How drought, waterlogging, and light availability shape patterns of tropical tree distributions, in French Guiana

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Thesis Abstract

Tropical forests display striking patterns in species richness along environmental gradients. At local scales, spatial and seasonal variation in soil-water and light availability are strongly linked to performance differences between species, and therefore compositional turnover between habitats. Understanding ecological responses to rapid environmental change is an urgent necessity in tropical forests as future tree distributions are likely to alter along lines delimiting wet and dry habitats. However, it is currently unknown what controls turnover of species between wetter and drier habitats and to what extent regeneration is controlled by the interactive effects of water and light.

As field gradients of drought, waterlogging, and light rarely occur independently from one another, or indeed from other important abiotic and biotic drivers, this confounding of variables make it particularly challenging to attribute observed distributions to environmental variation. I addressed these challenges by examining seedling and sapling performance under experimental and natural conditions of drought, waterlogging and light availability, utilising the contrasting wet and dry rainforest habitats of Paracou, French Guiana, South America, as the study system.

I conducted a shadehouse experiment involving seedlings of eleven co-occurring tree species with contrasting distributional patterns among the wet and dry habitats of Paracou. Using survival modelling techniques, I examined survival times of 1532 seedlings and 20,000 individual observations to investigate species variation in survival along an experimental irradiance gradient and in three contrasting water availability regimes, '*drought*', '*waterlogged*', and '*watered to field capacity*'. I calculated tolerance indices for drought, waterlogging, and shade based on survival time predictions, then assessed indices for evidence of interspecific trade-offs. I found evidence of non-interactive effects of water and light on seedling survival and species tolerance indices revealed a negative relationship between drought and shade tolerance. These results suggest that, when nutrients are not limiting and in the absence of root competition, shaded tropical seedlings are impacted more strongly by drought than seedlings in higher light conditions.

Then, I evaluated the roles of water and light availability in governing sapling survival in the field. I used data on the survival of 5374 individual saplings of 25 species, frequency of drought and waterlogging over 24 years, and detailed information on understory light availability. Utilising Generalised Linear Mixed Modelling techniques I showed that drought was the relatively more important factor determining differential species survival, as well as a likely important role of long-term soil instability associated with topographical water availability. By comparing survival responses of species with contrasting distributions among wet and dry habitats, I was able to infer that differential survival among wet habitat associated species may filter those species from drier habitats, whereas drier habitat associated species survive better than wet associated species in the driest habitats.

Finally, I used Generalised Linear Mixed Modelling techniques to assess the ability of experimentally derived species tolerances of drought, waterlogging, and shade to predict sapling performance in the field. I found evidence that abundance in topographic habitats defined by variation in water availability did depend on differential tolerance of drought, and waterlogging, but not shade. I found no evidence that sapling survival was related to any of the indices. Studies based on whole-plant tolerances can directly link plant performance to variation in resource availability and have been credited with improving the understanding of species distributions by providing mechanistic and predictive links between observed distributions and environmental conditions. This study provides positive first steps towards using shadehouse derived tolerance indices to achieve explanatory and predictive power regarding sapling performance across topographic habitats.

In summary, the results presented in this thesis strongly suggest that both water limitation and waterlogging are important factors limiting species performance and therefore structuring communities along environmental gradients. Under a scenario of increasingly dry weather, the forest of Paracou may see a turnover in species composition that would lead to more drought tolerant and fewer waterlogging and shade tolerant species. In this thesis, I have focussed on plant responses to locally contrasting soil-moisture availability. However, as plant responses at this scale are ultimately responsible for distributions at large as well as finer spatial scales, these results may be applicable more widely among neotropical and other tropical forests.

Declaration of authorship

I, Anna Deasey, declare that this thesis has been composed by myself and that it embodies the results of my own research. Where appropriate, I have acknowledged the nature and extent of the work carried out in collaboration with others.

Signed……………………..

Date………………………..

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1. General Introduction

Tropical tree distributions over environmental gradients

Patterns of species diversity exist (MacArthur 1965, Palmer 1994), and a central goal of ecology has been to understand and quantify what drives those patterns. In tropical forests, where tree species diversity reaches hyperdiverse proportions, a large number of mechanisms of coexistence have been hypothesised (Wright 2002). Niche concepts invoke a theoretical multidimensional ecological space, delimited at the points at which combinations of biotic and abiotic factors limit an individual's survival and reproduction (Hutchinson 1957). That so many species can coexist in tropical forests requires environments to differ sufficiently to support a variety of species strategies, and that species differ in their niche requirements.

Tree distributions vary at multiple scales. Over large spatial or long temporal scales speciation and historical or dispersal constraints influence regional species pools (Pavoine and Bonsall 2011). At local scales, the composition and structure of communities are influenced by environmental factors and biotic interactions (Hillerislambers et al. 2012, Kraft et al. 2015). When considering hydrological niches, plants respond to locally contrasting soil-moisture availability, which is ultimately responsible for distributions at large as well as finer spatial scales (Silvertown et al. 2015). Therefore, correlations between distributions at larger geographic and local scales are expected, and have been found for distributions related to drought tolerance in tropical tree species (Comita and Engelbrecht 2014, Silvertown et al. 2015).

At local scales, environmental factors shape plant communities in combination with biotic interactions such as competition, facilitation, disease and parasitism (Cadotte and Tucker 2017). Further, biotic processes such as omnipresent interactions with fungi and bacteria determine the outcome of environmental effects on host tree species, which are difficult, if not impossible to separate from the effects of the environment alone (Aguilar-Trigueros et al. 2017). Moreover, species-environment interactions are altered through niche construction modifications to the environment, such as shading by taller plants (Thakur and Wright 2017).

However, measuring the requirements of each species' niche would be an enormous task. In contrast, studies that correlate community structure components such as mortality or abundance with measures of environmental variability remain valuable tools to infer the importance of the environment in species persistence (Cadotte and Tucker 2017). By focussing on species demographic responses to variations in environmental factors it is possible to determine what constitutes suitable and unsuitable habitat for particular species (Pulliam 2000). Then, armed with knowledge of species and habitat suitability, it may be possible to predict the dynamics and distributions of species in places and times in which they have not been measured, or extend predictions to novel places or climatic conditions (Pulliam 2000, Toledo et al. 2012, Craine et al. 2012).

Understanding ecological responses to rapid environmental change has become an urgent necessity, and is especially important in tropical forests as these ecosystems are predicted to be among those most affected by fluctuating climate patterns (Sheldon 2019). In tropical regions, climate change scenarios forecast intensification of the seasons, where dry and wet seasons will become increasingly unstable in length and intensity (Neelin et al. 2006, Fu 2015). Therefore, future tropical tree distributions are likely to alter along lines delimiting wet and dry habitats and studies that explicitly consider how species sort along local hydrological gradients are of paramount importance.

Water availability as a driver of species distribution patterns across habitats

Tropical forests display striking patterns in species richness along a number of environmental gradients (Givnish 1999). Rainfall patterns and seasonality have been established as one of the most important factors governing regional species richness patterns in the tropics, where higher species richness is often associated with wetter forests (Wright, 1992; Clinebell *et al.*, 1995; Borchert, 1998; ter Steege et al., 2003). At local scales, spatial and seasonal variation in soil-water availability between habitats have been strongly linked to performance differences between species and compositional turnover (Comita and Engelbrecht 2009, Baltzer and Davies 2012).

The soil-water availability gradient is complex, with drought and waterlogging at either extreme harbouring two distinctly different sets of conditions for plants. Drought and waterlogging can occur in the same place at different times of the year during dry and wet seasons, which can vary in length and intensity. Drought and waterlogging can also occur simultaneously within habitat mosaics, with drier conditions on well-drained *terre firme* soil and higher ground, and waterlogging or flooding along watercourses and gley soils in lowlands. In recent years, there has been increased interest in uncovering the relative roles of these overlapping stresses in contributing to species turnover between habitats (ter Steege 1994, Pélissier et al. 2002, Baraloto et al. 2007, Parolin 2010, Miyazawa et al. 2014, Kenfack et al. 2014, Pires et al. 2018). Nevertheless, it is still not possible to answer with any certainty basic questions such as whether drought or waterlogging is the stronger driver of compositional turnover between wetter and drier sites.

Current evidence suggests that wet-forest distributed species may be excluded from drier forests mainly due to intolerance of seasonal drought, the possession of fewer adaptations to cope with water stress, and higher mortality during dry seasons in drier forests (Brenes-Arguedas et al. 2011). The factors that exclude dry forest origin species from wet forests are less clear, but may include covariation of wetter sites with greater pest pressure, lower soil nutrients, and lower light availability (Brenes-Arguedas et al. 2011).

In the field, hydrological gradients rarely occur independently from other abiotic gradients and biotic interactions can result in the same distributional patterns. This confounding of variables makes it challenging to attribute observed plant distributions to particular aspects of environmental variation (Dormann 2007). Abiotic factors that may covary and potentially interact with water availability to shape distribution patterns include not only light availability which may vary temporally and spatially with water availability (Brenes-Arguedas et al. 2011), but also soil nutrient status, where drought-prone and waterlogging-prone soils may differ in nutrient availability (Palmiotto et al. 2004), topography, where elevated and non-elevated areas are more susceptible to drought or waterlogging (Born et al. 2015, Freund et al. 2018), and temperature which covaries with light availability (Wright et al. 2009).

