scale productivity. Plant functional traits present a promising avenue for predicting productivity patterns and response to perturbation. Functional traits are plant attributes which directly relate to plant function and relate to the growth/survival strategies of plants and their adaptations to the environment[13]. Functional traits thus have the capacity to provide a mechanistic understanding of observed biomass and productivity patterns. Moreover, they now underpin the development of a new generation of ecosystem models for predicting carbon balance under global change[14]. These can include leaf morphological and chemical traits (e.g. leaf mass per area or leaf phosphorus content), wood structural traits (e.g. wood density) as well as physiological traits related to photosynthesis and plant water use[15].

Stand-level wood density has been shown to influence productivity in both Neotropical montane forests[16] and in lowland Amazon forests, where its spatial variation is an important driver of spatial variation in aboveground biomass[17, 18]. Leaf traits such as LMA and leaf nutrient concentrations could also be expected to affect tree growth through effects on photosynthetic capacity. These traits form the core of the leaf economic spectrum, whereby plant species can be classified along a fast-slow continuum characterised by acquisitive species with low LMA, high nutrient concentrations and high photosynthetic capacity occupy the ‘fast’ end of the spectrum and species with high LMA, low leaf concentrations and low photosynthetic capacity occupy the ‘slow’ end[19]. Studies linking leaf traits and growth rates in tropical forests have largely focused on single sites and have yielded contrasting results to date. For example, leaf traits were found to be important predictors of tree growth in restored forest area in Central Amazonia[20] and to have some explanatory power in predicting productivity in a very diverse old-growth forest in north-eastern Amazonia[21]. However, another study in Central Amazonia found that plant functional traits generally, including leaf traits, were very poor predictors of individual growth[21]. Holistic studies investigating the relationship between multiple functional traits and productivity at a large-scale across tropical forests have been lacking, despite the increasing availability of plant functional trait data, especially for Amazon forests[22].

Traits may also influence the response of productivity to global change, however this is highly uncertain as little research has been conducted to date. A recent study by Tavares et al. (2023)[15], found that variation in tree hydraulic safety margins were the only significant predictor of observed decadal-scale changes in forest biomass across 11 Amazon forests, with other traits such as LMA and wood density not influencing changes in carbon balance. However, the role of hydraulic traits on carbon balance was found to be mediated largely by influence on mortality processes rather than productivity processes. Trait controls on plant productivity trends over time across Amazon forests have never been formally evaluated, despite these trends varying considerably across Amazon forests[5]. Analysis of controls on productivity trends may offer insights into the response of the Amazon carbon sink to elevated concentrations of atmospheric carbon dioxide. There are concerns that the ability of many Amazon forests to continue gaining in biomass will be constrained by nutrient limitation, especially phosphorus, on productivity[23, 24]. A recent fertilisation experiments conducted on a phosphorus-depleted Central Amazon forest, for instance, found that net primary productivity increased exclusively with phosphorus addition[25]. While the impact of nutrient limitation on productivity has been demonstrated in modelling studies[24], space-for-time substitution studies across nutrient gradients[26], and in short-term fertilisation experiments[25], it has yet to be demonstrated at larger spatial and temporal scales.

Our study aims to evaluate the relationship between AGWP, climate and plant functional traits by combining AGWP data from a pan-Amazon network of long term forest inventory plots, with functional trait data collected in the same sites following standardised protocols. Given data availability, we focus on wood density, leaf mass per unit area, and leaf nutrients. Using this dataset, we investigate how functional traits mediate mean AGWP and long-term trends in AGWP. In addition to this, as our time series of data has coverage both before and after the 2015/2016 ENSO we will also investigate to what extent the response of AGWP to the ENSO was moderated by functional traits.

4.3 Results and Discussion

4.3.1 Methodological Overview

Long term mean, trends in AGWP and response of AGWP to a significant climatic anomaly, were calculated for a network of long term forest inventory plots distributed across Amazonia where leaf phosphorus, branch wood density, or leaf mass per unit had been also been collected (Figure 4.1, n = 33). Non-forest vegetation forms such as Cerrado were not included. To compare the relative predictive power of climate and functional traits, we also calculated maximum cumulative water deficit (MCWD) for all plots using remotely sensed precipitation[27]. MCWD was chosen as temperature, precipitation and MCWD were all highly correlated and so could not be in the same model due to multicollinearity issue, and testing indicated that MCWD explained the most AGWP variance of the three. The relationships between AGWP, climate, and community weighted average functional trait values were then investigated in a multivariate forward selection, regression framework to investigate the independent effect of functional trait controls on mean AGWP and AGWP trends, having accounted for variation in water stress. Spatial autocorrelation in the residuals of the best models based on AICc, were tested for and no significant spatial autocorrelation was found.

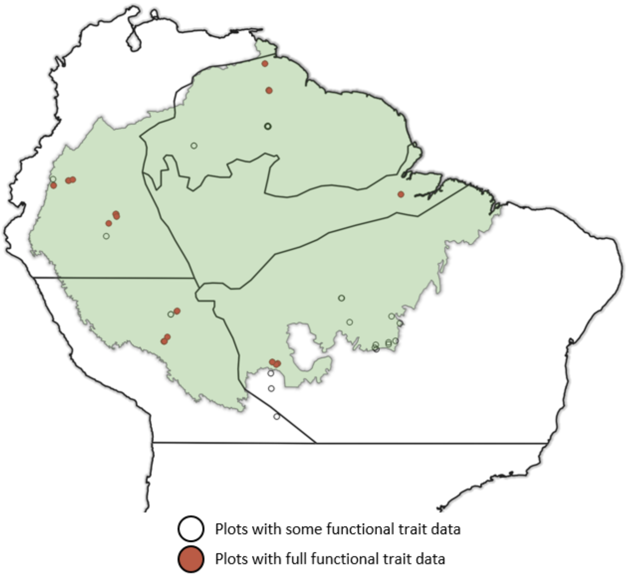

Figure 4.1: Spatial distribution of plots with at least one functional trait of interest (hollow circle) and plots for which all functional traits of interest have been collected (filled circle).

4.3.2 Controls on Long Term Mean and Trend in Aboveground Woody Productivity

Mean Woody Above Ground Woody Productivity

Our best model (based on AICc) accounted for 63% of observed variation in mean AGWP (Figure 4.2). Mean annual MCWD was the most important variable in the model and on its own explained 45% of the variation in mean AGWP. Mean annual MCWD represents a measure of background water stress with more negative values indicating a greater mean maximum annual water deficit and thus greater water stress. Our analysis shows that wetter forests with less seasonal water stress have greater mean AGWP, a result consistent with previous analyses based on the RAINFOR dataset[28].

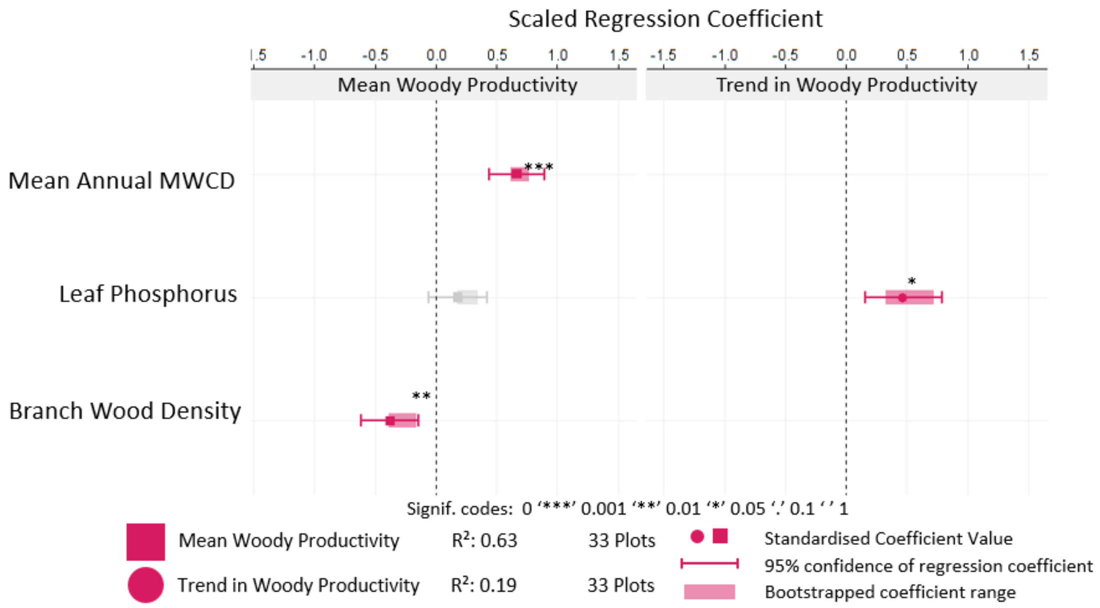

Figure 4.2: Standardised regression coefficients for the best models for predicting mean woody productivity (left) and trend in woody productivity (right) across Amazon forests. Points show the standardised coefficient value in the best model for each, wings show the 95% confidence interval, shaded rectangle represents the 95% range when the underlying dataset was subjected to moderate bootstrapped perturbation.

Branch wood density and leaf phosphorus content were also both in the best model, with the removal of either resulting in a worse model as evaluated by AICc, although of the two, only wood density was statistically significant. Plots with lower community-weighted branch wood density were associated with higher mean AGWP. Hence, for the same degree of water stress, plots with lower wood density tended to be associated with higher mean AGWP. This finding was confirmed in direction and magnitude in a separate univariate modelling of mean AGWP and wood density, leaf phosphorus and mean MCWD (SI C.1,C.2,C.3). This result is also consistent with previous RAINFOR analyses showing that wood density is generally lower in the more productive forests of western Amazonia[28], with other studies in tropical forests[29] and tropical semi-dry climate studies[30]. This result has been proposed to be due to soil properties which vary greatly across the Basin, with forests in Western Amazonia being characterised by fertile soils but with a poorer physical structure, which is associated with a more disturbance-prone regime[9]. These conditions favour lighter-wooded, more productive trees. The low wood density-high AGWP relationship has been previously attributed to a trade-off between wood strength and cost of construction[31], as high wood density is “expensive” in terms of carbon investment, leaving less for carbon for biomass accumulation and giving rise to a relatively conservative growth strategy. Thus, communities with a high average wood density are theoretically associated with a lower long-term mean AGWP which we find. We note, however, that this interpretation of the ecological role of wood density has been questioned by some studies which have an employed an engineering perspective to suggest that high wood density does not confer higher mechanical strength but may be associated with a lower maintenance respiration cost[32].

We do not see a significant phosphorus signal on mean AGWP in the multivariate analysis, despite a clear phosphorous gradient[25] that our plots sit across (Figure 4.2). However, a significant positive relationship between mean AGWP, and leaf phosphorous was observed in the univariate modelling of mean AGWP and leaf phosphorus, which makes use of a larger sample size than the multivariate analysis. (SI C.1,C.2,C.3 for all univariate analyses and bivariate plots). This relationship does become insignificant upon applying Holm–Bonferroni correction[33] for multiple comparison. Together this suggests that the weak signal we see is likely due to the relatively small sample size and may become significant with more data. The weak signal that our finding suggests, agrees with a previous study by Cleveland et al. (2011)[34] based on soil nutrients which found a significant, albeit weak, relationship between leaf phosphorus content and productivity across tropical forest. It also agrees with previous work that found moderately strong correlations between soil phosphorus content and productivity across RAINFOR plots[35, 36]. Our results contrast with the findings of Turner et al. 2018[26] who found a lack of a community level relationship looking across a steep phosphorus gradient in tropical rainforest plots in Panama. In their study they identified a pervasive species-specific phosphorus limitation on species productivity, however this relationship was not observed at the community level[26], as some species were able to grow rapidly on low phosphorus soils due to the evolution of multiple strategies for phosphorous acquisition and use, which enable a tight cycling of Phosphorous between plants, microorganisms and soils[37, 9]. It would have been interesting to investigate species-specific productivity-phosphorus relationships to see if the finding of Turner et al. 2018[26] could observed at a species level, but data availability with this dataset is currently insufficient to permit this.

Trends in Above Ground Woody Productivity

The longer time series of inventory data available allowed us to examine how AGWP is changing overtime, and whether functional traits and climate play a role in explaining the observed variation. Our final model for the trend in AGWP explained 19% of observed variation and thus accounted for a much lower amount of variation than our best mean AGWP model. Despite being important predictors of mean AGWP, MCWD and wood density were not found to be significant predictors of the trend in AGWP over time. Instead, leaf phosphorus content was found to be the only significant predictor of the trend in AGWP over time. Leaf phosphorus displayed a positive relationship with trend in AGWP indicating that plots with higher phosphorus concentration were associated with larger trends in AGWP over time. Our findings suggest that phosphorus availability is a key control on forest capacity to increase AGWP under increased CO2. Forests in phosphorus-rich regions where leaf phosphors is higher are apparently more able to exploit the increased resource availability to boost AGWP than those in more phosphorus-deficient regions. Phosphorus availability has recently been shown to limit total net primary productivity (but not specifically AGWP) in an experimental fertilisation study[25] and to influence productivity across space[38] but this is the first study to provide observational evidence that the ability of old-growth Amazon forests to increase productivity in time is limited by phosphorus availability. It is important to note, however, that the relationship is not strong, as there is considerable site-to-site variability (See SI C.1,C.2,C.3 for all bivariate plots). It is likely therefore that a range of other factors not considered in this study therefore also play a role and need further investigation, these include traits such as hydraulic safety margins[15], and thermal tolerance such as P50.

This relationship has a number of implications for global terrestrial models that assume that elevated atmospheric carbon dioxide, will stimulate Amazon rainforest productivity, and the system as a whole will continue, or increase its capacity to act as a carbon sink[24] (carbon fertilisation effect). Simulations suggest that phosphorus limitation could reduce the Amazon sink by as much as 50% in relation to simulations where no phosphorus limitation is assumed[24] but there has been no observational to support these predictions. Some caution is required, however, when making inferences based on AGWP. Wood production accounts for less than 40% of total Net Primary Productivity (NPP) across tropical forests[39] and changes in stem NPP cannot directly be taken to mean changes in total NPP over time.

4.3.3 Functional Trait Control of Response of Productivity to the 2015/2016 ENSO

During the time span which our dataset covers, a significant climatic anomaly occurred, in the form of the 2015/16 ENSO, giving us opportunity to investigate the role functional traits play in moderating AGWP response to pulse perturbations.

The final model modelled the productivity difference before and after the ENSO as a function of leaf nutrients, wood density, and mean MCWD anomaly during the ENSO. This model was able to explain 26% of observed variation and wood density was found to be the only significant predictor identified (Figure 4.3). The relationship between branch wood density and percentage change in AGWP due to the ENSO was positive, meaning that plots with higher branch wood density generally had higher AGWP percentage change following the ENSO relative to those with lower community average branch wood density. Examination of the biplot between branch wood density and percentage change in AGWP (Figure 4.3) revealed that above a wood density of 0.6 g/cm3 AGWP percentage change was generally positive, but percentage changed after this point continued to result in greater positive percentage change following the ENSO.