Hydrological heterogeneity affects not only individual trees and species directly but also their competitors and natural enemies (Uriarte et al. 2018). Pest and pathogen pressure may be amplified under wet conditions (Baltzer and Davies 2012), and ectomycorrhizal communities are responsive to variation in soil water availability that may affect mutualistic interactions (Cavender-Bares et al. 2009). Further, life history traits along the fast-slow continuum are likely to benefit performance in drier and wetter and habitats and interact with light availability (Ouédraogo et al. 2013, Sterck et al. 2014, Born et al. 2014).

Drought in tropical forests

Except for those occurring directly at the equator, most tropical forests experience pronounced seasonality with periods of low rainfall occurring once or twice a year for at least 15 - 30 days (Walsh and Newbery 1999, Markesteijn 2010, Comita and Engelbrecht 2014). Periods of abnormally low rainfall long enough to cause hydrological imbalance are associated with multi-year climatic cycles and are forecast to increase in frequency over the coming decades (Corlett 2016). During periods of low rainfall, water is lost from the soil via transpiration, exacerbated by evaporation caused by strong sunlight and high temperatures associated with dry seasons. Drying soils are a problem for plants because as soils dry the energy state of the water in the soil matrix is changed and soil water potentials become increasingly negative (Markesteijn 2010). This means that water becomes bound more strongly to mineral soil surfaces and more energy is required of plants to access water, leading to lowered leaf water potentials within the plant, which can eventually lead to cavitation, hydraulic failure, stomatal closure, leaf abscission, and death (Tyree et al. 2003).

Tropical tree species, like most plants, exhibit two main strategies to cope with reduced soil water availability during periods of low rainfall, desiccation tolerance, and desiccation avoidance (Comita and Engelbrecht 2014). Desiccation avoidance or delay strategies are those which minimise water loss in plants through stomatal control, increasing below-ground biomass, small thick leaves, or leaf shedding (Markesteijn and Poorter 2009, Delzon 2015). Desiccation tolerance strategies allow plants to survive periods of lowered plant water potentials, and include high osmotic potentials and rigid cell walls to maintain cell turgor, resistance to cavitation, and maintenance of cell processes (Comita and Engelbrecht 2014). Seedlings may be particularly susceptible to drought because of their shallow root systems, lack of water storage, and through interactions with biotic agents such as pests and pathogens that increase the stress caused by drought (McDowell et al. 2008, Parolin et al. 2010, Silvertown et al. 2015), while survival may be enhanced by non-structural carbohydrate levels (O’Brien et al. 2014).

Waterlogging in tropical forests

Waterlogged forest habitats are common in tropical regions. Waterlogged soil and flooding can be either a temporary state caused by increased rainfall in rainy seasons, or a more permanent state in lower terrain with a high water table. Waterlogging results in low soil oxygen, which consequently leads to reduced stomatal conductance, lower photosynthesis, plant hormonal imbalance, and poor water and nutrient uptake (Lopez and Kursar, 2003). Plants adapted to these habitats often exhibit enhanced root turnover rates, adventitious root formation, and formation of hypertrophic lenticels (Niinemets and Valladares 2006).

Low species diversity associated with seasonally flooded conditions in tropical forests has been attributed to low tolerance of flooding in many species (Lopez and Kursar 2007). However many species, including those not associated with flooded habitats, were relatively flood tolerant and therefore flooding tolerance alone could not explain the lower diversity found in floodplain forests (ter Steege 1994, Lopez and Kursar 2007). Seasonally flooded forests are often subject to annual periods of drying. Adult trees in floodplain areas may still be able to access the water table during dry periods, but seedlings with shallower root systems may be particularly susceptible during dry periods. Therefore drought resistance may be as important as flooding tolerance for species living in floodplain environments, particularly at earlier life stages (Parolin 2010).

Light availability

Light is recognised as a key limiting factor in tropical forests responsible for driving niche differentiation along light gradients (Kitajima and Poorter 2008). Light creates a high diversity of potential niches through fine scale habitat heterogeneity and high temporal variability, which contrasts with relatively more stable availabilities of water and nutrients. Typical light availability in the understory of mature tropical forests is around 0.5-3% of full sun, whereas treefall gaps can have between 10-40% of full sun (Kitajima and Poorter 2008). Species separate over the light gradient via physiological and morphological adaptations to perform optimally at some light availability and via tolerance of the extremes (high irradiance, and deep shade) (Valladares and Niinemets 2008). Classically, tropical trees are grouped as either light demanding pioneer species, or shade tolerant species based on germination and establishment requirements, however, newer research is refining these classifications into gradients of shade tolerance (Poorter 1999, Bloor 2003, Sendall et al. 2015, Feng et al. 2018).

Light is an essential resource for photosynthesis, but too high or too low intensities can compromise survival and growth (Valladares and Niinemets 2008). Light availability directly affects plant growth, survival, and recruitment, and indirectly via interactions with water availability. Higher light availability generally confers higher growth, unless availability is too high, or where water is limiting (Poorter 1999). Many tropical species are able to withstand light limited conditions in the understory for many years with very low growth until a gap is formed and they are able to take advantage of the increase in light (Popma and Bongers 1988).

Typically, plants living in low-light will allocate higher biomass to leaves, invest in thin leaves with high specific leaf area, reduce self-shading with large, spread-out crowns, and invest more in stem length over stem biomass to escape lower light levels (Givnish 1988, Poorter 1999, Chmura et al. 2017). Plants growing in high-light conditions may suffer adverse effects of increased radiation and temperature such as stomatal closure, turgor loss, wilting, bleaching of leaves, and damage to photosynthetic system (Poorter 1999, Teskey et al. 2015).

Interactions between water and light availability

The relationship between water and light availability and species niche partitioning in tropical forests is complex. Water and light are thought to covary along a productivity gradient where light decreases with increasing rainfall (Lohbeck et al. 2013, Amissah et al. 2015, Ouédraogo et al. 2016). Trade-offs in performance between wet and dry forests related to light availability are hypothesised to contribute to species distributions along water availability gradients (Brenes-Arguedas et al. 2011, Ouédraogo et al. 2013).

Different combinations and severities of both water and light provide opportunities for many niches and ecological strategies, where interactions between factors may increase the severity of the outcome, and potential conflicting responses from plants may result in heightened loss of performance. Further, adaptations to one factor may leave fewer resources available for other processes and may often result in trade-offs in specialisation. For example, dry forest origin species may be excluded from wetter sites because they are less able to cope with the lower light levels associated with wetter forests due to trade-offs in adaptations that allow them to take advantage of higher light associated with drier forests (Brenes-Argueda*s et al*, 2011). However, in a study on seedlings in Panama, no evidence was found for higher light requirements of dry forest species (Gaviria and Engelbrecht 2015).

An alternative hypothesis for the turnover in species between wet and dry forests is that wet distribution species may be associated with higher growth rates, and therefore competition for the limiting resource of light may be a strong determinant of success in wetter forests (Brenes-Arguedas et al. 2011). Differences in growth rates were found to underlie drought sensitivity in a wet forest in Central Africa where slow-growing species were found to be more drought tolerant and faster-growing species were more drought sensitive (Ouédraogo et al. 2013). Moreover, drought may have a greater negative impact on plants growing in deep-shade via a trade-off between greater belowground biomass adapted to efficient water uptake and greater aboveground biomass adapted to increased light capture. However, an opposing hypothesis predicts that plants subjected to drought under a canopy may be protected from the adverse effects of increased light such as high leaf and air temperature, high vapour pressure deficit, and oxidative stresses (Holmgren et al. 1997, Sack 2004).

Introduction to thesis chapters

In this thesis, I evaluated the relative roles of drought, waterlogging and light availability as drivers of differential species distributions across local scale habitats that varied in water availability, as well as other factors, in a seasonal wet tropical forest in French Guiana.

Chapter 2: Study site and species

This chapter provides an overview of the Paracou forest research site in French Guiana where this study was conducted, as well as an introduction to the study species and forest inventory data used in the study.

Chapter 3: The effects of drought, waterlogging and shade on the survival of tropical tree seedlings in French Guiana

Currently the relationship between seedling tolerance of drought, waterlogging, and light availability is unclear. Acclimation or adaptation to any one stress is energetically costly and may lead to a reduced ability to survive in another, and tolerance to any one stress is typically reduced by the presence of other co-occurring stresses. In this chapter, I report the results of a shadehouse experiment where I experimentally manipulated water and light levels creating combinations of drought, regularly watered and waterlogged conditions across a light gradient. Using survival times of 1532 seedlings and 20,000 individual observations. I modelled survival times to test theories of responses to combinations of multiple stresses. Using modelled survival responses, I calculated tolerance indices based on survival time predictions, then assessed indices for evidence of interspecific trade-offs.

Chapter 4: The relative importance of drought, waterlogging, and light availability in driving sapling distribution patterns in French Guiana rainforests

In tropical forests, variation in water availability between topographic habitats or soil-types is linked to local turnover in species composition. However, the relative importance of water and light in governing these relationships is currently unknown. Using data on the survival of 5374 individual saplings of 25 species and frequency of drought and waterlogging over a period of 24 years, and detailed data on understory light availability, I assessed the relative importance of drought, waterlogging, and shade in driving variation in sapling survival among habitats, and to what extent these relationships corroborate habitat associations in Paracou.

Chapter 5: Tolerances of drought and waterlogging but not shade predict tropical sapling performance in topographic habitats

Modelling approaches that incorporate species tolerance of environmental gradients could improve the understanding of species distributions by providing explicit links between species performance and environmental conditions. In this chapter, I tested the ability of experimentally derived species tolerance indices of drought, waterlogging and shade to predict observed species abundance and mortality patterns over the locally contrasting wet and dry topographic landscape of Paracou.

Chapter 6: Summary and conclusions

This chapter provides an overall summary of the results and limitations of the work presented in this thesis.

2. Study Site and Species

In this chapter, I present a general description of the forest plots and sapling census data, plot hydrology, and study species that are common to chapters 3-5.

This study took place in the Paracou experimental forest, a lowland tropical rainforest near Sinnamary, French Guiana, South America (5°18'N, 52°55'W) (Figure 2.1). In Paracou, continuous tree populations distributed across local-scale contrasting habitats provide an ideal opportunity to investigate the drivers of tree distributions along environmental gradients. Paracou is typical of Northern Guianan *terra firme* rain forests, with mean annual temperature of 26°C (annual range of between 1 - 1.5°C), and more than 500 woody species found on the site (Gourlet-Fleury et al 2004). The density of trees > 0.1m diameter at breast height averages 620 ha^{-1}, with a species richness of 140 species ha^{-1}, and mean tree height of 35m (Bonal et al. 2008).

Hydrology and light availability have been characterised across this well-studied landscape (Ferry et al. 2010, Wagner et al. 2012, Vincent et al. 2012). In addition, survival of saplings of 25 common tree species have been monitored for 25 years in a network of permanent forest plots (Gourlet-Fleury et al, 2004) (Figure 2.2). This abundance of data allowed the characterisation of resource availability, species distributions, and the vital rates of individual trees across the landscape. While the greenhouse growing facilities of the nearby Unité Mixte de Recherche EcoFoG, Kourou (40 km east of Paracou) allowed me to conduct the experiment in close proximity and similar conditions to the study site.

Rainfall

The site receives more than two-thirds of its annual 3041 mm of rainfall between March and June, with a pronounced dry-season between September and November when it often receives less than 50 mm per month (Wagner *et al.*, 2011). The length and severity of wet and dry seasons fluctuate annually (Figure 2.1), but severe dry seasons with at least 4 consecutive months of <50mm rain occur every 2-3 years whether there is an ENSO (El Niño Southern Oscillation) event or not (Bona*l et al*, 2008).

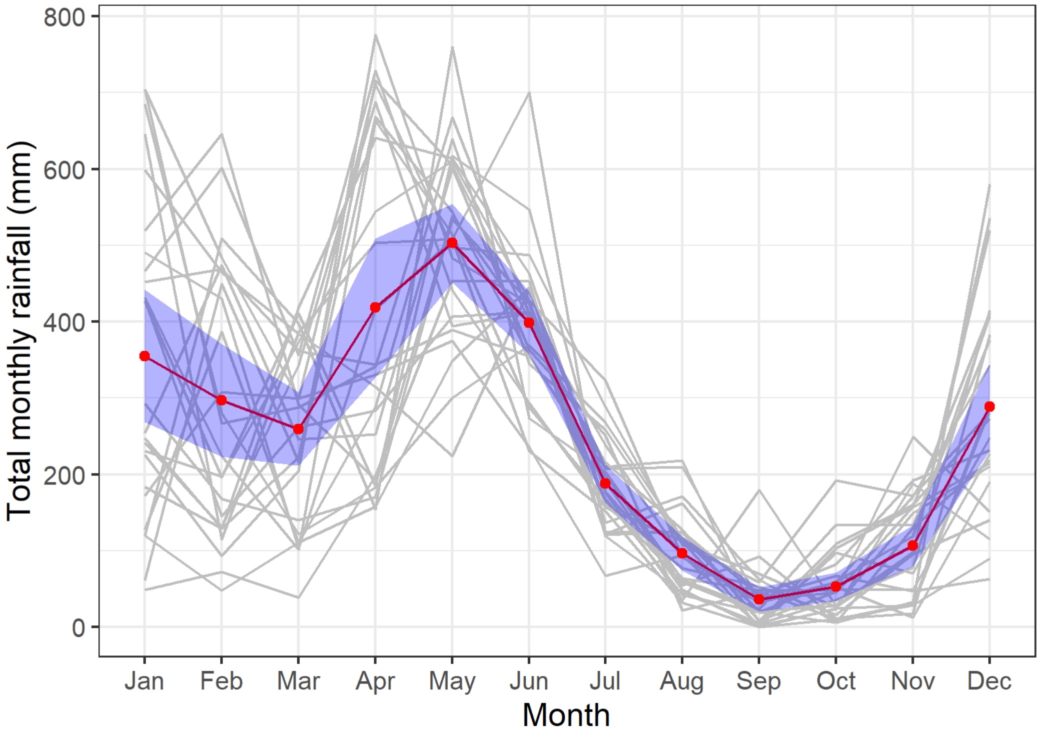

Figure 0.1. Total monthly rainfall (mm) in each year 1992 – 2016 with mean and 95% confidence intervals. Data taken at the Paracou experimental forest and from nearby meteorological stations (data courtesy of Fabian Wagner (Wagner et al., 2011).

Topography and soil water conditions

Paracou extends over 200 ha of undisturbed forest, where the parent material is a metamorphic formation of the Precambrian shield characterised by schists and sandstones (Epron et al. 2006). Elevation is between 0 – 45m (Figure 2.1). The site is characterised by a patchwork of hills 100 – 300 m diameter, with slopes between 25% – 45%, separated by narrow streams in humid valleys (Vincent *et al.*, 2011) (Figure 2.3). Topographical designations of hilltop, slope, and floodplains have been mapped for the site (Ferry et al. 2010). These categories refer to a gradient of soil water conditions and slope angle (summarised in Table 2.1).

Soils have been mapped using a soil classification system developed in French Guiana (Sabatier et al. 1997) and defined according to evolutionary stages in a feralitic soil, which is related to the soil's hydromorphic functioning and chemical properties (Sabatier *et al*, 1997; Wagner *et al*, 2011). Soils are mostly acrisols, limited in depth by a transformed loamy saprolite ≤ 1m deep which has low permeability, leading to lateral drainage during heavy rains (Epron et al. 2006). The upper permeable horizons are usually thickest on the hilltops and most shallow along slopes (Ferry et al. 2010). Seasonal waterlogging leads to bleaching of the surface soil horizons along streams (gleysols) and on slopes (Ferry et al. 2010). The soil types included in this study are referred to as Alt (red alloterite at a depth of less than 1.2m), SLD (superficial lateral drainage), UhS (uphill system), DhS (downhill system), and HS (hydromorphic soil) (Sabatier et al. 1997) (Table 2.2).

Soil Chemistry

Across Paracou, soil chemistry and fertility vary predictably across topographic gradients due to leaching of soils from the well-drained hilltops to the seasonally inundated floodplains (Allie et al. 2015). Lower nitrogen and higher phosphorus is associated with the Paracou floodplain soils compared to hilltops (Ferry et al. 2010). As well as a decrease in clay content and increase in nutrient content (base saturation cation exchange capacities) towards bottomlands and more acidic soils with high H, Al and C content on hilltops (Allie et al. 2015). The covariation of topography with soil hydrological properties and soil physico-chemical properties make it difficult to separate their effects on tree species distributions.

Table 0.1. Paracou regeneration plots topographic designation characteristics summary. Adapted from Ferry et al. 2010.

Topographic designation	**Slope**	**Water table**	**% of total regeneration plots**	**Total area (ha)**
Hilltops	< 25%	Consistently below 150cm	32.2%	1.27
Slopes	> 25%	Consistently below 100cm	43%	1.68
Floodplains	0 – 5%	Between 0–60cm depending on season	22.8%	0.9

Table 0.2. Paracou regeneration plots soil type characteristics summary and relationship with topographic designations.

Soil Type	Soil characteristics	Total area (ha)	% of plots in each topographic designation	
Alt	Water circulation is slow and always vertical. Found at the top of low slopes	0.63	Hilltops	13%
			Slopes	3%
			Bottomlands	0%
DhS	Downhill hydromorphic system. Found at the base of slopes near the permanent water table	1.1	Hilltops	3.3%
			Slopes	20.2%
			Bottomlands	5.2%
HS	Lowland hydromorphic soils. Corresponds closely to floodplains	0.73	Hilltops	0%
			Slopes	1.3%
			Bottomlands	17.6%
SLD	Superficial lateral drainage	0.92	Hilltops	11.3%
			Slopes	12.4%
			Bottomlands	0.3%
UhS	Uphill hydromorphic system. Top layer promotes accumulation of water, inducing hydromorphic conditions	0.47	Hilltops	5%
			Slopes	6.8%
			Bottomlands	0.4%

Description of Paracou forest plots and inventory

In Paracou, a network of permanent forest plots have been established and monitored for more than twenty years. The layout of the forest plots is shown in Figure 2.2, where small circular plots (represented as black dots on the map) are nested within larger plots of 6.25ha each. There are 768 small plots in total (64 per large plot), each measuring 4m radius (0.05ha, 50 m^2). Each plot has been classified with respect to topography and soil type (Table 2.1 & Table 2.2).

The small plots are referred to as regeneration plots, where irregular inventories of saplings have taken place in 1992, 1993, 1995, 2002, 2005, 2008, 2013, and 2016. Each inventory identified individual saplings between 1-10cm dbh (diameter at breast height) and above 1.3m in height and mapped each individual sapling location with respect to the centre point of each plot. At subsequent inventories, mapped individuals were monitored for growth and survival.