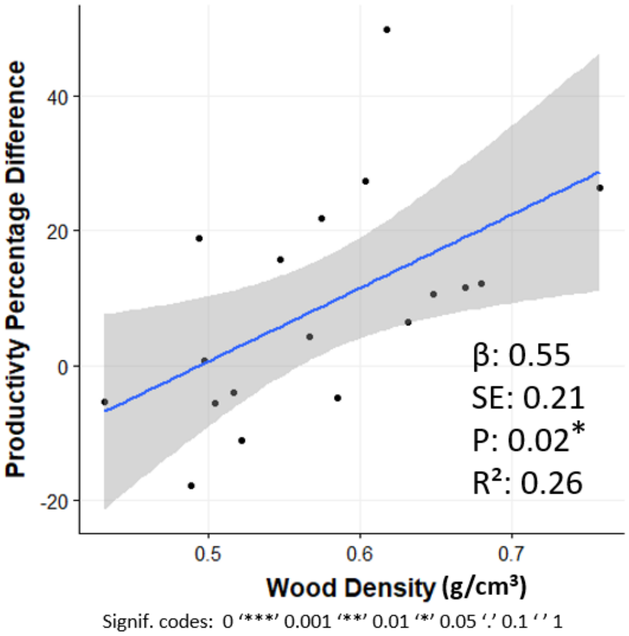

Figure 4.3: Productivity percentage difference before and after the ENSO plotted against community-weighted branch wood density.

The mechanistic link in this case may be that although higher wood density is an expensive investment, which results in lower long term average AGWP, it may confer enhanced xylem resistance to embolism[40] as well as greater resistance against mechanical damage[41]. Thus, species that have higher wood density may be more resistant to short term pulse droughts.

4.3.4 Conclusions

Our results indicate that nutrient availability and functional traits both play a role in determining long term AGWP patterns, as well as shorter term responses to climate perturbations. Wood density was found to be important as a control on background AGWP and response to short-term climate perturbations. An apparent trade-off seems to exist with communities with higher wood density having lower growth, and greater resistance to short term climate perturbation. This trade-off may be associated with wood density conferring enhanced xylem resistance to embolism[40], and hence increased resistance to drought but at the cost of lower AGWP. Leaf phosphorous was found to be the only significant predictor of long term trend in AGWP, with more productive forests having greater community-weighted mean leaf phosphorus content. This result may have significant implications for the maintenance of the Amazon forest sink, as it suggests that phosphorus availability may ultimately limit forest ability to sequester carbon in its vegetation.

4.4 Methods

4.4.1 Study Area

This study focuses on long term forest inventory plots within Amazonia which are part of the RAINFOR network[42]. Amazonia was delineated using the geographical boundaries described by Feldpausch et al. (2011)[43] which is based on a combination of climate, hydrology, flora, fauna and biogeography criteria. These regions vary markedly in forest composition and dynamics and have been used extensively to evaluate how forest structure and function vary across different biogeographical regions[1, 8]. We restrict our analysis to old-growth tropical forests with no recent history of anthropogenic disturbance.

4.4.2 Overarching Approach

Our study aimed to explore the different ways in which functional traits may mediate stem AGWP patterns, considering three distinct modes of AGWP: long-term AGWP, the trend in AGWP over time and in response to a significant climatic anomaly. To achieve this, we calculated AGWP and basal area-weighted community mean values of functional trait values collected in the same long-term forest inventory plots for which we had AGWP data. We constructed linear models for each AGWP metric that included both plant functional traits and climate drivers as predictors. Plots were excluded if they had less than two censuses periods (three censuses), or had data which covered less than ten years to give us confidence that these values were representative of the true average and trends.

The 2015/2016 ENSO event was associated with the most extreme drought and period of warming on record[44] and resulted in losses of aboveground biomass due to widespread tree mortality[45] and decreased gross primary productivity[46, 47]. Percentage productivity change between baseline AGWP, and AGWP immediately after the 2015/2016 ENSO was calculated per plot and functional trait information (leaf nitrogen, phosphorus and potassium, wood density, and leaf mass per unit area), as well as a measure of ENSO magnitude (average MCWD anomaly over 2015/2016) was used to explain the observed variation in a multiple regression framework.

4.4.3 Above Ground Woody Productivity Data

This study was carried out using inventory data provided by the ForestPlots[42, 48] network of long-term forest inventory plots networks, which collates inventory, and functional trait data from a widely distributed networks of permanent plot across the tropics and provides a platform for cooperation and collaboration of tropical vegetation research. All plots within Amazonia, flagged as containing old-growth forest for which plant functional trait data were available were used for analysis.

Productivity was calculated as AGWP per hectare per year, using the R package BiomasaFP[49] for all trees above 10 cm Diameter at Breast Height (DBH). Tree biomass was calculated using the Chave et al. 2014 allometric equation[50], requiring tree diameter, height and wood density to estimate AGWP. Tree height was estimated from recorded diameter using local height-diameter models based upon a three parameter Weibull model. To parameterise these models, we first removed trees for which height was poorly predicted at the biogeographic region level by fitting a three parameter Weibull model for height, and removing all individuals with a residual greater than the 99th percentile. For each plot the top ten trees with the largest recorded average diameter were then chosen, and from the remaining individuals forty were randomly selected without replacement. Local height-diameter models were then parameterised using this subset, before being used to predict height for all individuals. Wood density was obtained for all individuals from the Chave et al. 2009 wood density database[51]. Above Ground Biomass and Above Group Woody Productivity was then calculated for each census interval, for each plot. Code for the calculation of productivity is available in SI C.4.

Percentage change in AGWP was calculated as the percentage difference in AGWP at a plot level. Background AGWP was calculated for all plots that had at three or more censuses (hence at least two census intervals of AGWP) before 2015. Post ENSO AGWP was calculated from the first census period after 2016, including only plots that had a census within two years after 2016. Percentage difference was the calculated using Equation 4.1:

$$AGWPPercentageDifference = \frac{AGWP_{PostENSO} - AGWP_{baseline}}{AGWP_{baseline}} \tag{4.1}$$

4.4.4 Functional Trait Data

The functional trait data used in this study was also provided by the ForestPlots[42, 48] network. Plot level values of functional traits were calculated as the basal area weighted average of all individuals in a plot for any given functional trait, for most traits this was around twenty individuals per plot[22]. Individuals for which diameter was missing were therefore excluded from estimates.

For each plot, the basal area of individuals for which we had functional trait information was assumed to representative of all individuals of the same species at that plot, and their basal area was therefore added to the basal area for those species. The total basal area of species for which we had functional trait information was then summed, and converted to a percentage of the total basal area of all individuals at the plot. Any functional traits which had less than 25% of the total basal area were then removed from the analysis, as we cannot confidently say that they represent the community (SI C.5 for basal area distribution by plot). The code for the calculation of plot level functional trait values is available in SI C.4. Based on the available of functional trait data, plot level values were calculated for leaf phosphorous (Leaf P), leaf area per unit mass (LMA), and measured branch wood density (WD).

4.4.5 Climate Data

Precipitation data was obtained from the Climate Hazards group Infrared Precipitation with Stations dataset[27], covering the time period 1981 to 2021, at a spatial resolution of 0.05 °. Daily estimates were temporally resampled to monthly averages in Google Earth Engine[52] (code available in SI C.4), and then downloaded and used to calculate monthly precipitation and Maximum Cumulative Water Deficit (MWCD). MCWD was computed months as the difference between precipitation and Potential Evapotranspiration, with deficits accumulated over all months where precipitation was inferior to Potential Evapotranspiration and being reset to zero when precipitation exceeded Potential Evapotranspiration, a monthly evapotranspiration requirement of 100mm was assumed. Precipitation and MCWD monthly anomalies were then calculated using Equation 4.2:

$$StandardisedAnomaly = \frac{X_t - \overline{X}}{\sigma} \tag{4.2}$$

where $\mathrm{X_t}$ represents the mean precipitation/MWCD value of month t, $\overline{X}$ represents the mean precipitation/MCWD of month t between 1981 to 2021, σ the standard deviation of precipitation/MCWD month t between 1981 to 2021.

4.4.6 Statistical Analysis

To investigate the controls on long term mean and trend in AGWP, the mean and trend in AGWP was calculated per plot. Plots were excluded if they had less than two censuses periods (three censuses), or had data which covered less than ten years to give us confidence that these values were representative of the true average and trends. Long term mean AGWP was then modelled as a function of long term maximum cumulative water deficit, and basal area weighted functional trait averages at the plot level. Long term trend in AGWP was modelled as a function of the long term trend in climate variables and the same community-weighted functional traits at the plot level.

The relationship between functional trait variables was investigated before any analysis took place (SI C.4 for analysis) and on the basis of the correlation strength between variables the candidate variables was reduced to Leaf Phosphorus, Leaf Mass per unit Area, and Branch wood density, so as to not over-inflate models used to fit a relatively small number of data points (n=33).

Statistically analysing the relationship between AGWP, functional traits and climate was made difficult by the relatively lower number of plots that had overlapping functional trait data that allowed us to compare them. To this end we conducted a multiple regression approach, and a subsequent univariate approach of mean AGWP, and trend in AGWP as modelled by each functional trait, and MCWD to increase confidence that the results we saw were robust, and not due to low statistical power. For each trait a univariate linear regression was run, the total number of plots where it was greater than the number used for the multiple regression was down sampled without replacement to the number of plots used in the multiple regression to give the comparison approximately the same power. This down sampling was then bootstrapped 1000 times and mean, standard deviation and 2.5/97.5 quantiles were then calculated from the bootstrapped population. Variables for which the 95 quantiles crossed zero were excluded from analysis as the direction of their relationship with AGWP could not be reliably inferred.

Variable selection for the multiple regression model was undertaken using a backward-forward selection algorithm based on AICc. Starting with a model with just an intercept, baseline AICc was calculated. For each following step each variable was added to the model one at a time from the selection of possible variables the change in AICc calculated. The variable which resulted in the greatest increase in AICc was then added. This process was repeated until the addition of any variable resulted in an increase in AICc of less than 2 producing the final model for interpretation. After each addition each variable was also removed and the change in AICc, again calculated, to ensure that the order in which variables enter the final model doesn't bias their inclusion/exclusion which may occur when relationships between variables exist.

Model stability was investigated using a bootstrapping approach[53] to quantify the extent to which our final model was stable to mild to moderate perturbation, and thus to what extent we can rely on the final model for inference. The underlying dataset was bootstrapped (n=1000), for each bootstrap iteration, 70% of the data used was selected at random, the final 30% was then randomly sampled with replacement to introduce perturbation. Forward elimination was then used to produce a final model as outlined previously. Mean, standard deviation and 2.5/97.5 quantiles were then calculated from the bootstrapped population. Variables for which the 95 quantiles crossed zero were excluded from analysis as the direction of their relationship with AGWP could not be reliably inferred.

Given the spatial nature of the response and explanatory variables, the residuals of the final model were investigated for spatial dependency which may violate the linear regression assumption of independence of error. A data drive approach was used to investigate a range of different spatial structures, including 1,2,3, and 4 nearest neighbours, and distance and inverse distance weighted neighbours within the bounds of 100km, 200km, 500km, 1000km and assuming all sites were connected. Moran's I was then calculated for each spatial structure, with statistical significance being investigated using a monto carlo permutation approach.

All statistical analysis was conducted using R version 4.2.2[54]. Data visualisation was performed in R using the ggplot2[55] package and QGIS[56]. Sample size for univariate and multivariate analyses can be found in C.2/

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Chapter Five

Discussion

Forests can be found across boreal, temperate, subtropical and tropical climatic domains. In total, they cover 4.06 billion ha (40 million km^2)[1], nearly a third of the planet's land surface[2]. Across these climatic domains forests vary widely in form and function, including tropical and temperate rainforests, coniferous, deciduous, mangrove, boreal, and montane forest, to name but a few. Despite the critical role they play in human wellbeing[3], at a global level forests have historically[4, 5], and continue to, experience a wide range of threats[6]. The value of forests is widely discussed in the literature, and is ultimately as much a political and philosophical exercise as it is a scientific one. However, no matter the methodology used, the world's forests are consistently valued extremely highly[7]. Ultimately, because of the role that forests play in sustaining life and maintaining human wellbeing, we should as a global community care a great deal about their status, and their future, as any threat to them is a threat to global human wellbeing.

A key observation when examining forests, is that there is considerable diversity in how forests respond to stress[8]. Some forests when experiencing drought, for instance, show relatively little change, while others for a similar magnitude drought show dramatic responses in productivity[9], mortality[10], community composition or ecosystem service provision. Understanding why these differences exist, and what factors moderate the response of forest to stress is one of the core research questions of this thesis, and lies in the realm of an area of research known as ecosystem stability.

The field of ecosystem stability straddles conceptual and applied ecology and is extensively discussed by both. In this thesis, two core paradigms from the ecosystem stability literature have been used in order to guide the development of research questions, methodologies, and the interpretation of results to help us better understand the underlying stability of forests. The first paradigm is the stability landscape[11], which allows us to describe and define components of stability using a metaphor of a how a ball may move across a landscape with varying topography. The second paradigm is the phrasing of all stability studies in the question of “stability of what, to what?” [12] which allows us to design research questions and methods that provide information that can easily be linked to an aspect of ecosystem stability.

There are a number of different aspects to ecosystem stability, and so stability is often broken down into a number of subcomponents[11]. Considerable variation exists in the literature in how these different aspects of stability are labelled, and so for the purpose of this thesis we define stability as having four components, resistance, resilience, latitude and precariousness. A variety of methods, and indices exist in the literature to estimate these different components, with resistance and resilience being the most commonly studied. A number of seminal papers exist in the forest-stability literature, but beyond these few papers, stability is not commonly discussed, and relevant results are often not linked back to ecosystem stability theory, leading to there being surprisingly little literature on how forest stability varies globally.

The role that species richness and diversity plays in moderating stability is extensively discussed in the literature, with numerous studies finding contradictory results on the direction and magnitude of this relationship. There is a growing consensus, that it may be functional diversity, or the value and range of species traits, rather than number of species, or specific species per se, which most strongly determines ecosystem functioning and stability[13].

Bar a few exceptions forest ecosystem stability is often studied at small spatial scales, often single plots, or over small areas. In many papers once an element of stability is measured, there is no further investigation as to what variable influences this stability, and even more rarely is the relative importance of multiple potential controls on stability investigated. The primary aim of this thesis was therefore to develop a deeper understanding of the underlying variables and processes that influence variation in forest productivity, and stability of productivity to climate, and climate perturbations. A particular focus has been put on exploring the role biodiversity and functional trait diversity play in mediating these relationships.

This thesis will focus on exploring the general principles that govern these relationships at landscape scales, rather than site specific, or local scaled examples. To this end, remotely sensed data will be relied on throughout in a variety of forms to allow larger spatial extents and time series to be studied, than realistically could be collected at a plot level.

5.1 Overview of findings

5.1.1 Chapter summaries

In chapter two we examined the photosynthetic response of Amazon forests to the 2015/16 El Nino-Southern Oscillation (ENSO) event. Productivity was proxied using remotely sensed solar induced fluorescence (SIF). We compared the relative importance of ENSO-associated climate anomalies, background climate, and soil characteristics in explaining the observed variation in basin-wide forest photosynthetic anomalies during the ENSO. Our final model explained 25% of forest photosynthetic response, and highlighted that the background climate that a forest has experienced, and its soil conditions are more important in determining the productivity response to the ENSO, than the magnitude of the ENSO that that forest experienced. We found marked sensitivity differences across Amazonia, with North-Western forests being the most sensitive (least resistant) to precipitation anomalies, likely relating to variation in forest species composition and background water stress.

In chapter two we focused on stability to a single short term press event, to build on this in chapter three, we focused on exploring longer term climate resistance in temperate forests using the United Kingdom (UK) as a case study. Remotely sensed normalised difference vegetation index (NDVI) was retrieved for all pixels identified as forest in Forest Research's subcompartment database[14]. For each forest pixel the NDVI time-series was modelled as a function of precipitation and temperature anomalies in a generalised linear framework. The climate coupling (variance explained by the model) and climate sensitivity (standardised regression coefficients for temperature and precipitation anomalies) were then extracted from each pixel model as measures of forest stability to climate. Our result indicate a marked differences in climate-sensitivity and coupling across the UK, with significant spatial patterns in both climate coupling and sensitivity being found. We show that forests in the north-west, west and south-east respond in fundamentally different ways to climate extremes. Forests in the north-west and west of the UK when experiencing drought have historically tended to increase productivity, while those in the south-east when experiencing drought have tended to decrease productivity. We compared the relative importance of background climate, soil characteristics and forest attributes in explaining the observed variation in climate sensitivity using a random forest framework. The final model explained 72% of the observed variation in temperature sensitivity, and highlighted the importance of background climate, and forest attributes in explaining NDVI-temperature sensitivity, again likely explained by variation in community composition.

In the first two chapters, forest productivity was proxied using remotely sensed data in order to assess the drivers influencing stability patterns at a landscape scale. Remote sensing while a powerful tool that allows for large spatial and temporal extents to be analysed, comes at the cost that productivity is never directly being measured, but instead inferred from satellite imagery. To this end, in chapter four, we used a long term, pan-Amazon network of forest inventory plots to directly observe productivity, to explore the role that functional traits and climate play in moderating both long term productivity patterns, and short term productivity response to climate anomalies. Modelling revealed that functional traits played a key role in moderating all aspects of productivity measured. For long term mean productivity, wood density and average maximum cumulative water deficit (MCWD) were the only significant variables in the final model, for long term trend in productivity just leaf Phosphorous was found to be significant, and just wood density was found to be significant in the final model for productivity response to the 2015/16 ENSO. Our results highlight the importance of functional traits in moderating productivity responses both in the long term, and in response to climate anomalies. They also support an increasing body of literature that suggests that the Amazon forests ability to maintain, or increase its carbon sink ability may be limited by nutrient availability, with significant implications for the global carbon balance in face of the ongoing trend in atmospheric carbon emissions.

5.2 Appraisal of Thesis Aims

In this section I will review the overarching questions developed at the start of this PhD, and listed in the introduction to this thesis, in light of the research and insights obtained during the course of this PhD.

5.2.1 How can we measure forest stability across large spatial extents to understand landscape scale stability?

One of the findings of the literature review conducted at the start of this PhD was that of the existing literature, only a handful of studies had explicitly studied the stability of forests at larger spatial scales. Although more examples could be found for smaller spatial scales, single sites, or within site variation, scaling up these findings to landscape scale processes is difficult, and in many cases not reliable as it's likely that the factors moderating stability at a landscape scale are different to those moderating stability at small spatial scales[15]. To this end we decided that in this thesis we would explicitly examine the factors and processes that influence forest stability at landscape scales in order to better our understanding of the large scale processes that moderate forest stability.

Four different methods were developed over the course of the PhD to quantify the stability of forests to climate, and climate perturbation. This next section will review each of the different methods that were developed, the underlying logic of how each conceptually links to stability, and any limitations of the methodology that were realised during, or after, its development.

Modelling of productivity anomalies to a large press disturbance using climate anomalies and other variables

The first method that we trialled was to examine the response of forest productivity to a single large pulse perturbation. We chose the 2015/16 ENSO, and the impact that it had on Amazon forest productivity during the peak of the event. The 2015/16 ENSO event was chosen as it was associated with the most extreme drought and period of warming on record[16] for the Amazon, and thus offered an ideal first case study in terms of the strength of signal to noise ratio.

In this case, stability was assessed using an anomaly methodology. We computed standardised anomalies for productivity, temperature and precipitation, defined as:

$$StandardisedAnomaly = \frac{X_t - \overline{X}}{\sigma} \tag{5.1}$$

where $\mathrm{X_t}$ represents the mean SIF/climatic value during the October to December 2015 period, $\overline{X}$ represents the mean and σ the standard deviation of the baseline period (October to December) between 2007 and 2014 (excluding 2015).

This productivity anomaly was modelled as a function of climatic anomalies, background climate and soil characteristics. Stability was quantified by examining the relationship between productivity anomaly and precipitation/temperature anomaly. A strong relationship, as indicated by large standardised coefficients, or high model R^2 (in a model of just productivity and climate anomalies) indicates a low overall resistance of productivity to climate anomalies. Conversely, a weak relationship between productivity and climate, indicated by a small standardised coefficient, or low model R^2 (in a model of just productivity and climate anomalies) would indicate higher resistance, as the variation in climate anomalies do not explain the observed variation in productivity anomaly.

This methodology was designed to quantify the resistance of Amazon forests to short-term climate anomalies, and was inspired by the definition of resistance, "The ability of an ecosystem to withstand perturbations and remain unchanged", and existing literature that had looked at forest resistance at large spatial scales[17].

One of the key challenges that was faced designing a methodology to look across large spatial scales is that productivity changes at a pixel level cannot be directly compared to each other, as sites will vary in their baseline productivity, so what would constitute a significant decline in productivity in one area, may be trivial for another area that has a much larger natural variation in productivity. To overcome this problem an anomaly approach was utilised in which the productivity change during the ENSO was standardised by subtracting the long term productivity mean, and dividing by the long term standard deviation of productivity for that pixel. This transformed the units of change into standard deviation units relative to the mean and variance of that pixels history. This therefore made it possible to directly, and fairly, compare forested pixels across the Amazon and to use a single model to investigate spatial variance in resistance.

A potential limitation of this methodology is the assumption of linearity between productivity anomaly, and climate anomalies, implicit in the use of the generalised linear framework that we used for statistically inference. Linear models were chosen as they are simple to interpret, and generally considered to be robust to minor violation of their assumptions, where sample size is sufficiently large[18]. To address potential non-linearity in the relationship between productivity and climate anomalies we considered both linear and quadratic terms for temperature anomaly to better represent its non-linear relationship with productivity as suggested by the literature[19].

Modelling of productivity over a long time period using a time series of climate data

In the first method we focused on describing stability in terms of the response of forest to a single large perturbation, however, these large perturbations are relatively rare (although with climate change they are predicted to increase both in frequency and intensity[20]). It is also possible that the resistance quantified by looking at the response to such large events is not representative of the resistance that forest has to smaller magnitude climate perturbations. To explore this, the second method we developed to quantify stability used a 20 year long time series of productivity (proxied by NDVI) and climate data. For each pixel, the NDVI time series was modelled as a function of precipitation and temperature anomalies in a linear regression framework. All variables were standardised by subtracting the long term mean, and dividing by the long term standard deviation for that pixel, to facilitate fair comparisons with other pixels. Stability was then quantified for each forested pixel by extracting the variance explained by its model (climate coupling), and the standardised coefficients (climate sensitivity/resistance) for temperature, and precipitation anomalies as measures of how resistant the forest in that pixel is to climate perturbations of varying magnitudes over longer times periods. The interpretation of these variables was similar to the first method, with larger climate coupling/sensitivity indicating that variation in climate more strongly controlled variability in productivity, and thus the forest in that pixel is less resistant to climate fluctuations.

Using this methodology we aimed to capture forest productivity resistance to climate variability more generally by including a range of different strength climate perturbations. This type of methodology is often referred to in the literature as forest productivity-sensitivity[21, 22] to climate, rather than being referred to as resistance, however for consistency with the terminology of this thesis it will referred to as resistance.

A number of issues arose during the development of this methodology. As a time series of productivity data was used, we found that in young forests productivity-climate relationships were hard to disentangle from growth patterns as growth appeared to more strongly influence NDVI patterns than any observable climate effect. We therefore restricted our analysis to mature forests by using the planting age detailed in the National Forest Estate Subcompartments (SCDB) 2019[14], and restricted the analysis to subcompartments that have been planted for at least 30 years. This threshold was determined by grouping pixels by age classes and examining NDVI time series for each group, selecting the age for which the NDVI no longer showed growth curves (SIB.5 for details).

A further issue that arose during the development of this methodology was spatial autocorrelation. Autocorrelation in the model residuals in all chapters was tested by creating a wide range of spatial weight matrices including, 1,2,3,4 nearest neighbours, distance and inverse distance matrices ranging from the smallest distance required for all points to have at least one neighbour, and increasing in increments of 100km. Moran's I was then calculated using each of these matrices, and the most significant, in terms of p-value, chosen to best represent the spatial structure of the residual information. In the second and third, but not the fourth chapter, statistically significant spatial autocorrelation was detected in the residuals. Accounting for this residual spatial autocorrelation using a spatial lag, or spatial error model would certainly be an interesting way to further investigation in both of these studies.

Another potential limitation of this study is that it produced noisy results, which complicated statistical analysis, and restricts the power of this methodology. From examining the NDVI-climate responses in detail, at least part of this noise is attributable to low signal to noise ratios for low magnitude climate perturbations. For these small magnitude climate perturbations, it appears that the impact that it has on productivity is harder to quantify, as other unmeasured processes have larger impacts on the productivity signal.

A final limitation that was realised during the analysis of the NDVI time series was the impact that cloud cover can have on the amount of remote sensing data available for analysis. The UK over the course of a year can experience significant cloud cover, as we employed cloud masking to remove cloudy pixels as they can adversely impact calculation of NDVI, some pixels were left with relatively little data for regression over the 20 year period. This means that the quality of the linear regression is lower in some areas, compared to others. To quantity the impact that this may be having on our results, we reran the analysis removing all pixels for which the model R^2 (climate coupling) was below the mean nationwide average, therefore leaving us just with models in which we could have greater confidence. Rerunning the Random Forest with just this subset showed similar results for all key findings, thus giving us greater confidence in the full dataset. (SI B.3 for details).

Modelling of average productivity, and trend in productivity using climate and other variables

The first two methods used remotely sensed productivity as the dependent variable, as it is a relatively easy method to obtain data over a large spatial scale. However, as mentioned previously this comes at the cost that productivity is never directly being measured, but instead is being inferred from satellite imagery.

The third methodology we developed therefore aimed to investigate how stability can be measured using ground sourced productivity data. To this end we made use of a pan-Amazon network of long term inventory plots[23, 24, 25] in order to investigate climate-productivity relationships. For each plot, above ground woody productivity was calculated for each census interval, and these time series used to calculate long term mean productivity, and the long term trend in productivity. Controls on the spatial patterns in both these variables were explored using long term climate trends/averages, and community weighted functional trait values. Within the conceptual framework used, this doesn't neatly fall into any specific aspect of stability, and instead allows us to explore more generally the productivity-sensitivity of Amazonian forests.

Modelling the percentage change in productivity to a large press disturbance using climate anomalies and other variables

The final method that we developed as part of this thesis was based on the same data[23, 24, 25] as the previous method, and took advantage of the fact that during the time series for which we had forest inventory data, the 2015/16 ENSO occurred allowing us to investigate productivity response to a short term press perturbation using plot productivity data.

Percentage change in above ground productivity change was calculated between before, and immediately after the 2015/16 ENSO at a plot level, to account for variance in plot baseline productivity. Stability was inferred through modelling the percentage change as a function of average MCWD over 2015/16. A strong relationship, as indicated by large standardised coefficient, or high model R^2 (in a model of just productivity and MCWD) indicates a low overall resistance of productivity to drought (as proxied by MCWD).

Given the experience gained developing the previous two methods, the third method for quantifying stability is relatively straightforward and no significant issues were encountered. Most of the difficulties of this method arose from the use of plot data, which requires a significant amount of pre-processing and site specific data knowledge, in order to assure that the data used for statistical inference is of high quality. This required a significant amount of time, as the metadata for this screening of site level data is not easily accessible, and often lies with individuals rather than being recorded in a database. Additional quality screening involved selecting sites that had sufficient data, to ensure that long term means, and trends could be reliably estimated.

The main limitation of this method, is how representative the network of sites that we used is of the Amazon more widely. Although we had plots from each of the biogeographic zones delimited by Feldpausch et al (2011)[26] of the Amazon (Figure 5.1), we can see that there is a clear lack of plots from the central Amazon, meaning that our results are less representative of this region.

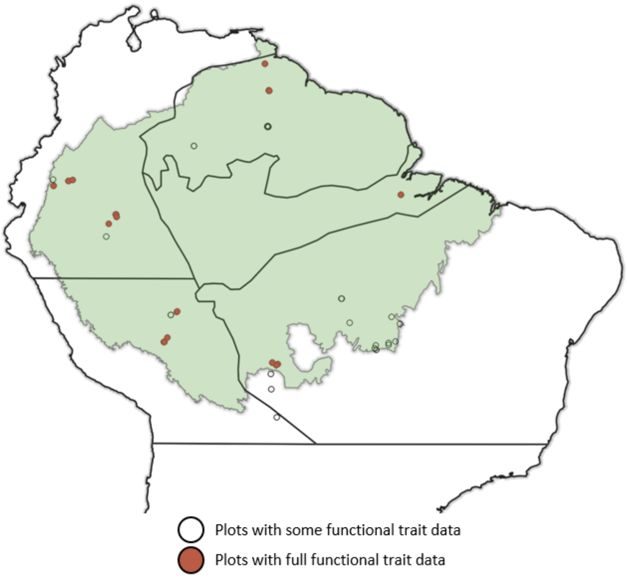

Figure 5.1: Spatial distribution of plots with at least one functional trait of interest (hollow circle) and plots for which all functional traits of interest have been collected (filled circle).

Another limitation of this methodology was sample size for the purpose of statistical analysis. With the remote sensing methods that we used sample sizes were very large, allowing for robust statistical analysis. However, with plot based studies in the Amazon, data collection is time consuming, difficult and expensive. Furthermore, as we wished to investigate the role of functional traits, intersecting the plots for which we had both inventory data and functional trait information reduced the number of sites further. The end result of this was a relatively small total sample size that had to be analysed with caution to avoid statistical problems, and prevented the use of more sophisticated statistical tools. In the previous methods, backward elimination methods were used for variable selection, as the large sample size meant that we could be confident in this process producing reliable results. However, with the sample size for this analysis being just 33 plots, statistically it would have unreliable to perform backward selection starting with four variables as the estimation of coefficients would be untrustworthy with such small sample sizes. To account for this we instead used a forward selection methodology, which because of its iterative nature starting with just a single variable, accounts for the problem of too few data points per variable, by using the AICc to access whether the trade off of adding a variable and its effect on prediction error, is penalised as a function of the number of variables in the model. This variable selection method is relatively under-powered compared to backwards elimination, but removed the risk of going beyond what was statistically supportable by the sample size available.

In addition to these challenges, the irregularity of when data was collected also presented a problem. As this was not a bespoke dataset collected for the purposes of analysing the impact, therefore although we wished to compare productivity before and immediately after the ENSO, very few plots happened to be sampled during the exact dates required. Therefore, a window of two years after the ENSO was used to increase the sample size for collection with the acknowledgement that the percentage change for such plots will be a combination of the impact of drought, and subsequent recovery.