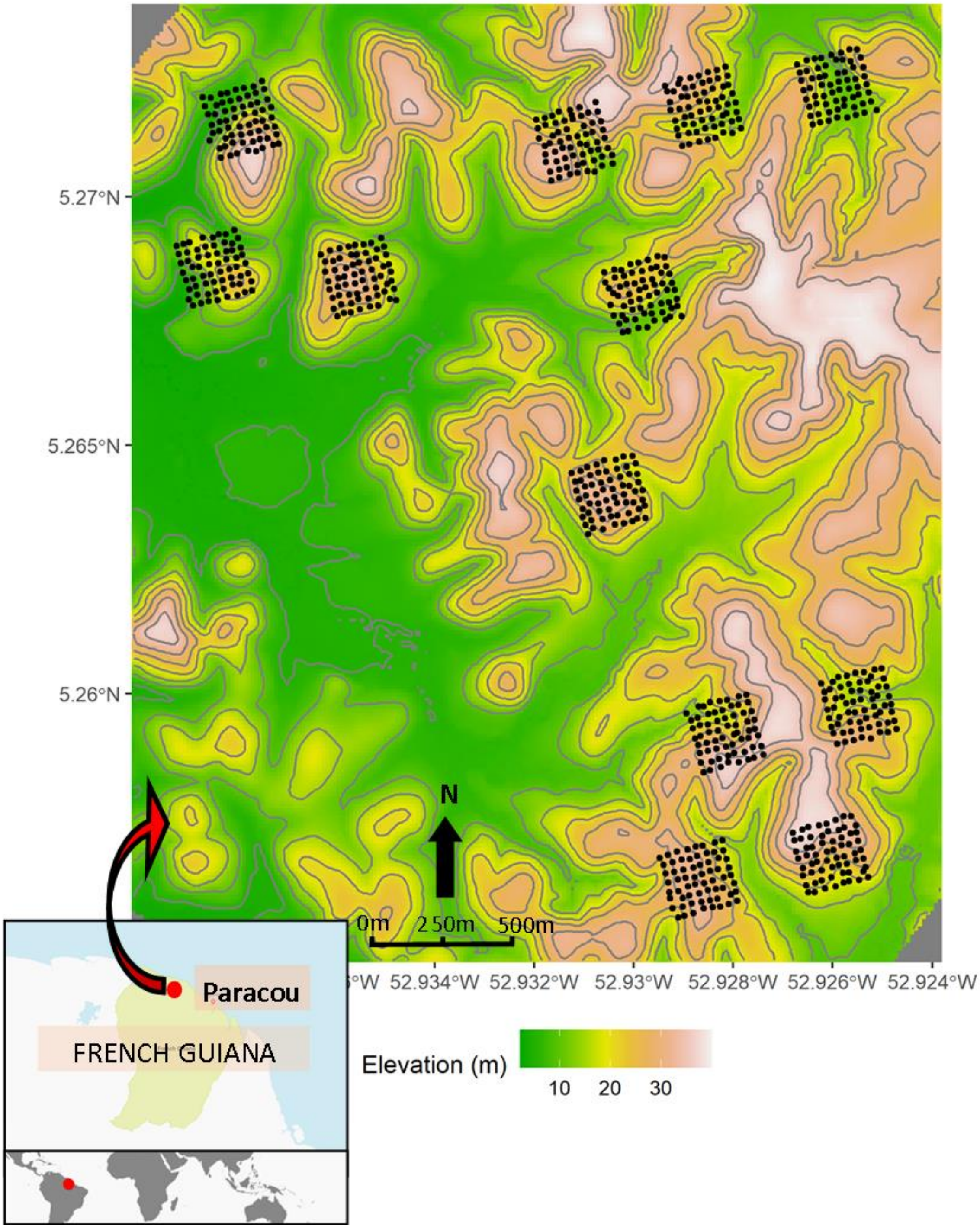

Figure 0.2. Permanent forest regeneration plots at Paracou Research Station, French Guiana, South America. Within each of 12 square plots there are sixty-four 4m radius small circular plots laid out in a grid, indicated by black dots on the map. The 768 small circular plots are used to monitor forest regeneration by monitoring abundance, growth, and survival of 25 common tree species at the sapling stage (see text for details). Shown with elevation map created from a digital terrain model derived from LiDAR data acquired across the Paracou site in 2013.

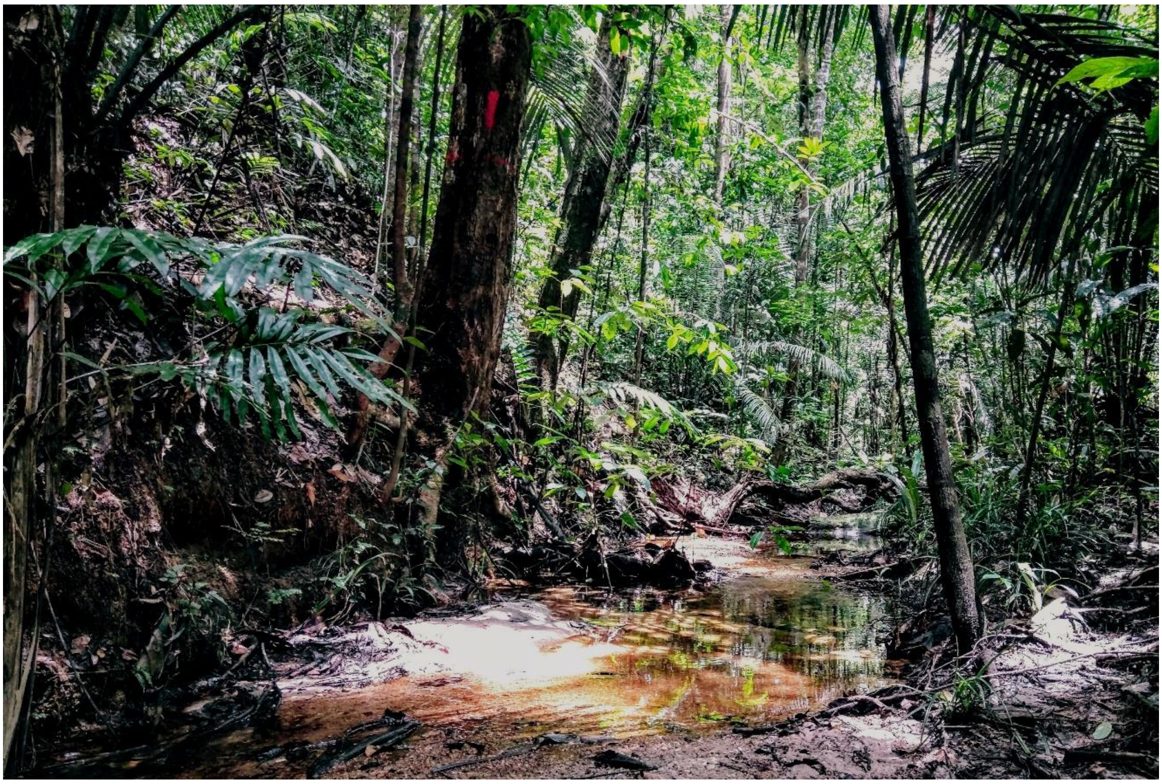

Figure 0.3. Photograph of a regeneration plot located in a valley bottom with steep slope in Paracou experimental forest. Photo taken April 2016 during the 2016 regeneration census.

Study Species

The full set of study species consisted of twenty-five common species for which reliable census survival data was available (Table 2.3). A subset of eleven of these was studied in greater depth in chapters 3 & 5 (highlighted species in Table 2.3). Each species was chosen to be part of the sapling regeneration survey at Paracou because they were abundant across the landscape and were easily identified at the juvenile stage (Gourlet-Fleury *et al* 2004). Previous work characterised the life history strategy in terms of shade tolerance for each species (except *V. surinamensis*) based on the maximum height, recruitment, mortality, wood density and growth rates of adult trees larger than 10cm diameter at breast height (dbh) in logged and unlogged permanent forest plots in Paracou (Favrichon 1994). For example, the mean characteristics of light-demanding species display faster growth and lower wood density than other species (Ferry et al. 2010).

More recently, studies characterised habitat associations for these species in Paracou using the torus translation method to account for spatial autocorrelation by permuting rotations of habitat coordinates relative to those of trees (Baraloto et al. 2007), and pairwise association of spatially structured maps (Allie et al. 2015). It is important to note that species were not evenly represented in different classes. Eleven species in total were associated with hilltops compared to nine with the bottomlands, a further one species had no association and three were unknown (Table 2.3). Of those species studied in greater depth, only three species were included with association to the hilltops compared to six with the bottomlands, one further species with no association to any of the three topographic habitats and one species of unknown habitat association. This uneven distribution may introduce bias to the results, which is discussed in the relevant chapters.