In terms of implications, for stability research the methods developed during the course of this PhD represent a significant contribution towards developing and testing methods to analyse forest stability over large spatial, scales. As there are relatively few methods published in the literature this represents a sizeable increase in the number of methods available. In terms of ecological research, the implications are significant. By providing methods to measure stability at large spatial scales, the base data to investigate what moderates the stability of forest, and other ecosystems to a wide range of stressors, and perturbations can now be generated, and investigated using any variable that for which data is available.

5.2.2 At a landscape scale can we disentangle climate, biodiversity, and functional trait influences on moderating productivity?

When examining the response of forest to perturbation, conceptually the response that we see is a combination of the magnitude of the perturbation, modified by the community and functional trait composition, biodiversity effects, and all other variables that contribute to the systems stability to that particular perturbation.

To understand what variables influence stability, we therefore want to examine the explanatory power of candidate stability variables having accounted for spatial variation in perturbation strength. In this thesis we made use of two different methods to achieve this separation, one for single short term pulse perturbations, and the other when examining perturbations of varying magnitude, over a longer length of time.

In the first method, the ecosystem productivity change, or the productivity at the peak of the perturbation, is modelled in a regression framework using both measures of the perturbation strength, and the candidate stability explaining variables themselves. Both dependent and independent variables are standardised before regression so that their relative importance can be evaluated by directly comparing the magnitude of the coefficients. The regression framework means that the coefficient of any variable should be interpreted as the change in the dependent that occurs for a unit increase in that variable, all other variables in the model held constant. This choice of statistical tool therefore allows us to examine the independent effects of both magnitude of the perturbation, and candidate stability variables in order to explore what variables are important in understanding stability to perturbation.

The second method that we developed in this thesis was designed to look across a time series of productivity for a forested area, in order to summarise how the ecosystem responded to a range of different magnitude perturbations. This was achieved through modelling productivity for each area as a function of climatic variables in a regression framework. The total variance explained by the model, and the standardised coefficients of each of the climatic variables were then extracted. These values were assigned to that forested area to characterise the magnitude and direction of the relationship between productivity and climate anomalies. This was repeated for all forested areas in the target domain. The spatial variation in these measures of productivity-climate stability were then modelled themselves as a function of the candidate stability variables in order to explore what variables were important in explaining the spatial variation in stability. In the third chapter this was conducted using a Random Forest framework, while in the fourth chapter a linear regression framework was used.

Both of these methods were successful in allowing us to explore what variables moderate response of productivity to short term climate perturbations and average response over a range of different magnitude perturbations. Their primary limitations arise from the various statistical assumptions that the modelling processes relies on. In the second, fourth and the first half of the third chapter methodology linear regression frameworks are used. Linear regression frameworks make a number of assumptions, however perhaps the most pertinent is the assumption of linearity between dependent and independent variables. This assumption restricts the relationship between productivity and both the climate perturbation, and the candidate stability variables to a linear one. While many systems in nature demonstrate linear characteristics[27], and a linear approximation of a more complicated relationship may be sufficient to understand if any relationship exists, given the complexity of ecosystems the exact relationship could well be non-linear and so this approach would miss such details.

The implications of these results for ecological and stability research are significant, as these methodologies give us a framework to rigorously assess the independent contribution of candidate variables in moderating ecosystem responses to perturbation. Further to this, because the framework is generic, this can easily be applied to a wide range of ecosystem descriptors, and candidate variables with the only real limits being enforced by the sample size required to have confidence in the findings of these statistical models.

5.2.3 At the landscape scale, what factors are responsible for moderating long-term productivity, and short term response to climate anomalies?

This third question represents the core question of this PhD, and to which all three data chapters of this thesis were developed primarily to answer. In order to make our results more widely applicable we developed studies examining ecosystem responses to different types of perturbation, across a range of temporal scales, and in tropical and temperate forests. This section will draw from all data chapters in order to explain our key findings and conclusions from this work.

A.Stability needs to be accounted for When Examining Productivity Variability

Our first key finding is that accounting for ecosystem stability is crucial in order to be able understand the variability we see in the response of forests to perturbation. In the second chapter for instance, modelling of SIF anomalies in response to the 2015/16 ENSO showed that a model containing only measures of the magnitude of the ENSO, had very little explanatory power. Examining the spatial patterns in SIF anomalies it became clear that despite significant spatial variation in the magnitude of the drought associated with the ENSO, the photosynthetic response was fairly uniform across the region. This suggested that some form of compensatory response at a landscape scale was occurring. In this case it was only by including metrics of the long term climatic conditions that different forested areas had historically experienced, that we were able to explain a significant portion of the observed variation. These historic variables, as I will go into more detail later, likely act as a proxy for the historic selection pressure that has acted in that area. With areas with historically lower rainfall for instance, selecting for species and traits over time that are better able to cope with water stress.

All three data chapters showed a similar pattern, whereby models of productivity responses to perturbation that did not include some measure of either, historic climate, functional traits, or biodiversity which act as a proxy for community resistance to perturbation, had relatively little explanatory power. This is not to say that the magnitude of the perturbation is unimportant, indeed both temperature and precipitation anomalies were significant in the final model explaining SIF response to the ENSO in the first data chapter, just that they are relatively of lower importance compared to the variability seen in forest resistance.

B.Forest Resistance Varies Considerably Spatially

Our next key finding, is that considerable variation exists in forest resistance to climate perturbations, which may be explained by resistance, however it is achieved, being costly in terms of the resource investment required. This high investment cost may result in lower growth, and subsequently a lower competitive ability (when there is no drought) compared to species, or communities that do not invest in traits that confer resistance. This trade-off between growth and resistance is most clearly shown in the results of the fourth chapter (Figure 5.2), where we were able examine the role of functional traits on productivity on both long term productivity, and the productivity response to perturbation. Our results indicate that plots with higher average community wood density had lower long term mean productivity, but generally had a more positive percentage productivity change in response to the ENSO. The mechanistic link in this case may be that although higher wood density is often considered an expensive investment, which results in lower long term average productivity, it conferrers enhanced xylem resistance to embolism[28] as well as greater resistance against mechanical damage[29]. Therefore, communities with higher wood density grow slower, but have an enhanced ability to short term pulse drought perturbation.

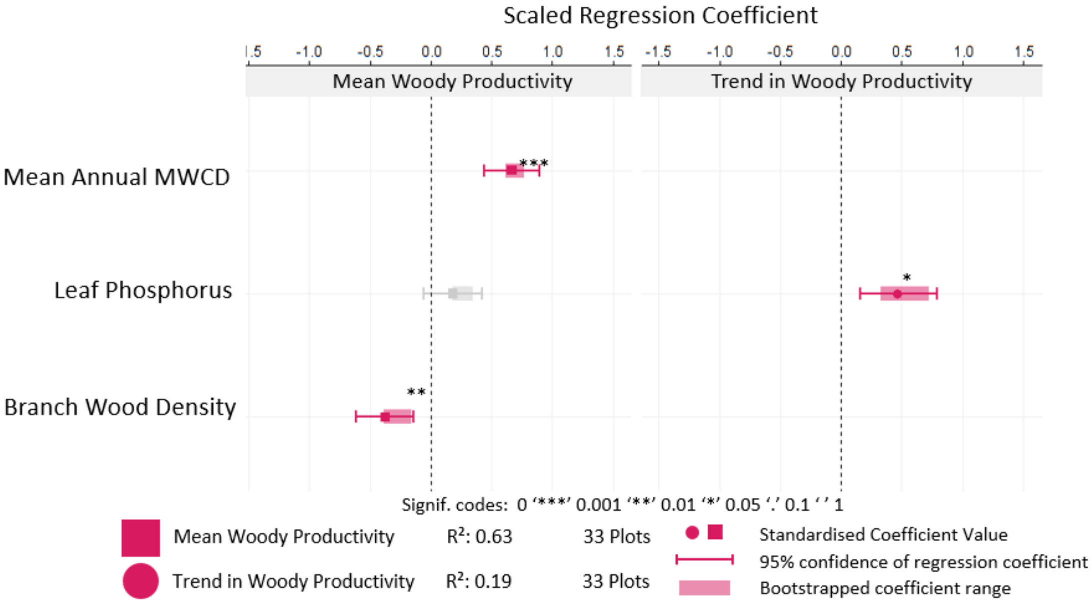

Figure 5.2: Standardised regression coefficients for the best models for predicting mean woody productivity (left) and trend in woody productivity (right) across Amazon forests. Points show the standardised coefficient value in the best model for each, wings show the 95% confidence interval, shaded rectangle represents the 95% range when the underlying dataset was subjected to moderate bootstrapped perturbation.

This result is consistent with the core concept of the leaf economic spectrum[30] which has previously found that species with more conservative growth tend to be associated with more "expensive" functional traits such as high wood density. Species with these conservative strategies tend to be slower growing, because resources are finite and investing in high cost strategies, leaves less for biomass accumulation, therefore resulting in slower growth[30]. The economic spectrum appears to link through to stability as many of these high cost strategies, including high wood density as found in this thesis, or high leaf mass per unit area[31], have been found to confer increased resistance to perturbation. Higher wood density for instance has been found to confer resistance to drought by decreasing the chance of embolism[28] due to water stress, and higher LMA has been found to increases resistance to mechanical damage[29]. The extremes of the leaf economic spectrum may therefore provide a link through to understanding stability with the two extremes being species that invest heavily in order to survive perturbation, but consequently have lower growth, and species that do not invest in such expensive traits, prioritising instead high growth and who risk mortality during perturbation by lacking these adaptations.

It should be noted that while the low wood density-high above ground woody productivity relationship has been previously attributed to a trade-off between wood strength and cost of construction[32], this interpretation of the ecological role of wood density has been questioned by some studies which have an employed an engineering perspective to suggest that high wood density does not confer higher mechanical strength but may be associated with a lower maintenance respiration cost[33].

Spatial variation in forest resistance to climate perturbation can therefore be seen to represent an evolutionary equilibrium based on the probability of climate perturbation. In low probability areas it is the "better" strategy to grow fast, outcompete slower more conservatively growing communities, as the risk of mortality due to perturbation, is low and vice versa in high perturbation probability areas. With climatic anomalies predicted to become more frequent in the near future[20], the distribution of these historic probability areas are likely to change rapidly as the areas at risk of climate perturbation change, meaning that the community level strategies we see may well predict how forest will respond.

C.Variation in Community Species and Functional Trait Composition is Key

That community composition, either in terms of species or functional trait composition is important in understanding stability to climate perturbation is well supported by published literature. Seasonal water stress for instance has been found to exert a fundamental control on the biogeographical distributions of Amazonian tree species, with many species being restricted in range to the wetter regions of the Amazon[34]. Over more local scales, variation in water table depth can also strongly influence community species composition, with near complete species turnover observed in closely occurring forest plots on shallow water tables compared to those on deeper water tables[35]. Such large differences in floristic composition along water availability axes are likely associated with differences in community-level drought tolerance. It has been shown for example that species occurrence along hydro-topographic gradients in Central Amazonia is underpinned by differences in embolism resistance[36], as species occurring on water-limited plateau areas are considerably more embolism-resistant than those occurring in valley areas with more access to water([36]. Community-level differences in hydraulic traits have been found to explain why a more seasonal Amazon forest experiencing a strong drought anomaly during the 2015/16 ENSO presented a similar canopy conductance response to a less seasonal forest experiencing a weaker climatic anomaly[37].

In both the second and third chapters' historic climate variables were the single most important group of variables, with seasonality of rainfall actually featuring in both as the most important variable. Rainfall seasonality has been found in studies looking at intra-species trait variation to be important in explaining spatial patterns of trait adaptation[38], and our findings demonstrate a similar effect at the community level. This results combined with the fourth chapter where we explicitly test functional traits and find them important, indicates that in all of our studies the functional trait makeup of the community likely played an important role in determining its stability to perturbation. It is interesting to note that this holds true across both the temperate and tropical forests we examined, which are very different ecological systems, and for both resistance to short term extreme perturbation as well looking across a range of different perturbation strengths.

In the third chapter we had the opportunity to test the relative explanatory power of community functional trait composition (as proxied by historic climate), and species identity directly to see which matters more in their contribution to resistance. In this chapter remotely sensed NDVI was retrieved for all forests identified in Forest Research's subcompartment database[14]. For each forest pixel the NDVI time-series was modelled as a function of precipitation and climate in a generalised linear framework. For each of these pixel level models, the climate coupling (variance explained by the model) and climate sensitivity (standardised regression coefficient for temperature and precipitation) were extracted as measures of forest stability to climate. Climate coupling and climate sensitivity were then modelled as a function of historic climate and biodiversity information from the subcompartment database, including the most common genus in the subcompartment. Modelling both background climate variables, acting as a proxy for functional trait composition, as previously described, and genus in the same framework allowed us to directly compare their relative explanatory power. We found that genus was significant, and had some clear and consistent patterns. Betula genera were associated more often with high resistance forests, and Fagus and Fraxinus genera were more often associated with lower resistance, however in terms of relative importance the historic climate variables were far more important, indicating for the subset of UK forests that we tested, that community trait composition is more important than the genera present per say.

The comparison we make in this chapter should we viewed with the caveat that the forests in the UK forests have low species richness, and are highly managed systems which may weaken the relationship between perturbation and response through compensatory management options which may act to lessen the impact of climate perturbation on forests. Furthermore, due to evolutionary relationships, genus and functional trait composition are likely correlated, and thus disentangling them statistically may be difficult.

D.Other Controls on Resistance

The final finding that I wish to highlight is related to what other major factors we identify as important. In the third chapter, we find a significant role of a number of background climate variables most of which fit into the narrative of the community composition reflecting historic climatic selection pressure. However, long term mean growing season temperature in the third chapter, was found to have a relationship with temperature sensitivity opposite to expectation. Forests with higher mean growing season temperatures were more commonly associated with more negative productivity values during droughts compared to forests located in areas with lower mean growing season temperatures. This finding is perhaps unsurprising given the climate context of the UK, as temperate forests often have mean growing season temperatures (mean growing season temperature found in this study was 13°C +/- 2°C) well below the photosynthetic optimum temperature for the majority of broadleaf (between 23°C and 30°C)[39] and coniferous tree species (between 10°C and 20°C)[39]. Therefore, water and nutrients permitting such forests may be expected to respond positively to higher temperatures[40, 41, 42] associated with drought periods.

Evidence of further controls on productivity responses were also found in the fourth chapter. In this chapter we found that the only significant control on the long term trend in productivity was leaf phosphorus. The relationship between the two was positive indicating that plots with larger mean community leaf phosphorous concentrations, were more often associated with larger productivity trends. This finding identifies phosphorus availability as a control on productivity. The ramifications of this may be that while elevated carbon dioxide levels may act to stimulate productivity, we may not see any further productivity increases in many areas, especially in the eastern Amazon, due to phosphorous limiting the capacity of these systems to increase productivity. The key role that phosphorous, and other such limited nutrients plays in moderating changes in productivity has been found now from a number of different types of study examining the question from a variety of angles including experimental fertilisation[43], ecosystem modelling[44, 45] and examination across phosphorous gradients[46].