Table 0.3. Information on the twenty-five species used in this study. Included are life history strategies in terms of shade tolerance (Favrichon 1994), *(where ST = strongly shade tolerant; T = shade tolerant; MT = mid shade tolerant; and H = heliophilous); known habitat associations to either Hilltops (dry) or Bottomlands (wet) at the adult stage* (*Baraloto *et al.*, 2007; **Allie *et al.*, 2015)*; seed dispersal method* (from Baraloto and Forget, 2007)*; and, dry seed size class* (from Baraloto and Forget, 2007)*. Yellow shading identifies those species studied in greater depth in Chapters 3 and 5.*

Species name	Family	Life History Strategy	Habitat association	Dry seed size
Andira coriacea	Fabaceae	MT	Hilltop**	20g
Bocoa prouacensis	Fabaceae	ST	Hilltop**	2.5g
Carapa surinamensis	Meliaceae	H	Bottomlands**	7.5g
Dicorynia guianensis	Fabaceae	MT	Hilltop**	0.5g
Eperua falcata	Fabaceae	MT	Bottomlands*	7.5g
Eperua grandiflora	Fabaceae	MT	Hilltop*	20g
Goupia glabra	Goupiaceae	H	Bottomlands**	0.01g
Iryanthera hostmannii	Myristicaceae	ST	Bottomlands*	0.5g
Iryanthera sagotiana	Myristicaceae	ST	Hilltop*	2.5g
Jacaranda copaia	Bignoniaceae	H	Bottomlands**	0.05g
Moronobea coccinea	Clusiaceae	MT	Unknown	7.5g
Platonia insignis	Clusiaceae	MT	Hilltop**	7.5g
Pradosia cochlearia	Sapotaceae	T	Hilltop**	0.5g
Qualea rosea	Vochysiaceae	MT	No association**	0.5g
Recordoxylon speciosum	Fabaceae	MT	Bottomlands**	0.5g
Schefflera decaphylla	Araliaceae	H	Unknown	0.05g
Sextonia rubra	Lauraceae	MT	Hilltop**	2.5g
Sterculia pruriens	Malvaceae	H	Bottomlands**	0.5g
Sterculia multiovula	Malvaceae	H	Unknown	0.5g
Symphonia globulifera	Clusiaceae	MT	Bottomlands*	7.5g
Symphonia sp. 1	Clusiaceae	MT	Hilltops*	2.5g
Tachigali melinonii	Fabaceae	H	No association**	0.5g
Virola michelii	Myristicaceae	H	Hilltops*	2.5g
Virola surinamensis	Myristicaceae	Unknown	Bottomlands*	0.5g
Vouacapoua americana	Fabaceae	T	Hilltops**	20g

CHAPTER 3

3. The effects of drought, waterlogging and shade on the survival of tropical tree seedlings in French Guiana

3.1 Abstract

In tropical forests, water and light availability are two of the most important factors affecting forest regeneration. Fundamental questions remain as to what extent seedling survival is affected by the interactive effects of water availability and light. I report the results of a shadehouse experiment involving seedlings of eleven co-occurring tropical tree species and survival times of 1532 seedlings using 20,000 individual observations. I modelled survival times to investigate within and between species variation in seedling survival along an experimental irradiance gradient and in three contrasting water availability regimes, '*drought*', '*waterlogged*', and '*watered to field capacity*' and calculated tolerance indices for drought, waterlogging, and shade. Intra-specific relationships between survival times in different water treatments across the light gradient provide evidence of positive, negative, and nonlinear effects of light. Species tolerance indices revealed a negative relationship between drought and shade tolerance, but no evidence of an association between waterlogging tolerance and either shade or drought tolerance. Overall, these results suggest that, when nutrients are not limiting and in the absence of root competition, shaded tropical seedlings are impacted more strongly by drought than seedlings in higher light conditions. Given that climate projections predict increasing frequency and severity of both droughts and flooding for tropical regions, these relationships may have profound implications for species compositional changes in the tropical forests of French Guiana.

3.2 Introduction

Seedling survival along resource gradients varies between species and is a key factor controlling plant community structure and dynamics (Grubb 1977, Silvertown 2004, Sánchez-Gómez et al. 2006). Understanding the drivers of seedling survival is important as the early life stages of tree communities are a critical bottleneck for shaping forest composition (Green et al. 2014). Differential seedling tolerance of environmental conditions and trade-offs in tolerance of multiple conditions restrict optimal performance to certain habitats (Grime 1977, Niinemets and Valladares 2006). As the availability of different resources can vary simultaneously along spatial and temporal gradients an understanding of how plant performance is affected by combinations of multiple resources is fundamental to predicting the effects of environmental change (Niinemets and Valladares 2006, Holmgren et al. 2012, Craine et al. 2012).

Seedling tolerance of hydrological conditions is related to niche separation along fine-scale soil-moisture gradients and is a major determinant of species compositional turnover between habitats in tropical and temperate forests (ter Steege 1994, Wright 2002, Metz 2012, Letten et al. 2015, Silvertown et al. 2015). Many environmental variables co-occur with soil-water availability, however,and tolerance of hydrological conditions is likely to be affected by the co-occurrence status of other key drivers (Niinemets and Valladares 2006, Lucas et al. 2013, Laanisto and Niinemets 2015).

Along the hydrological gradient, insufficient water, i.e. drought, and the opposite extreme, waterlogging or flooding, impose two uniquely harsh environments for tropical seedlings. Habitat partitioning in tropical seedlings has been linked to differential mortality related to both drought (Delissio and Primack 2003, Slot and Poorter 2007, Lopez and Kursar 2007, Comita and Engelbrecht 2009, Itoh et al. 2012), and flooding (Lucas et al. 2013, Born et al. 2015, Fortunel et al. 2016), while in forested systems subject to seasonal wet and dry periods, tolerance of both drought and flooding regimes is crucial to establishment (Urbieta et al. 2008, Parolin et al. 2010, Teshera-Levye et al. 2020).

Another key driver in forest understory regeneration success is sunlight (Brokaw 1982, Denslow 1987, Canham et al. 1990, Valladares et al. 2016). Lack of sunlight can impose severe energy stress in seedlings as they inhabit forest floors where less than 1% of sunlight may penetrate through intact canopies (Valladares and Niinemets 2008). Tolerating shade affects the ability of plants to survive and grow as well as to cope with other stressors (Valladares et al. 2016). Shade tolerance plays a key role in seedling establishment under closed canopies in tropical and temperate forests (Montgomery and Chazdon 2002, Bloor and Grubb 2003, Zhu et al. 2014, Lin et al. 2014).

In forested systems water and light levels are often negatively correlated (Brenes-Arguedas et al. 2011, Holmgren et al. 2012). Wetter forests are associated with greater plant production which results in dense canopies that reduce light availability in the understory (Niinemets and Valladares 2006). Whereas drier forests can be associated with increased understory light availability related to adaptations for smaller leaves, leaf abscission during droughts, as well as increased solar radiation related to decreased cloud cover (Givnish 1988, Wright and van Schaik 1994). Nevertheless, wet and light conditions can occur as a result of increased tree falls in waterlogged soils (Ferry et al. 2010), as well dry and shady conditions can result following extended dry periods in dense forests (Veenendaal et al. 1996, Holmgren et al. 2012).

Plant species may have adaptations to perform better in wetter, drier or more shaded conditions. For example, during periods of drought, the risk of death in seedlings is determined by the ability of the plant to avoid hydraulic failure and drought-induced cavitation by controlling water potentials via stomatal control, increase allocation to roots, and produce smaller leaves (McDowell et al. 2008, Comita and Engelbrecht 2014, Blackman et al. 2019). During periods of soil waterlogging survival may depend on a plants ability to produce adventitious roots, lenticels, aerenchyma, and leathery xeromorphic leaves to cope with reduced stomatal conductance, reduced photosynthesis, and poor water and nutrient uptake resulting from oxygen depleted soils (Lopez and Kursar, 2003; Parolin et al. 2010). Typically, characteristics that help a plant survive in low-light conditions include greater allocation of resources to above-ground traits such as larger leaves and investment in stem and stem growth (Poorter et al. 2012c).

Acclimation or adaptation to any one of these stresses is energetically costly and may lead to a reduced ability to survive in another, and tolerance to any one stress is typically reduced by the presence of other co-occurring stresses (Niinemets and Valladares 2006, Dragičević 2015, Menezes-Silva et al. 2019). Fundamental questions remain as to what extent plant performance is affected by the interactive effects of drought and light (Prider and Facelli 2004, Sack 2004, Amissah et al. 2015), and waterlogging and light (Lenssen et al. 2003, Niinemets and Valladares 2006, Infante-Mata et al. 2019). Given that disturbance and extreme weather events such as droughts and intense rainfall are set to increase in tropical regions (Cochrane and Barber 2009), an understanding of plant mortality in relation to each driver and their interactions is important to be able to predict how species may respond to future environments (Craine et al. 2012).

At the intraspecific level, the trade-off hypothesis predicts that as a result of contrasting biomass allocation strategies drought will have a stronger impact on plants growing in low-light and similarly that plants will become less tolerant of shade when growing in dry conditions (Smith and Huston 1989, Sack 2004). For example, a given species growing in low-light will have greater allocation to above-ground biomass at the expense of allocation to roots, thereby increasing light capture over water capture (Smith and Huston 1989, Sack 2004). Similarly, survival in waterlogged conditions may be achieved by increased root turnover and energetically costly adventitious root formation, which is not favourable to survival in low-light conditions (Niinemets and Valladares 2006).

An alternative hypothesis relevant to plants exposed to water and thermal stress is that the presence of low-light may reduce water limitation in seedlings by reducing air temperature, leaf temperature and transpiration demands which therefore weakens the effect of drought (Holmgren et al. 1997, Sack and Grubb 2002). This facilitative interaction where plants grow and survive better under the shade of other plants is thought to be widespread among plant communities (Bertness and Callaway 1994, Holmgren et al. 2012). The facilitative effect of a dense canopy can also be relevant in waterlogged sites. For example, increased canopy interception created sheltered microsites with lower risk of waterlogging which facilitated seedling emergence and survival in Mediterranean oak forest ecosystems (Urbieta et al. 2008).

With regards to drought, a further 'interplay' hypothesis reconciles the contrasting trade-off and facilitative hypotheses where at both high and low irradiances the effect of drought may be strong, whereas at intermediate light levels the effect of drought may be weaker (Holmgren et al. 1997, 2012, Sack and Grubb 2002).