5.3 Suggestions for Future Research

In order to further advance our understanding and address knowledge gaps, this section delves into key recommendations and potential avenues for future research in the field.

In the conception of this thesis we explored and defined stability as being resistance, resilience, latitude and precariousness to draw clear distinction between components which are often confused and conflated in the literature. In the end, we focused primarily on exploring forest resistance, and what variables moderate resistance to short term climate perturbations, as at a landscape scale there is still a great deal of uncertainty in understanding this relationship. Building on this work, it would be interesting to examine different components of stability, develop methodologies for measuring them consistent with the conceptual framework outlined in this thesis, and to examine whether the controls we have identified in this study are also important for other moderating other components of stability.

By measuring different components of stability it would then be possible to examine relationships, between the different stability components. Trade-offs, for instance between forest resistance and resilience to extreme climate perturbation have been identified by a global study examining gymnnosperms[47]. It would therefore be interesting to examine why these trade-offs exist, and what variables moderate such trade-offs, as they would provide a fascinating insight into the underlying mechanics of the stability landscape and the constraints it works within.

Continuing with the topic of stability, the case studies used in this thesis provided snapshots in time, or long term averages in the case of the case study of the UK. It is an interesting question to ask if these values are stable over time, and if a forest that is considered stable in response to one perturbation, is also considered stable to a subsequent one accounting for any difference in the magnitude of the perturbation itself. This result would be an important one, as if found to be stable then it would lend weight to the argument that we can use modern, or historic evaluations of stability to inform, or at least better quantify the uncertainty, of how those same forests will respond to future perturbation.

In this thesis we argue that the background climate variables we use act as proxies for community composition both in terms of species present, and functional trait composition, mediated through the idea that long term climate patterns would select for certain species or functional trait compositions. However, it would be interesting to explicitly investigate this assumption through examining gradients of background climate and ground collected inventory and functional trait databases to see to what extent species and functional trait composition correlates to background climate.

Continuing with functional traits, the Forest Plots functional trait dataset that we used in the final chapter has a great deal more potential for investigating how functional traits moderate the response of Amazonian forests to climate perturbation. It has a great deal more functional traits available beyond those tested in this thesis, and it would certainly be interesting to see to what extent other traits explain observed variance in productivity average, trends, and in response to perturbation. It would also be interesting to further investigate the correlation observed between the leaf economic spectrum paradigm, and the response of stability to ascertain if this was a study specific response or a more generally applicable finding.

5.4 Conclusions

The primary aim of this thesis was to develop a deeper understanding of the underlying variables and processes that influence variation in forest productivity, and stability of productivity to climate, and climate perturbations. Given the evidence presented in this thesis, I believe it is fair to say that this aim has been achieved.

The methods presented here demonstrate that it is possible to quantify and describe spatial patterns in stability of forests to climate perturbations at landscape scales, and to understand the mechanisms behind the variation in stability that we observe. The flexibility of the conceptual framework we utilised allowed us to examine forest stability in a range of different circumstances including, single large perturbations, a time series of climate perturbations, as well as long term mean and trends in productivity. The methods developed are equally applicable to remotely sensed data, geospatial databases, as well as ground sourced data, and provide a means to statistically disentangle the effects of climate, biodiversity, and functional trait covariates.

Our results highlight the importance of understanding forest stability when seeking to explain landscape scale variation in forest response to climate perturbation. In all chapters when investigating climate perturbation, the magnitude of the perturbation alone was insufficient to explain productivity patterns. Therefore, any examination of productivity response to perturbation without considering variance in stability will be missing a crucial component.

Investigation of which variables were important in explaining variation in response to perturbation revealed that for both tropical and temperate forests, the background climate that a forest has experienced was the single most important group of explanatory variables in all cases, except when functional traits were directly included in models. Background climate, I argue, ultimately acts as a measure of the selective pressure acting on the community, and thus is informative of the community composition in terms of species and functional traits present. This finding is given further support by the final data chapter of this thesis in which we have direct measurements of both background climate and functional traits, and find that in understanding the response to perturbation only functional traits were in the final model explaining the variation in productivity response.

The finding that functional traits are important in understanding the response of forest ecosystems joins a growing body of literature highlighting the power of a functional trait approach to understanding variation in productivity responses, and offers a mechanistic understanding of the processes underlying stability, and giving us valuable insights into how these forests may respond to ongoing climate change.

Overall these results represent an important advance in our knowledge of the stability of forest productivity to climatic perturbation, and hopefully will pave the way for further forest stability research that will continue to improve our understanding of our planets forests.

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Appendix One

Chapter Two Supplementary Materials

A.1 Supplementary Figure 1

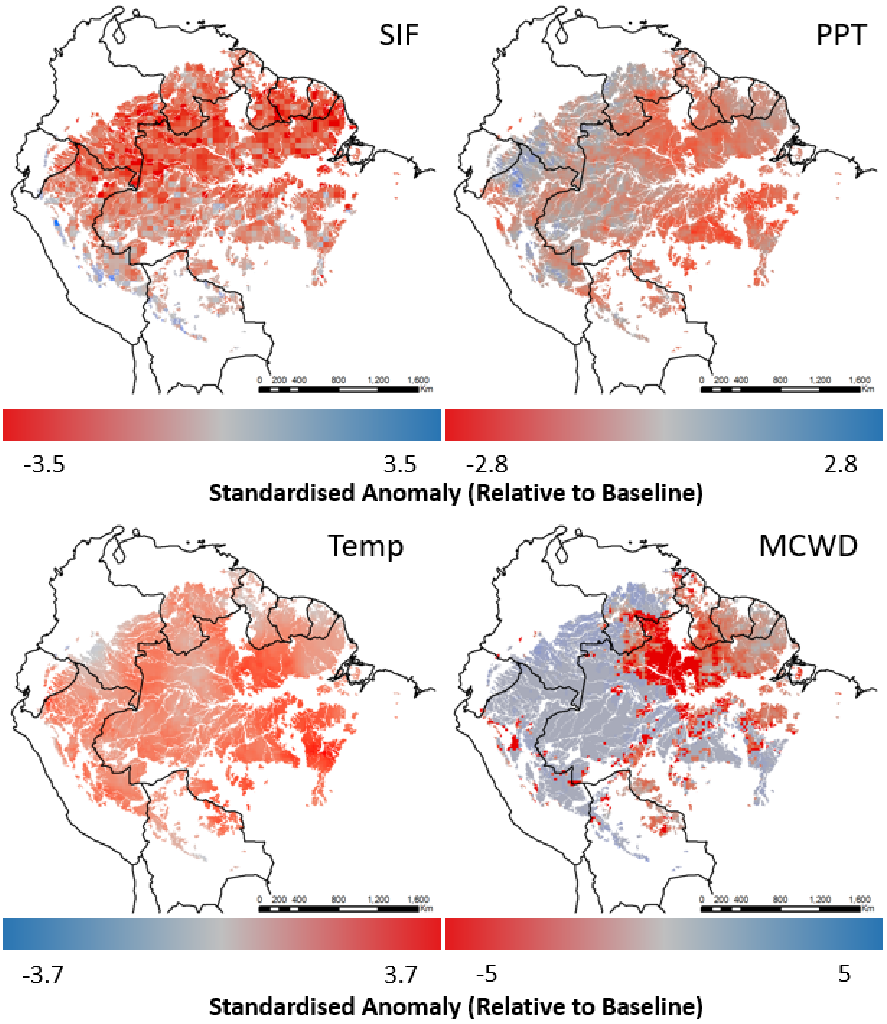


Figure A.1: The spatial distribution of solar induced fluorescence, precipitation, temperature and Maximum Cumulative Water Deficit anomalies for October to December 2015, compared to a baseline of October to December 2007 to 2014.

A.2 Supplementary Figure 2

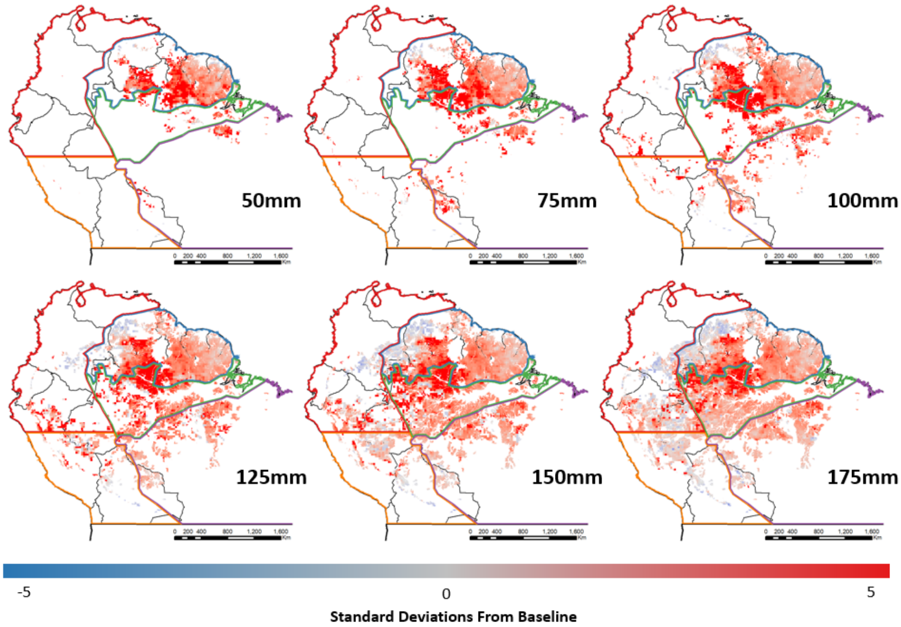


Figure A.2: Maximum Cumulative Water Deficit (MCWD) calculated using a range of assumed evapotranspiration requirements.

A.3 Supplementary Figure 3

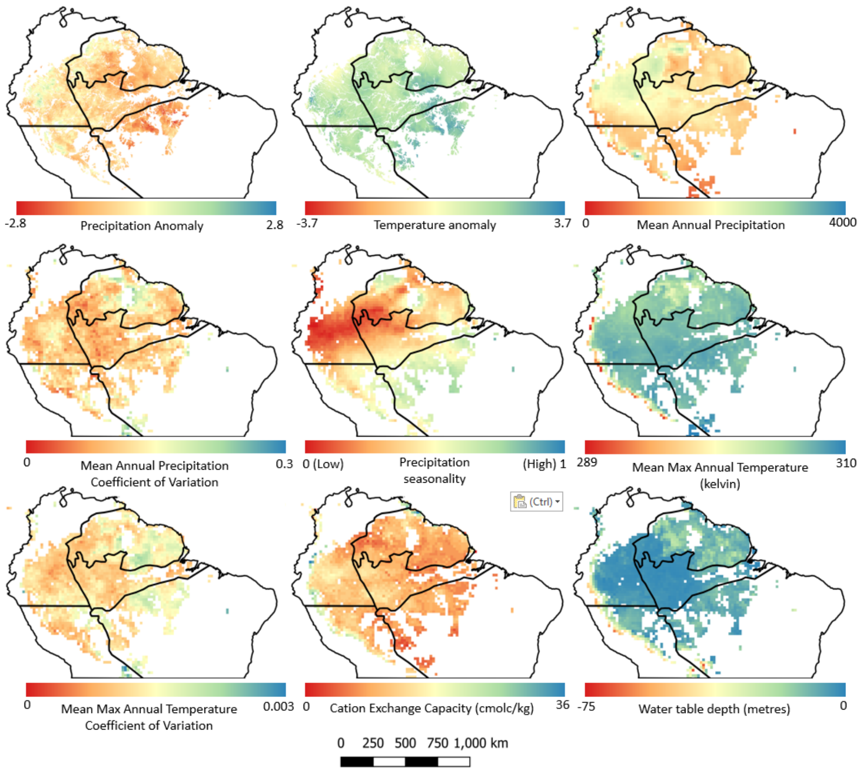


Figure A.3: Spatial distribution of all variables in the final model.

A.4 Supplementary Figure 4

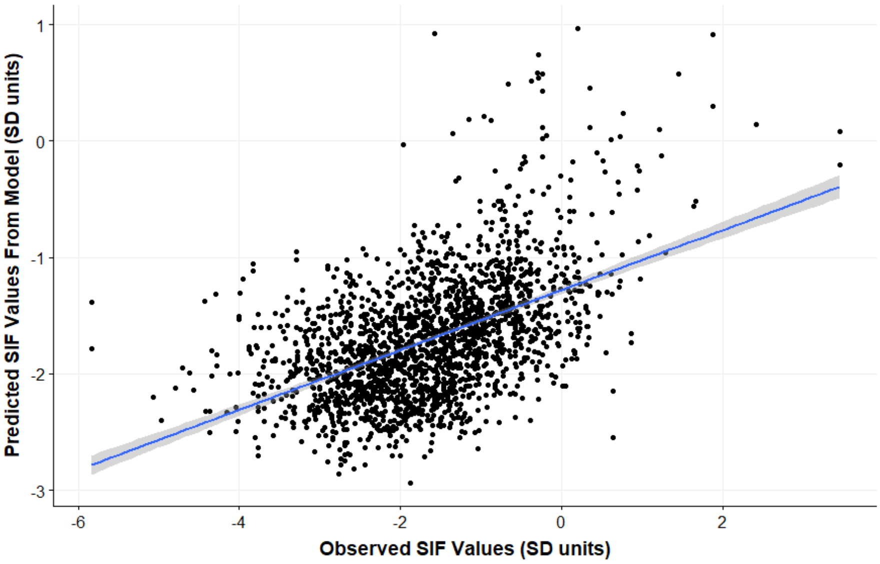


Figure A.4: Modelled SIF values from the final selected model against observed SIF values, blue line represents the trend line, and shaded area around this line representing the standard error.