Interspecific trade-offs may also govern tolerances of drought, waterlogging and low-light, and selection for particular biomass allocation patterns may underlie these trade-offs as well (Smith and Huston 1989, Sack 2004). For example, species with greater tolerance of low-light may be particularly vulnerable to drought compared to light demanding species as a result of selection for allocation to stems and leaves rather than roots (Sack 2004). In contrast, co-tolerance to pairs of environmental factors may be achieved if functional trade-offs within a species support survival in the presence of both stressors (Vinebr*ooke et al*, 2004). For example, some of the same functional and anatomical characteristics that allow plants to cope with drought conditions also alleviate the stress of waterlogged conditions (such as increased root allocation) (Parolin et al. 2010, Grubb 2016).

Untangling the effects of each driver on seedling performance is difficult in natural systems, but manipulation studies offer the opportunity to isolate variables of interest and directly assess the impact on seedling performance (Paine et al. 2018). In this chapter, I report the results of a shadehouse experiment involving seedlings of eleven co-occurring tropical tree species that vary in life-history strategies and habitat associations. I used survival modelling to investigate within and between species variation in seedling survival along an experimental irradiance gradient and in three contrasting water availability regimes, drought, waterlogged, and regularly watered. I asked two broad questions. In the absence of root competition and when nutrient availability is not limiting:

1) To what extent does species' survival in the shadehouse under drought, waterlogged, and watered conditions vary over a gradient of light availability?

2) To what extent do experimentally assessed species' tolerance of drought, waterlogging, and light trade-off?

3.3 Methods

Study site

A general description of the site and environmental conditions can be found in Chapter 2. The experiment reported here was conducted in two shadehouses at the Unité Mixté de Recherche EcoFoG, Kourou, French Guiana (40km east of Paracou, Figure 2.1). The climate is tropical with an average annual temperature of 26.1^0C and average annual rainfall 3041 mm. Kourou experiences the same wet and dry season pattern described for Paracou, where the months of March to June see the heaviest rainfall and dry season extends from around September to the end of October.

Experimental design

In this shadehouse experiment, I imposed three levels of water availability in a factorial split-plot design: 'drought' (no watering since the commencement of the study), 'waterlogging' (water maintained at or above the soil surface) and 'watered' to field capacity (watered every 2-4 days). Inside two experimental shadehouses with imposed gradients of shade (detailed below) I arranged six blocks (each approx. 1m x 1.5m) per watering treatment (36 blocks in total) in evenly spaced rows with one block per treatment allocated randomly to each row (Figure 3.1). Arrangement in replicate blocks suited the logistical needs of the experiment as individuals in different water treatments needed to be kept separate. Individuals in 'drought' blocks were placed on bamboo or wooden slats to elevate them from the ground to prevent water absorption into the pots, and 'waterlogging' individuals were kept in large flooded boxes (see Figure 3.2).

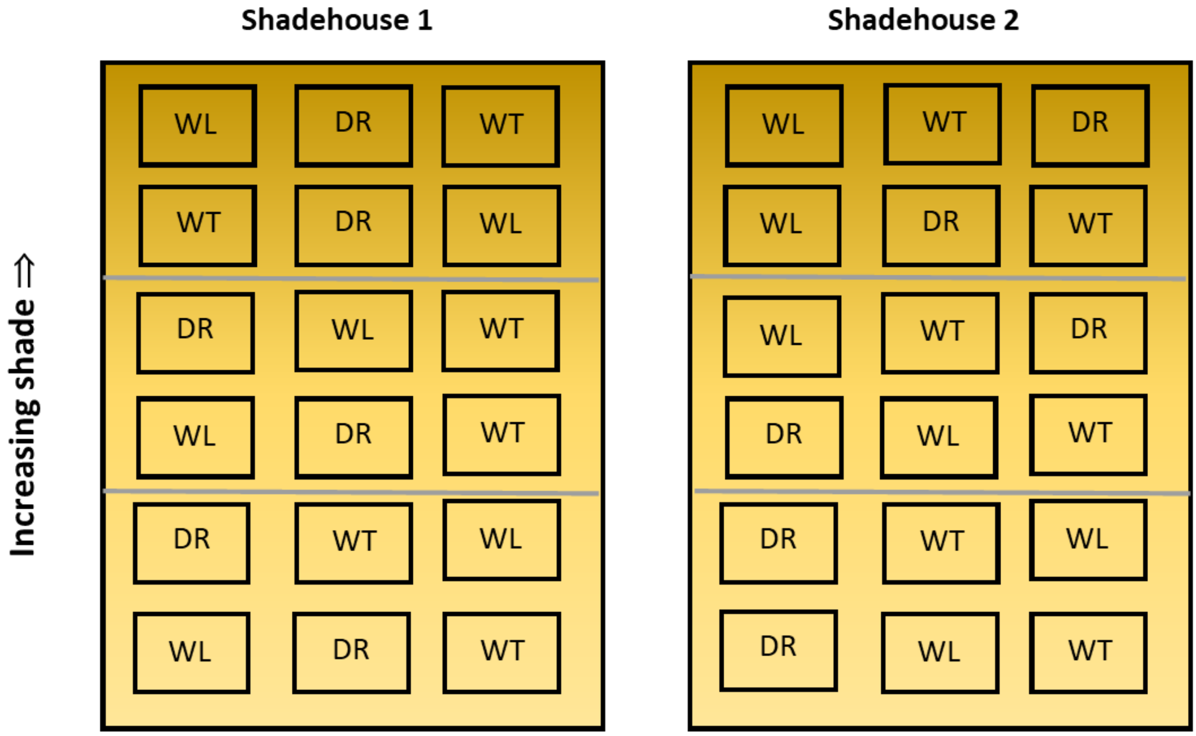

Figure 3.1. Experimental design of manipulation experiment. Shown are the two shadehouses each with a gradient of light availability that increased in shade from front to back; the location of each of treatment block with the three treatments, drought = 'DR', waterlogging = 'WL', and the control treatment watered to field capacity 'WT'; internal 'walls' of hanging shadecloth are shown as grey horizontal lines. Individual treatment blocks are arranged with six blocks per water treatment per shadehouse. Blocks were arranged in a 3 x 6 grid, where treatments were randomly allocated to each block, ensuring that each treatment is located once per row to allow an even distribution over the range of light availability values.

Experimental shadehouse set-up

Two high tunnel style shadehouses were located adjacent to each other running east to west. Each shadehouse was 10m long x 4.2m wide x 2.2m high, with a space of 2m between the tunnels to avoid shading of the neighbouring tunnel (Figure 3.2A).

The three sections of each tunnel were covered in shadecloth, and layered to create a continuous gradient of high- low shade environments (Figures 3.1 & 3.2) (see section 'Light availability measurements' below for details on how the light gradient was measured and monitored). The levels of light availability in shadehouse studies have received criticism for being less than realistic (see Bloor, 2003). For this investigation I mitigated concerns over light conditions by creating a gradient of light availability ranging from 0.2% - 27% of full sunlight. This gradient spans the range typically found in understorey tropical forests (Canham et al. 1990, Kobe 1999, Bloor and Grubb 2003, Sánchez-Gómez et al. 2006), and importantly includes the very lowest end of the gradient which is often not included in studies and may be the most relevant for partitioning survival abilities in shade tolerant species (Bloor 2003). Each shadehouse was split into three equal sized sections separated by layers of shadecloth acting as internal walls (Figure 3.2B).

To control water availability inside the shadehouses, each was covered in a layer of plastic to prevent rain from entering. I created plastic covering-free gaps at either end of the tunnels and around the sides to encourage air-flow and reduce humidity (Figure 3.2A). Flooding containers for experimental treatments were built using wooden frames with plastic walls and floor (Figure 3.2B & 3.2C).

A third shadehouse of the same dimensions with a medium-sunlight environment created using shadecloth and no plastic rain cover was used as a nursery to house seedlings collected in the field before they entered the experiment.

Temperature inside each of the two experimental shadehouses was monitored using a temperature logger (HOBO Pendant UA-002-64) which logged temperature at 30-minute intervals between 10:00 and 16:00 daily during the experimental period.

Figure 3.2. Experimental set-up. ***A****) Outside view of both shadehouses. In view are the green shadecloth coverings with plastic rain cover over the top. Rain covers are rolled up at either end and along sides to encourage ventilation. Flooding containers are seen before placement in the experiment.* ***B****) Inside middle section of one shadehouse during the experiment. At the top of the picture is the shadecloth 'wall' that partitions the darker section. At the front of the picture not in view is the second shadecloth 'wall' partitioning the lighter section. Flooding containers filled with water can be seen. Bamboo slats elevating drought treatment seedlings from the ground to prevent absorbing moisture from the ground can also be seen.* ***C****) Inside dark section of one shadehouse during the experiment. Several light sensors monitoring light availability are in view.*

Light availability measurements

The percentage of full sunlight inside each shadehouse was measured at a resolution of 0.25m^2. I did this by creating 50cm x 50cm grid squares on the floor of each shadehouse and giving each a coordinate reference, then systematically measured light availability at the centre point of ~80% of all grid squares. For all grid squares monitored, the light environment was logged for a mean of 2.4 days (range 1 – 29 days). Sensors were placed at the centre of grid squares at a height of 75cm from the ground (Figure 3.2C).

Light intensity was measured in lux using multiple HOBO light sensors (HOBO Pendant UA-002-64) logged at precise intervals between 10am-4pm. The HOBO light logger has a planar sensor designed for measurement of light intensity between 150-1200 nm. All sensors were placed on a flat surface to reduce measurement error between sensors from differing levels of intensity from direct and indirect light.