A.5 Supplementary Figure 5

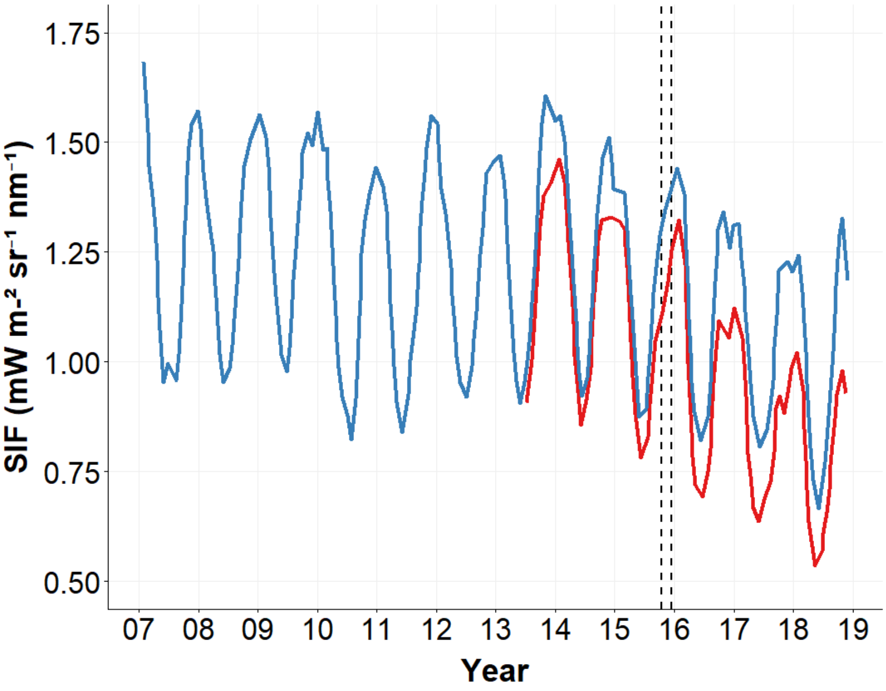
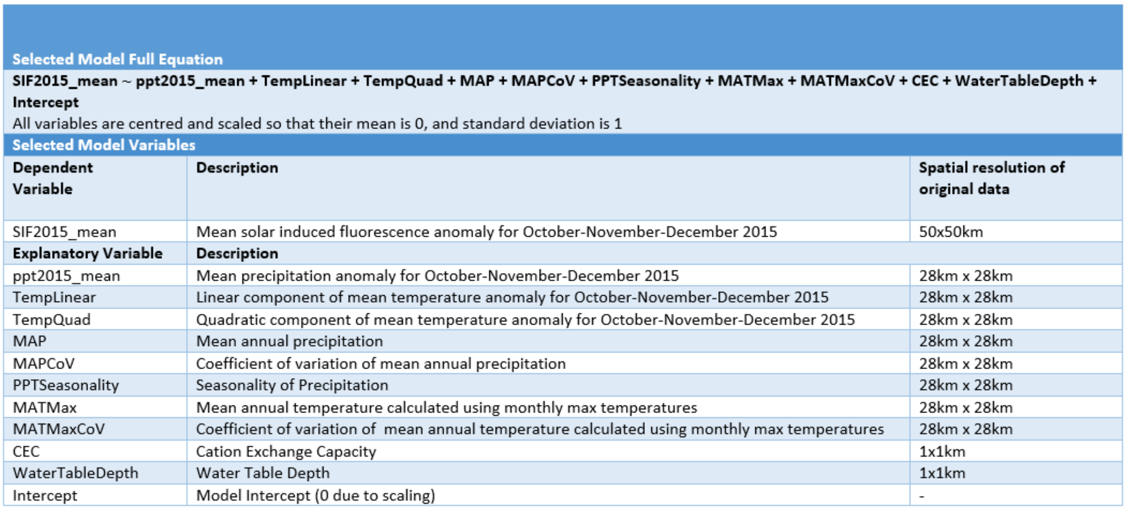


Figure A.5: Mean SIF for the SIFTVERv2 product for the Amazon Region (0-15°S, 70-55°W) with (blue), and without (red) the correction for sensor degradation, reproduced from van Shaik et al. 2020[1]. Vertical lines denote the study period (October 2015 – December 2016).The vertical lines depict the study period.

A.6 Supplementary Figure 6



Selected Model Full Equation		
SIF2015_mean ~ ppt2015_mean + TempLinear + TempQuad + MAP + MAPCoV + PPTSeasonality + MATMax + MATMaxCoV + CEC + WaterTableDepth + Intercept All variables are centred and scaled so that their mean is 0, and standard deviation is 1		
Selected Model Variables		
Dependent Variable	**Description**	**Spatial resolution of original data**
SIF2015_mean	Mean solar induced fluorescence anomaly for October-November-December 2015	50x50km
Explanatory Variable	**Description**	
ppt2015_mean	Mean precipitation anomaly for October-November-December 2015	28km x 28km
TempLinear	Linear component of mean temperature anomaly for October-November-December 2015	28km x 28km
TempQuad	Quadratic component of mean temperature anomaly for October-November-December 2015	28km x 28km
MAP	Mean annual precipitation	28km x 28km
MAPCoV	Coefficient of variation of mean annual precipitation	28km x 28km
PPTSeasonality	Seasonality of Precipitation	28km x 28km
MATMax	Mean annual temperature calculated using monthly max temperatures	28km x 28km
MATMaxCoV	Coefficient of variation of mean annual temperature calculated using monthly max temperatures	28km x 28km
CEC	Cation Exchange Capacity	1x1km
WaterTableDepth	Water Table Depth	1x1km
Intercept	Model Intercept (0 due to scaling)	-

Figure A.6: Selected model full equation, variables and explanation

Appendix Two

Chapter Three Supplementary Materials

B.1 Supplementary Figure 1

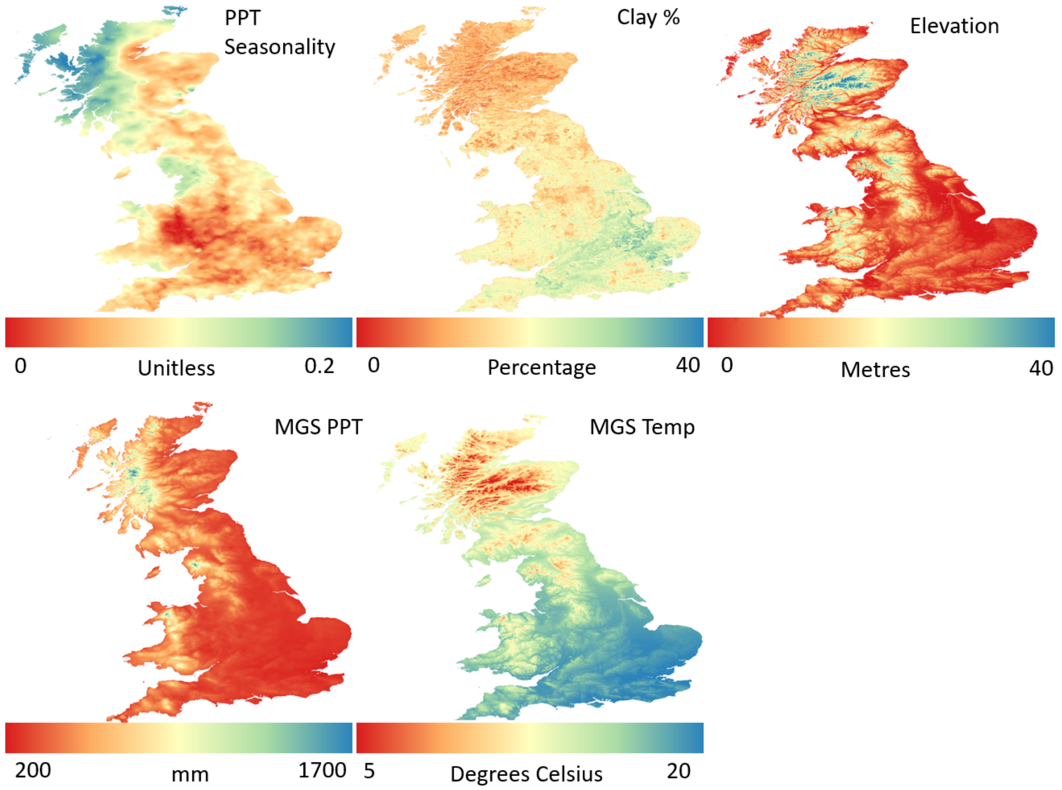


Figure B.1: Spatial distribution of the explanatory variables used in the Random Forest modelling.

B.2 Supplementary Figure 2

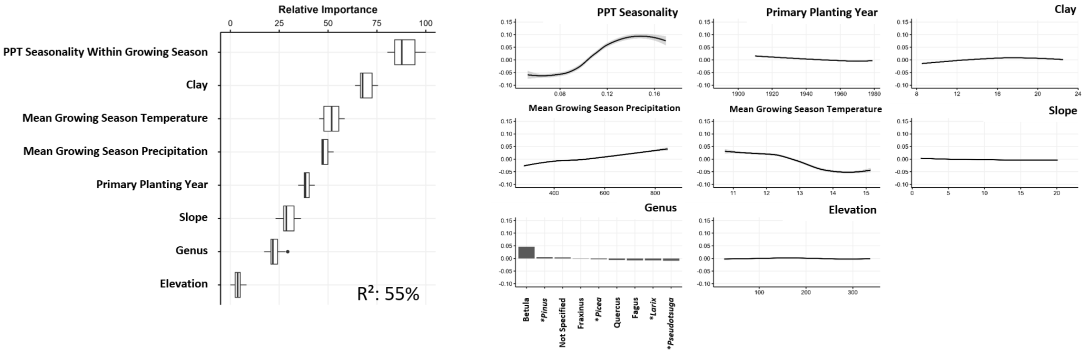


Figure B.2: Modelling of drought coupling, relative importance of variables as deteremined by Boruta score (left) and accumulated local effects plots (right)

B.3 Supplementary Figure 3

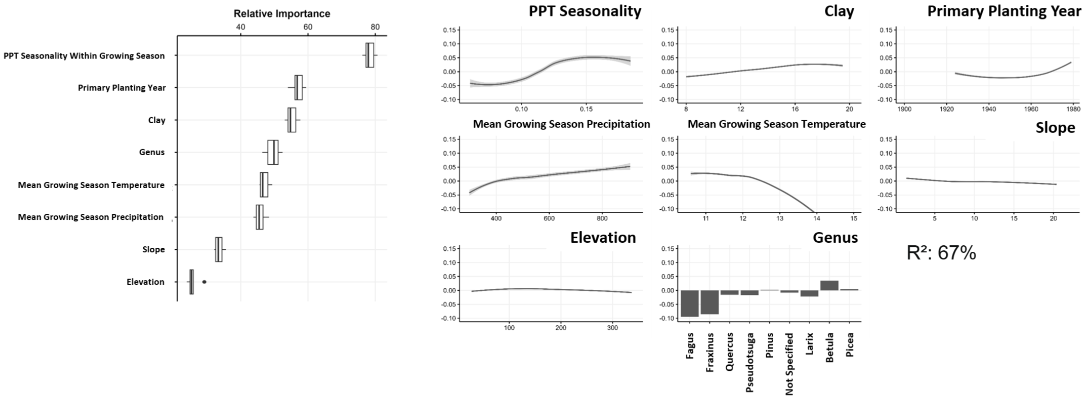


Figure B.3: Modelling of temperature drought sensitivity, only using pixels who have a R^2 greater than the average R^2 calculated in the main analysis (16%), relative importance of variables as determined by Boruta score (left) and accumulated local effects plots (right)

B.4 Supplementary Table 1

All data made available through Google Earth Engine require the creation of a Google Earth Engine account `https://earthengine.google.com/`

NDVI data - MOD13Q1.061 Terra Vegetation Indices 16-Day Global 250m `https://lpdaac.usgs.gov/products/mod13q1v061/`

Precipitation data – Gridded estimates of daily and monthly areal rainfall for the United Kingdom (1890-2019) [CEH-GEAR]

`https://catalogue.ceh.ac.uk/documents/dbf13dd5-90cd-457a-a986-f2f9dd97e93c`

Temperature data - Climate hydrology and ecology research support system meteorology dataset for Great Britain (1961-2017) [CHESS-met]

`https://catalogue.ceh.ac.uk/documents/2ab15bf0-ad08-415c-ba64-831168be7293`

Long term climate temperature - ERA5 Monthly Aggregates - Latest Climate Reanalysis Produced by ECMWF / Copernicus Climate Change Service

`https://cds.climate.copernicus.eu/cdsapp#!/dataset/10.24381/cds.f17050d7?tab=overview`

Hansen Global Forest Change v1.9.

`https://earthenginepartners.appspot.com/science-2013-global-forest/download_v1.7.html`

SRTM Digital Elevation Data Version 4.1

`https://cgiarcsi.community/data/srtm-90m-digital-elevation-database-v4-1/`

B.5 Supplementary Figure 4

As the data at the pixel level has been standardised (mean centred and divided by the standard deviation) model coefficients for temperature, and precipitation, can be directly compared to assess their relative importance with a larger variable coefficient being interpreted as that variable being of relatively higher importance. To aid in the understanding the percentage contribution of each coefficient to the absolute sum of the three coefficients was calculated using equation B.1 at a pixel level. This allows us to understand the importance of each sensitivity component relative to each other, as well as to assess the spatial patterns in this relative importance.

$$Component percentage contribution = \frac{abs(\beta_{temp/ppt/date})}{abs(\beta_{temp}) + abs(\beta_{ppt}) + abs(\beta_{date})} \times 100 \quad (B.1)$$

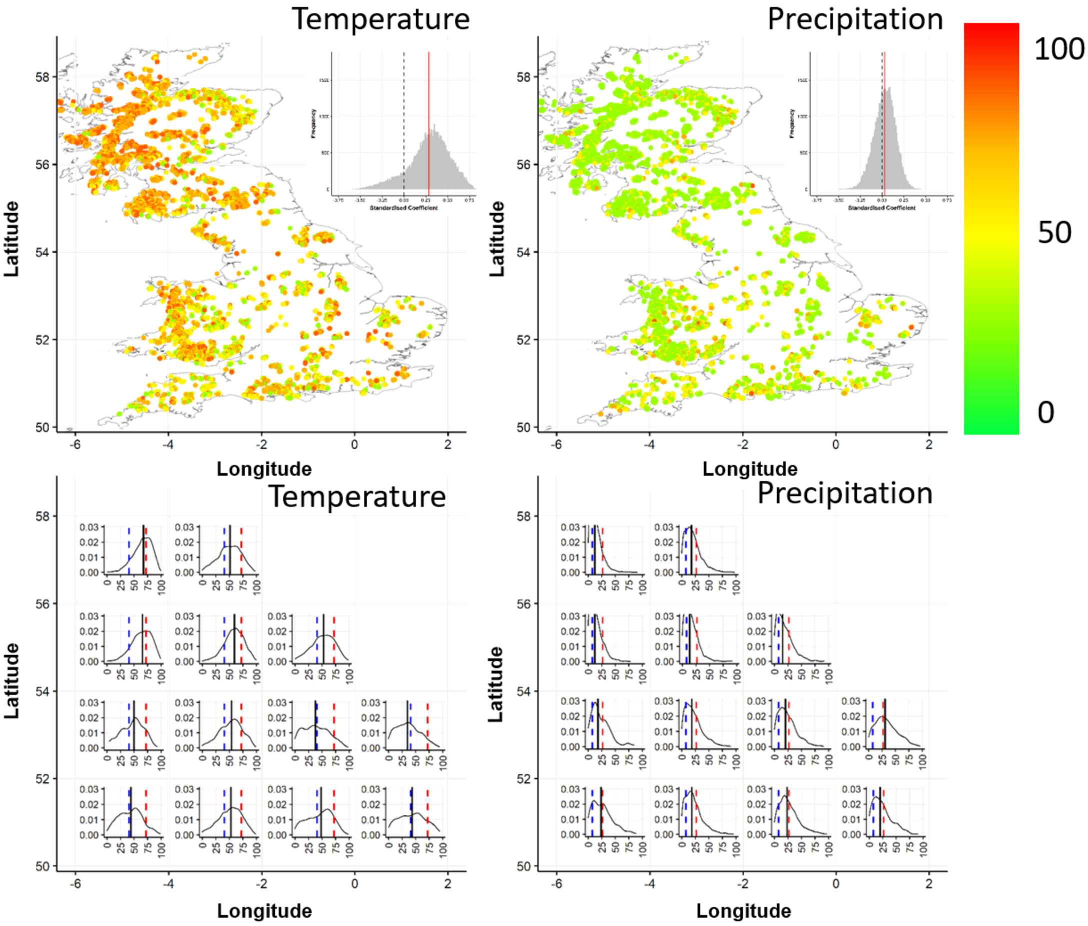


Figure B.4: Relative importance of sensitivity components shown spatially for temperature top left, and precipitation top right. Precipitation shows relatively low importance across the UK, with a few localised areas of higher importance. Temperature by contrast shows itself to be highly important nearly everywhere, with a slight East-West gradient across the UK. This figure was produced by dividing the absolute temperature or precipitation coefficient by the absolute sum of the temperature, precipitation and date coefficient. As all data are standardised prior to calculation, this produces an easy to interpret measure of relative importance. For instance an area with a temperature importance of near 100% would indicate that all of the climate sensitivity is explained by the temperature component rather than the precipitation or date coefficient. Bottom plots show the same information, but summarised for each 2x2 degree square, by frequency distribution for temperature (bottom left) and precipitation (bottom right), the blue and red lines represent the 25% and 75% for visual reference

Figure B.4 displays the spatial and frequency pattern of this relative importance, from examining these distributions several interesting features can be observed. First, sensitivity to temperature is the single most important contributor to overall sensitivity with average temperature sensitivity being approximately ten times that of the average contributions of precipitation, and long-term trends (0.28, vs 0.03 respectively numbers). Second, there is significant spatial variation in which component is most important. The relative importance of temperature for instance has very high percentage contributions in the northwest and north Wales with the percentage contribution dropping towards the northeast and southeast. Finally, precipitation sensitivity shows a more even distribution, being of relatively low importance everywhere, with slightly higher importance in the southeast.

B.6 Supplementary Figure 5

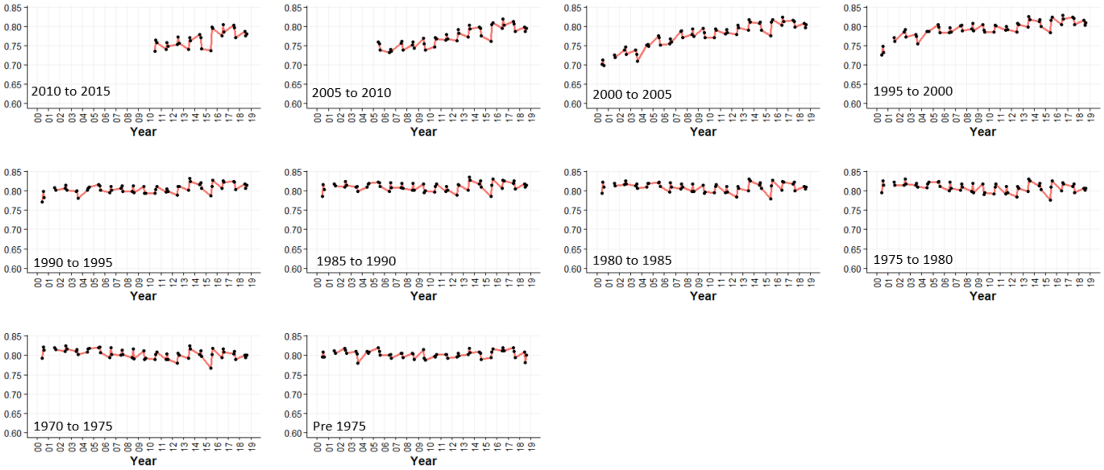


Figure B.5: NDVI averaged for each age cohort labelled over time, restricted just to the growing season of each year.

B.7 Code Availability

All code for this chapter is freely available for download from `https://github.com/maxfancourt42/uk_ndvi_forest_stability_paper.git`.

B.8 Supplementary Table 2

Table B.1: Table showing the results of considering all pairwise interactions within the random forest model, variable importance is calculated for each pair of variables (paired column), for each variable separately (Var 1 and Var 2) and then finally also the summed importance of the two variables together (summed column). A large positive or negative difference between ”paired” and ”additive” indicates an association that is worth considering, if the univariate variable importance for each of the paired-variables is also reasonable large.

Variable Pair	Var 1	Var 2	Paired	Additive	Difference
mat:map	0.0193	0.018	0.0353	0.0373	-0.002
mat:clay	0.0193	0.0103	0.0279	0.0296	-0.0017
mat:pptseasonality	0.0193	0.013	0.0263	0.0323	-0.006
mat:PRI_PLYEAR	0.0193	0.0054	0.0219	0.0247	-0.0027
mat:genus	0.0193	0.0047	0.0217	0.0239	-0.0022
mat:slope	0.0193	0.0023	0.0201	0.0215	-0.0014
mat:elevation	0.0193	0.0012	0.0198	0.0204	-0.0007
map:clay	0.018	0.0104	0.0262	0.0284	-0.0022
map:pptseasonality	0.018	0.013	0.0251	0.031	-0.0059
map:PRI_PLYEAR	0.018	0.0054	0.0204	0.0234	-0.003
map:genus	0.018	0.0046	0.0202	0.0226	-0.0025
map:slope	0.018	0.0023	0.0187	0.0203	-0.0016
map:elevation	0.018	0.0012	0.0185	0.0192	-0.0007
clay:pptseasonality	0.0103	0.013	0.0191	0.0233	-0.0042
clay:PRI_PLYEAR	0.0103	0.0054	0.0139	0.0158	-0.0019
clay:genus	0.0103	0.0046	0.0143	0.015	-0.0007
clay:slope	0.0103	0.0023	0.012	0.0126	-0.0006
clay:elevation	0.0103	0.0012	0.0111	0.0115	-0.0004
pptseasonality:PRI_PLYEAR	0.013	0.0054	0.016	0.0184	-0.0024
pptseasonality:genus	0.013	0.0046	0.0158	0.0176	-0.0019
pptseasonality:slope	0.013	0.0023	0.0141	0.0153	-0.0012
pptseasonality:elevation	0.013	0.0012	0.0135	0.0142	-0.0007
PRI_PLYEAR:genus	0.0054	0.0046	0.0087	0.0101	-0.0014
PRI_PLYEAR:slope	0.0054	0.0023	0.0073	0.0077	-0.0004
PRI_PLYEAR:elevation	0.0054	0.0012	0.0063	0.0066	-0.0003
genus:slope	0.0046	0.0023	0.0066	0.0069	-0.0004
genus:elevation	0.0046	0.0012	0.0056	0.0058	-0.0002
slope:elevation	0.0023	0.0012	0.0033	0.0035	-0.0002

B.9 Supplementary Figure 6

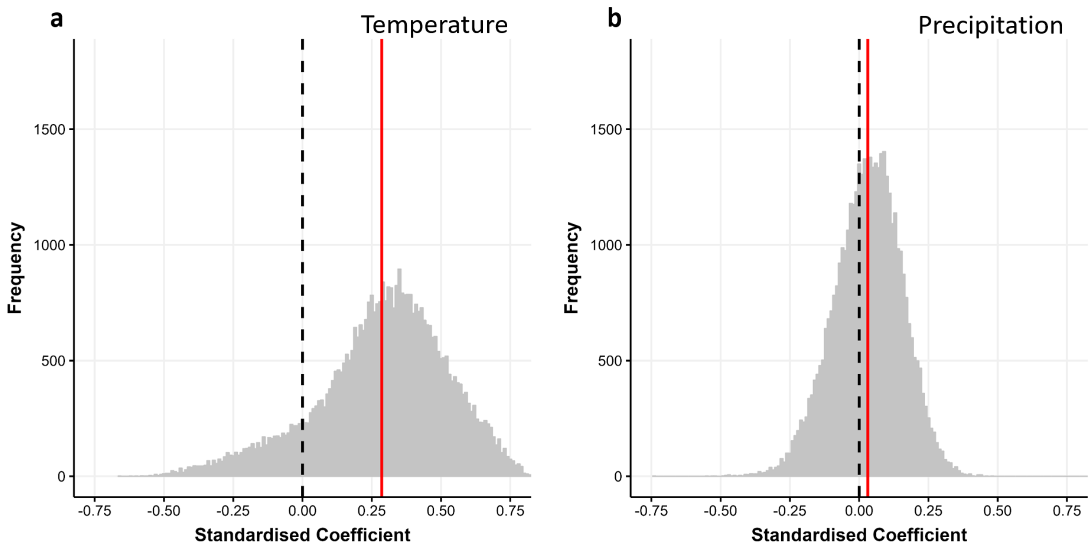
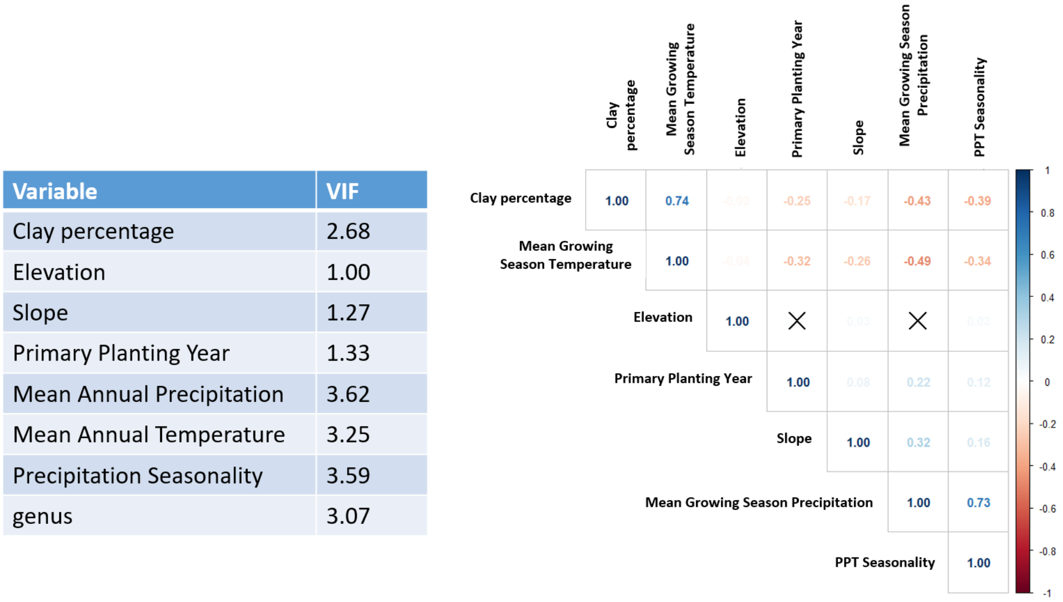


Figure B.6: Frequency distribution of standardised regression coefficients for **a)** temperature anomalies **b)** precipitation anomalies. Red-solid line represents the mean sensitivity, black-dashed line highlights 0 to be used in comparing to the mean.

B.10 Supplementary Figure 7



Variable	VIF
Clay percentage	2.68
Elevation	1.00
Slope	1.27
Primary Planting Year	1.33
Mean Annual Precipitation	3.62
Mean Annual Temperature	3.25
Precipitation Seasonality	3.59
genus	3.07

	Clay percentage	Mean Growing Season Temperature	Elevation	Primary Planting Year	Slope	Mean Growing Season Precipitation	PPT Seasonality
Clay percentage	1.00	0.74	-0.03	-0.25	-0.17	-0.43	-0.39
Mean Growing Season Temperature		1.00	-0.04	-0.32	-0.26	-0.49	-0.34
Elevation			1.00	✕	0.03	✕	0.03
Primary Planting Year				1.00	0.08	0.22	0.12
Slope					1.00	0.32	0.16
Mean Growing Season Precipitation						1.00	0.73
PPT Seasonality							1.00

Figure B.7: Variance inflation factors, and correlation matrix for all variables used in the final random forest model, correlation between variables was investigated using Peason's correlation coefficient, and a rule of thumb of 4 was used to filter variables by VIF (with variables more than 4 being excluded.

Appendix Three

Chapter Four Supplementary Material

C.1 Supplementary Figure 1a

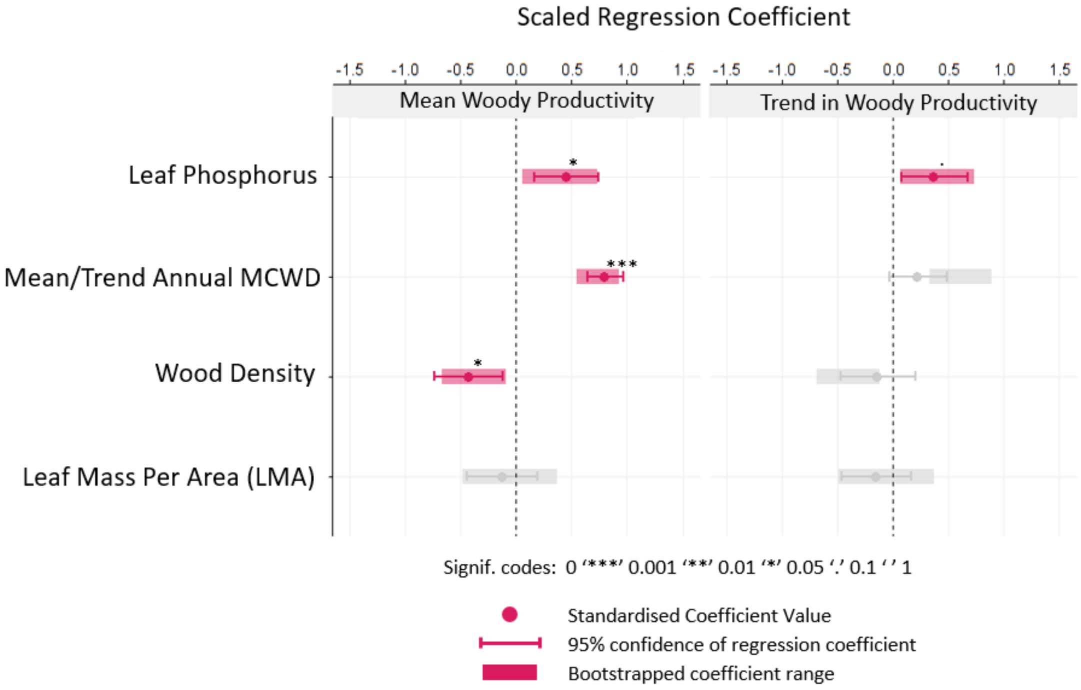


Figure C.1: Standardised univariate regression coefficients for the best models for predicting mean woody productivity (left) and trend in woody productivity (right) across Amazon forests. Points show the standardised coefficient value in the best model for each, wings show the 95% confidence interval, shaded rectangle represents the 95% range when the underlying dataset was subjected to moderate bootstrapped perturbation.