Light availability in the shadehouses was calculated as a percentage of that measured in an open location. Measurements taken by two HOBO loggers placed in full sunlight outside the shadehouses were averaged and compared against loggers placed in mapped locations inside the shadehouses. Results were averaged to give a daily estimate for each grid square monitored. These data were then used to predict a light availability surface estimate for the inside of each shadehouse (Figure 3.3) using a kriging method (Nychka et al. 2019). This allowed prediction of light availability for all individually mapped seedling locations.

The difference in light availability between full sunlight and light inside Shadehouse-1 ranged between 0.2% - 25%, and in Shadehouse-2 between 0.6% - 27% (Figure 3.3). The light gradient in each shadehouse was not exactly the same, therefore replicate blocks are not replicates of light availability. This does not affect analyses however, as each individual seedling was given its own light availability measure.

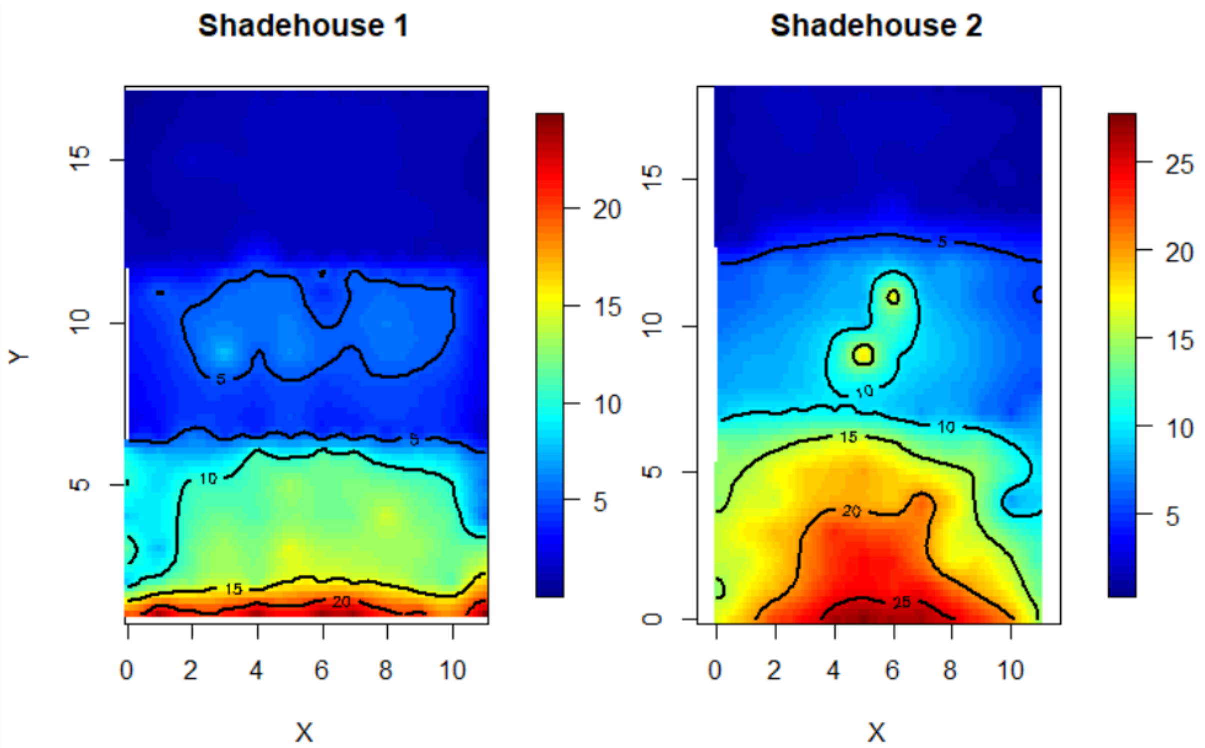

Figure 3.3. Light availability surface estimate inside both experimental shadehouses. Light availability is shown as the percentage difference between full sunlight and light inside the shadehouses. Light intensity was measured in lux using multiple loggers at different locations simultaneously (see text for details).

Species and seed / seedling collection

All species were collected from the Paracou experimental forest, a lowland tropical rainforest near Sinnamary, French Guiana (5°18’N, 52°55’W) (described in detail in Chapter 2) with permission for seed and seedling collection granted by Cirad (Centre de coopération internationale en recherche agronomique pour le développement), French Guiana. Individuals of eleven species of canopy trees were collected as seeds, or seedlings that had established during 2016. The species are listed in Table 3.1 with details of numbers of individuals, collection and experiment start dates. Photographs of each species are in Figure 3.4. The eleven species vary in light requirements and soil-moisture related habitat preferences (see Table 2.3 in Chapter 2 for details).

Groups of individuals of *D. guianensis* and *S. rubra* were collected multiple times so they could be run through the experiment at different times of the year to allow comparisons of performance for the same species between time periods. If performance within a species was similar during different time periods, this would suggest that the conditions were similar over the entire experimental period.

All seeds or seedlings were planted in individual plant pots in the nursery within two days of collection. A lot of consideration was put into the choice of pot size for this experiment, as the wrong choice of pot size may induce nutrient limitation, and may affect biomass accumulation independently of nutrient levels through root restriction (Poorter et al. 2012a). I opted for tall and wide with approx. 22L of soil per pot. This was based on the recommendations given by Poorter, Bühler, et al*.* (2012) for ratio of plant size to pot size of <1g dry biomass L^{-1} and expected size of seedlings. This was also realistically and logistically the largest pot size that could be in this experiment due to space limitations. Polythene grow bags 30cm x 35cm (25 litres) were filled with a two-parts local provenance top-soil, one-part white-sand mix. Each pot was filled to depth of approximately 25cm. All plants received regular watering during the nursery phase where species spent 2-7 months.

For the vast majority of the seedlings in this study the choice of pot size meant that they were not limited in growth potential. Most seedlings did not outgrow the ratio of <1g dry biomass L^{-1} recommended by Poorter, Bühler, et al*.* (2012) and none were larger than 2g dry biomass L^{-1} (destructive harvest data not published). However, nutrient limitation may have affected some individuals grown in the '*watered'* treatment and high-light conditions. For some of these individuals the symptoms of chlorosis was noted during the first run of the experiment. A slow-release fertiliser was therefore administered to all seedlings, and in subsequent trials the same dose of fertiliser was administered at the same point in the experiment. Following this only few yellowing leaves were noted which may have been due to nutrient limitation, but this was only on larger plants at the final stages of the experiment so was unlikely to bias the survival results.

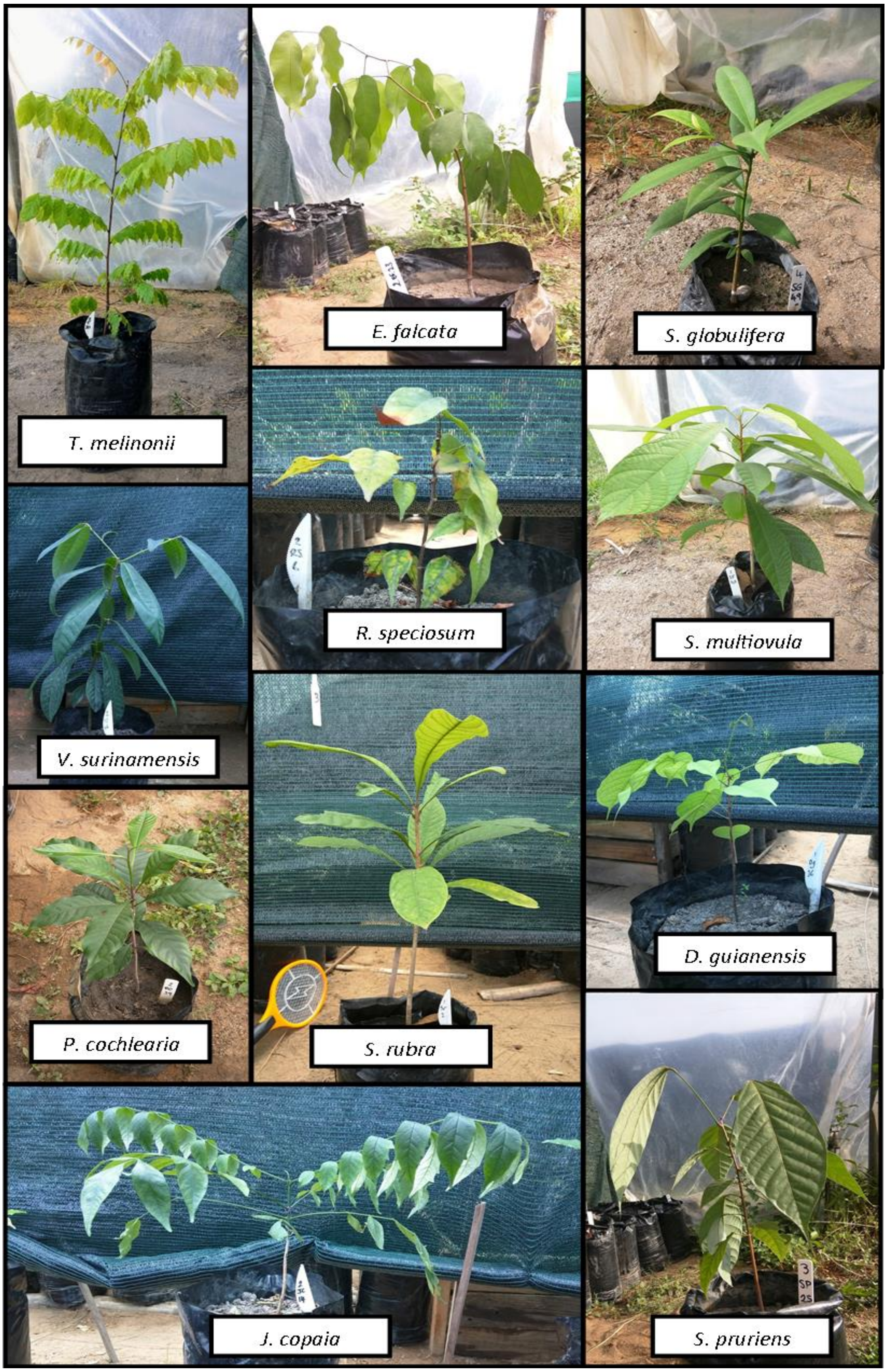

Figure 3.4. Photographs of each of the eleven species used in chapter 3. Refer to Table 3.1 for details of each species.