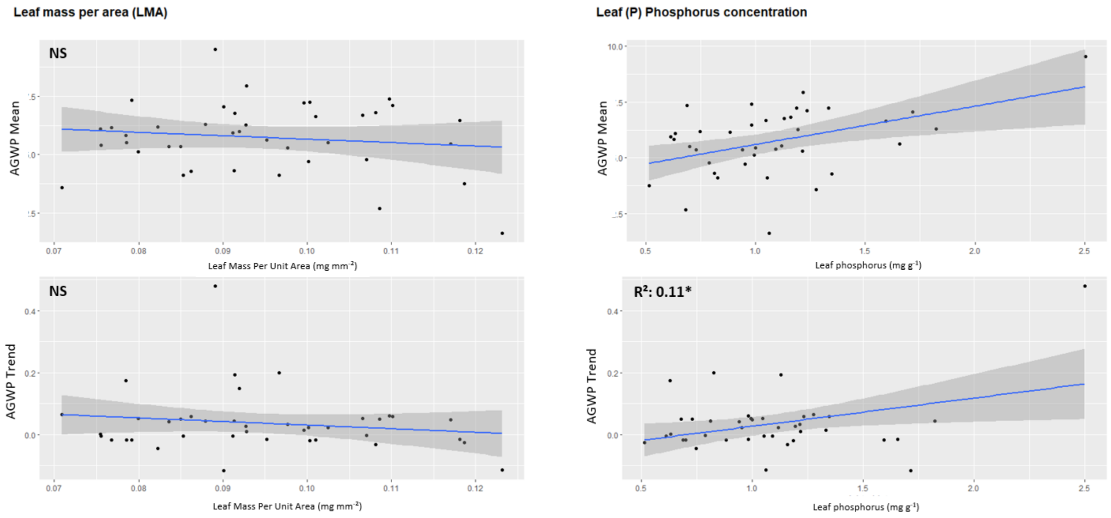


Figure C.2: Biplots for Leaf mass per unit area, and leaf phosphorus, for AGWP mean, and AGWP trends. Basal area weighted functional trait averages were calculated using the closest available census date to the date the functional trait data was collected. As functional traits are only collected once per plot in our dataset, the average calculated for each plot are assumed to be constant.

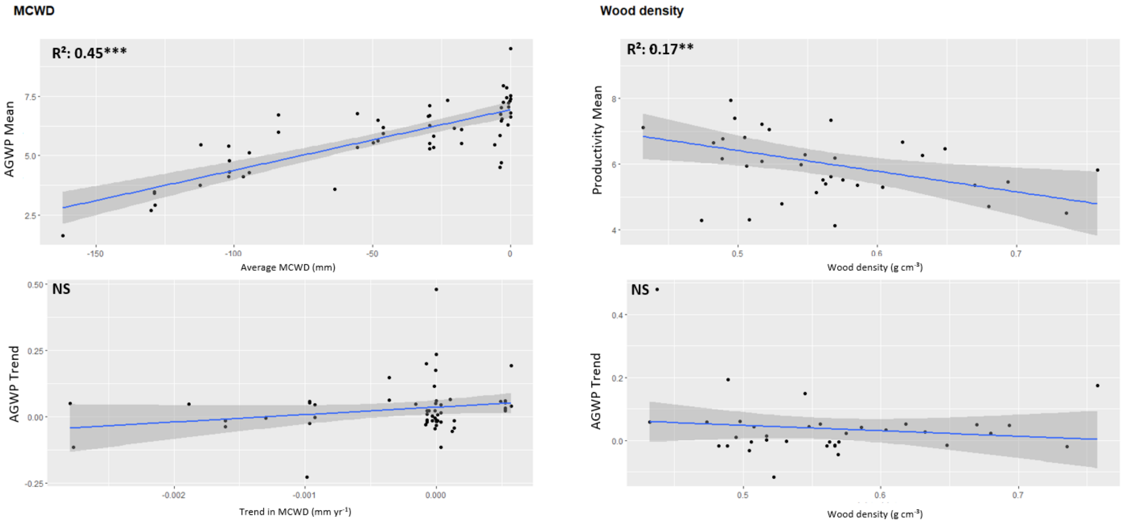


Figure C.3: Biplots for MCWD, and wood density, for AGWP mean, and AGWP trends, note for MCWD vs AGWP trends. . Basal area weighted functional trait averages were calculated using the closest available census date to the date the functional trait data was collected. As functional traits are only collected once per plot in our dataset, the average calculated for each plot are assumed to be constant

C.2 Supplementary Figure 2

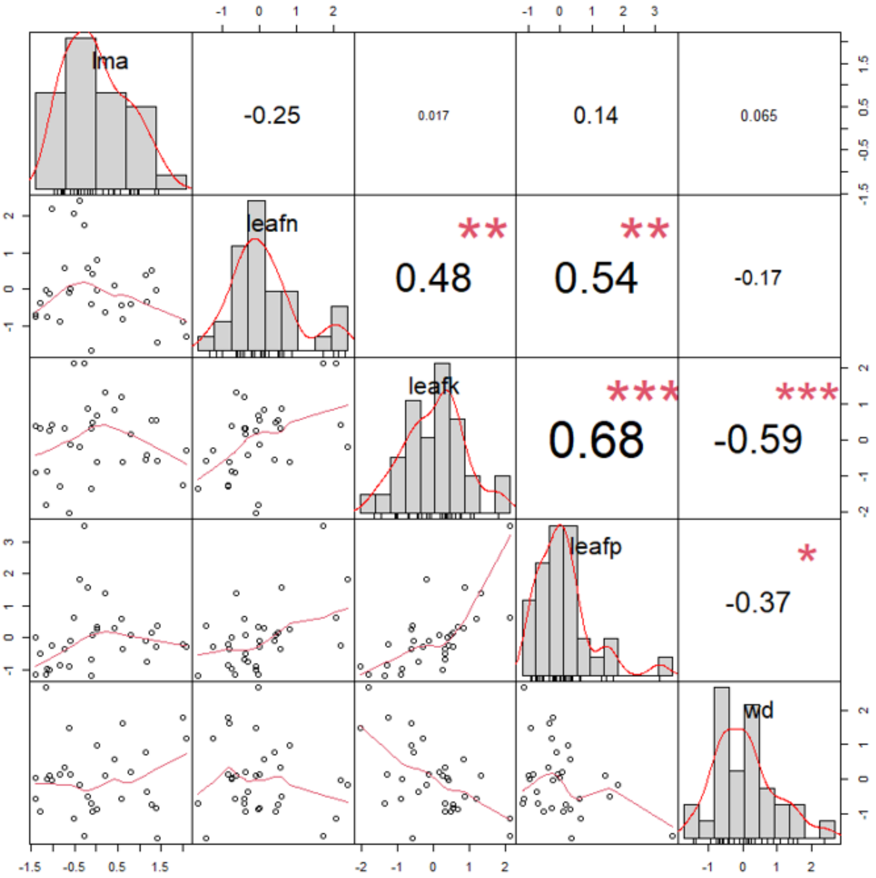


Figure C.4: Correlation matrix for functional traits, high correlation can be observed between leaf N, leaf P and leaf K, this high correlation would likely result in multicollearinty issues during stastitical modelling. To this end leaf P was chosen as it had the lowest correlation with LMA and wood density out of the the tree leaf nutrient variables making it most suitable for modelling

C.3 Supplementary Figure 3

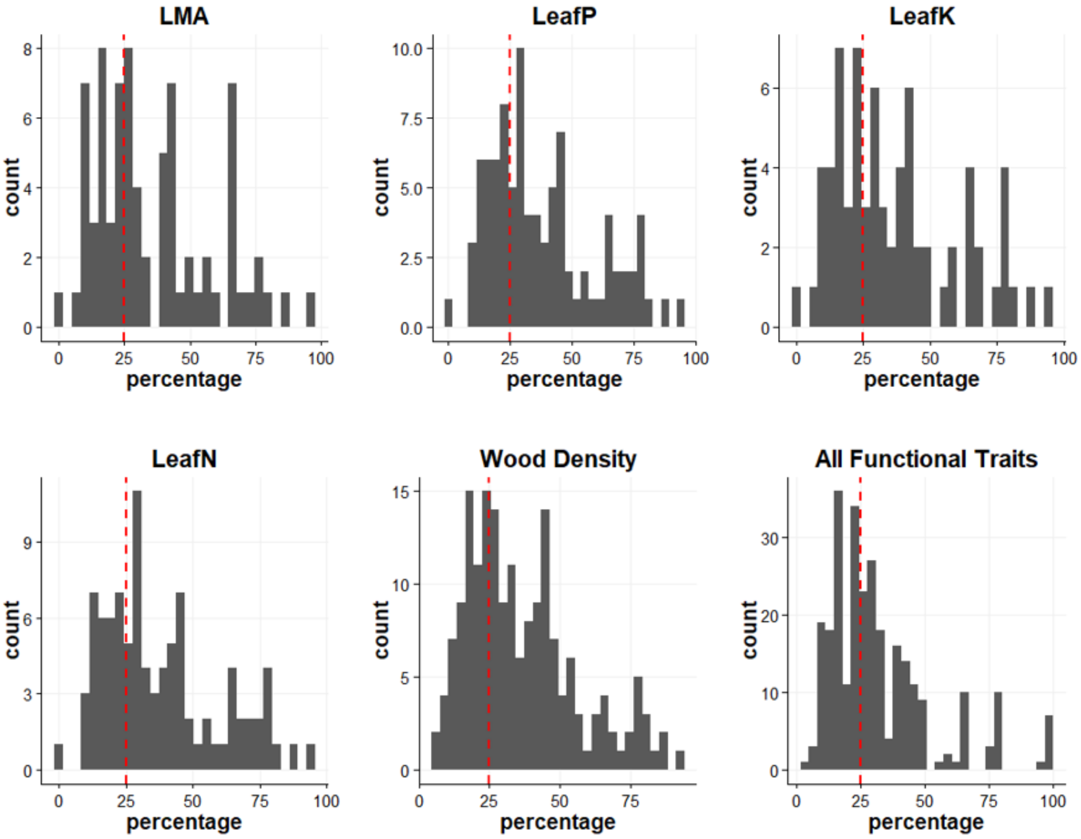


Figure C.5: Historgrams showing the frequency distribution of basal area for all function traits, a 25% threshold was chosen on the basis that sites with less than this basal area would be unlikely to fully represent the community, and a higher threshold would remove too many sites making statistical analysis unreliable.

C.4 Code Availability

All code for this chapter is freely available for download from `https://github.com/maxfancourt42/amazon_AGWP_functional_traits.git`.

C.5 Supplementary Table 1

Plot	Leaf N	Leaf P	Leaf K	Leaf Mass Per Unit Area	Wood density
AGP-01	1	1	1	1	1
AGP-02	1	1	1	1	1
ALC-01	1	1	1	1	
ALC-02	1	1	1	1	
ALF-01	1	1	1	1	

Plot	Leaf N	Leaf P	Leaf K	Leaf Mass Per Unit Area	Wood density
ALP-01	1	1	1	1	1
ALP-02	1	1	1	1	1
ALP-30	1	1	1	1	1
BNT-04	1	1	1	1	
BOG-01	1	1	1	1	1
BOG-02	1	1	1	1	1
CAX-01	1	1	1	1	1
CAX-02	1	1	1	1	1
CHO-01	1	1	1	1	1
CPP-01	1	1	1	1	1
CUZ-03	1	1	1	1	1
DEC-06				1	
DOI-01	1	1	1	1	1
DOI-02	1	1	1	1	1
ELD-01	1	1	1	1	1
ELD-02	1	1	1	1	1
ELD-03	1	1	1	1	1
ELD-04	1	1	1	1	1
ETA-01					1
ETA-02					1
ETA-03					1
ETA-04					1
ETA-05					1
ETA-06					1
ETA-07					1
ETA-08					1
ETA-09					1
ETA-10					1
ETA-11					1
ETA-12					1
ETA-13					1
ETA-14					1

Plot	Leaf N	Leaf P	Leaf K	Leaf Mass Per Unit Area	Wood density
ETA-15					1
ETA-16					1
ETA-17					1
ETA-18					1
ETB-01					1
ETB-02					1
ETB-03					1
ETB-04					1
ETB-05					1
ETB-06					1
ETB-07					1
ETB-08					1
ETB-09					1
ETB-10					1
ETB-11					1
ETB-12					1
ETB-13					1
ETB-14					1
ETB-15					1
ETB-16					1
ETB-17					1
ETB-18					1
ETB-19					1
ETC-01					1
ETC-02					1
ETC-03					1
ETC-04					1
ETC-05					1
ETC-06					1
ETC-07					1
ETC-08					1
ETC-09					1

Plot	Leaf N	Leaf P	Leaf K	Leaf Mass Per Unit Area	Wood density
ETC-10					1
ETC-11					1
ETC-12					1
ETC-13					1
ETC-14					1
ETC-15					1
ETC-16					1
ETC-17					1
ETC-18					1
ETC-19					1
ETD-01					1
ETD-02					1
ETD-03					1
ETD-04					1
ETD-05					1
ETD-06					1
ETD-07					1
ETD-08					1
ETD-09					1
ETD-10					1
ETD-11					1
ETD-12					1
ETD-13					1
ETD-14					1
ETD-15					1
ETD-16					1
ETD-17					1
ETD-18					1
ETD-19					1
ETD-20					1
ETD-21					1
ETD-22					1

Plot	Leaf N	Leaf P	Leaf K	Leaf Mass Per Unit Area	Wood density
ETD-23					1
ETE-01					1
ETE-02					1
ETE-03					1
ETE-04					1
ETE-05					1
ETE-06					1
ETE-07					1
ETE-08					1
ETE-09					1
ETE-10					1
ETE-11					1
ETE-12					1
ETE-13					1
ETE-14					1
ETE-15					1
ETE-16					1
ETE-17					1
ETE-18					1
ETE-19					1
ETE-20					1
ETE-21					1
ETE-22					1
ETE-23					1
ETE-24					1
ETE-25					1
ETE-26					1
ETE-27					1
ETE-28					1
ETE-29					1
ETF-01					1
ETF-02					1

Plot	Leaf N	Leaf P	Leaf K	Leaf Mass Per Unit Area	Wood density
ETF-03					1
ETF-04					1
ETF-05					1
ETF-06					1
ETF-07					1
ETF-08					1
ETF-09					1
ETF-10					1
ETF-11					1
ETF-12					1
ETF-13					1
ETF-14					1
ETF-15					1
ETF-16					1
ETF-17					1
ETF-18					1
ETF-19					1
ETF-20					1
ETF-21					1
HCC-21	1	1	1	1	1
HCC-22	1	1	1	1	1
JAS-02	1	1	1	1	1
JAS-03	1	1	1	1	1
JAS-04	1	1	1	1	1
JAS-05	1	1	1	1	1
JEN-11					1
JEN-12					1
JRI-01	1	1	1	1	1
LFB-01	1	1	1	1	1
LFB-02	1	1	1	1	1
LOR-01	1	1	1	1	1
LSL-01	1	1	1	1	1

Plot	Leaf N	Leaf P	Leaf K	Leaf Mass Per Unit Area	Wood density
LSL-02	1	1	1	1	1
MON-01				1	
POR-02	1			1	1
RIO-01	1	1	1	1	1
RIO-02	1	1	1	1	1
SCR-04	1	1	1	1	1
SCR-05	1	1	1	1	1
SIP-01	1	1	1	1	
SUC-01	1	1	1	1	1
SUC-02	1	1	1	1	1
SUC-03	1	1	1	1	1
SUM-01	1	1	1	1	1
TAM-01	1	1	1	1	1
TAM-02	1	1	1	1	1
TAM-03	1	1	1	1	1
TAM-04	1	1	1	1	1
TAM-05	1	1	1	1	1
TAM-06	1	1	1	1	1
TAM-07	1	1	1	1	1
TIP-03	1	1	1	1	1
TIP-05	1	1	1	1	1

C.6 Supplementary Table 2

Table C.2: Sample size for univariate and multivariate analyses.

Univariate	Sample size
LMA	40
Leaf N	40
Leaf K	39
Leak P	39
Wood density	35
Multivariate	33

Bibliography

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