Experiment timings

The experiment was carried out between Nov. 2016 – Jan. 2018. Owing to limited space in the shadehouses it was not possible to carry out the whole experiment at one time. Instead a rolling experimental protocol was implemented whereby when a species was removed at the end of their experiment time, it was replaced by a new species entering the experiment (see dates in Table 3.1). Individual plants were placed at random within blocks. Individual pots were placed within grid squares (four pots per 50cm x 50cm square) which allowed mapping of individual seedling location and light availability. Pots were turned regularly to prevent and check for roots growing out of or into pots. At two-monthly intervals individuals within blocks were re-randomised which controlled for spatial effects within blocks.

The experimental schedule for each species included an initial 30-day acclimation period following the placement of the plants into the experimental shadehouses. Any mortality observed during this period was not included in the analysis to allow for individuals that may have died due to the shock of being moved. Following this, all seedlings were subject to a 'shade acclimation' period, which varied between 21- 50 days depending on species. During this time seedlings were exposed to the light availability treatments and were watered regularly. This was followed by commencement of the water treatments, which continued for between 2-4 months.

From commencement of the shade acclimation period, individuals were monitored for survival at least weekly. Seedlings were determined to have died when severe wilting, necrosis, or leaf abscission were observed. For individuals where death was difficult to determine, a thin section of bark was cut to check for stem death. Some individuals of each species were re-watered after 'death' was thought to have been observed to check for resprouting. Resprouting was observed for three individuals of *Recordoxylon speciosum*. These individuals were reclassified as 'not dead' with 'undetermined' survival time. Further mortality observations for this species were confirmed by checking stem health and no further resprouting after rewatering was observed.

Table 0.1. Details of species entered into experiment. Includes whether they were collected from the forest as seeds, seedlings, or as seedlings with seeds still attached (Seedlings²); the number of parent trees; the date the particular species entered the experiment; the total number of individuals that entered the experiment; and the total number of individuals that died during the experiment.

Species name (species code)	**Collected as seeds or seedling**	**No. of parent trees**	**Date entered experiment**	**Total seedlings entered experiment**	**Total seedlings died during experiment**
Dicorynia guianensis (DG)	Seedlings	3	Jan-17	108	41 (37.9%)
	Seedlings	1	Oct-17	9	2 (22.2%)
Eperua falcata (EF)	Seeds	4	Jul-17	117	12 (10.3%)
Jacaranda copaia (JC)	Seedlings	3	Jan-17	129	60 (46.5%)
Pradosia cochlearia (PC)	Seedlings	3	May-17	150	45 (30%)
Recordoxylon speciosum (RS)	Seedlings^2	3	Jan-17	144	40 (27.8%)
Sextonia rubra (SR)	Seedlings^2	3	Jan-17	100	39 (39%)
	Seedlings^2	1	May-17	28	13 (46.4%)
	Seedlings^2	1	Oct-17	14	5 (35.7%)
Sterculia pruriens (SP)	Seedlings^2	3	Sep-17	204	20 (9.8%)
Sterculia multiovula (SM)	Seedlings^2	2	Sep-17	118	19 (16.1%)
Symphonia globulifera (SG)	Seedlings^2	4	Sep-17	153	18 (11.8%)
Tachigali melinonii (TM)	Seedlings	3	Jan-17	116	44 (37.9%)
Virola surinamensis (VS)	Seedlings^2	3	Jan-17	142	17 (12%)

Data analyses

Individual species survival models

I examined survival times of 1532 seedlings using 20,000 individual observations. I carried out a multi-step data analysis whereby individual survival models were built for each species, then based on those models I predicted survival times in different treatments and assessed them for evidence of intraspecific trade-offs. I calculated tolerance indices based on survival time predictions, then assessed indices for evidence of interspecific trade-offs.

I performed parametric survival analyses using the survreg() function from the Survival package in R (Terry and Therneau 2016), in which the outcome variable of interest is *time until an event occurs.* This approach allowed comparison of the timing of mortality across species and treatments, and prediction of the median time to death for each species in each of the nine treatment combinations. Models were fit using a Weibull error distribution as these produced lower error variances when compared with other commonly used survival distributions ('logistic', 'loglogistic', 'exponential'). The Weibull distribution is biologically appropriate for seedling survival studies, as it allows mortality risk to vary over time (Fox 1993, Walters and Reich 2000).

Coding for the response variable followed convention whereby the two vector response variable 'event' was coded as '0' if the seedling remained alive, or '1' if mortality was observed, and 'time in days' to the final observed event. For those individuals coded as '0' i.e. 'no event', the 'time in days' value corresponds to either the last day of the experiment, or the day they were last observed alive before removal from the experiment (some individuals were removed for destructive harvesting and others lost their identification tags). These are 'censored' seedlings, which are individuals for which I have some survival information, but I do not know the exact time of death.

The full survival model for each species included terms for the categorical predictor '*water treatment*', with the '*watered'* treatment set as the reference level against which survival in '*drought'* and '*waterlogged'* treatments were compared. Light availability was included as a continuous linear predictor. To account for the potential nonlinear effect of light, whereby low and high light levels may negatively affect survival, resulting in a U-shaped response curve, I also included a quadratic light availability term. Seedling height at the start of the experiment was included as a covariate to account for differences in starting condition. The number of leaves belonging to each seedling at the start of the experiment correlated with seedling height so was not used. Interaction terms were included for each predictor variable. All numerical predictors were scaled and centred prior to analyses by subtracting the mean and dividing by the standard deviation to allow direct comparison of the relative importance of each predictor on sapling performance and to ensure no collinearity between the light and quadratic light term (Schielzeth 2010).

No mortality was observed in some species/treatment combinations (Figure 3.2), Therefore, I added 1 dummy dead seedling of each species to each treatment on day one to allow calculation of reasonable survival estimates. When no mortality was observed for some treatment combinations, the model became unstable and resulted in unreasonable estimates of survival time. By adding a dummy dead seedling on the first day of the experiment, I forced the survival probabilities to be less than one for all species/treatment combinations without biasing the results. Survival of each species was modelled independently.

Model simplification was carried out by fitting the maximal model, then iteratively removing non-significant terms, starting with interaction terms (Crawley 2007). I tested for significance of removed terms by comparing nested models using likelihood ratio tests. The most parsimonious model kept all main additive effects, but only kept interactions if they were significant. Parental provenance of seedlings was included in maximal models and found to be significant for only one species, *Sterculia multiovula*. This was the only species for which seedlings were collected from only two different parent trees. All other species were collected from either three or four parents (Table 3.1). Shadehouse, and blocks within shadehouses, were also included in maximal models. The effects of these variables on seedling survival were found to be non-significant and so were excluded from further analyses.

Change in survival in different water treatments over a light gradient

To assess how survival changed in water treatments over a light gradient I predicted the median time until death (i.e. time in days until 50% of the seedlings died) for each species based on model results. Here, the change in survival among treatments rather than the predictions of survival times were the focus of interest. Given that zero or very little mortality was observed under conditions of regular watering and plenty of light for many seedlings within the bounds of the experimental period, models were unable to estimate realistic survival times for these treatments. However, even though estimates of actual survival times were unreliable the change in survival estimates was reliable as they were derived in a consistent way from a robust method.

I made predictions for each of the three water treatments, '*drought*', '*waterlogging*', and the reference treatment '*watered*', over the full range of light availability experienced by the seedlings in the experiment, 0.2 – 27% of full sunlight.

Generating and testing tolerance indices

My second research question asked, to what extent do species tolerance of drought, waterlogging, and shade trade-off? To answer this question, I generated three separate indices based on the relative difference in survival time in '*least-stressful*' vs '*stressful*' conditions (Figure 3.7). In this study, the '*watered*' treatment is considered to be the least-stressful water treatment. It was more difficult to designate a particular light level as the 'least-stressful' as the effect of light was likely to vary between species and treatments. I chose 8% of full sunlight as the comparison level as seedlings located at this level in the experiment appeared not to suffer any effects of irradiance stress, it was the mid-level at which most seedlings were located.

To generate drought and waterlogging tolerance indices I calculated the relative proportional difference between the predicted median time of survival in the watered treatment at 8% light availability and median survival time in drought and waterlogging treatments at 8% light availability. To generate the shade tolerance index I calculated the relative proportional difference between predicted median time of survival in the watered treatment at 8% light availability and median survival time in the watered treatment at 1% light availability. Generating tolerance indices based on relative differences in survival times rather than using the actual predicted survival times resulted in indices that were comparable between species.

Testing for evidence of interspecific trade-offs

I tested for evidence of trade-offs in tolerance indices using standardised major axis regression (SMA; (Warton et al. 2012). SMA is used to estimate and test hypotheses about a line of best fit between two variables in which the direction of causality is unclear. This differs from simple linear regression in which one predicts *y* from *x*. With SMA the relationship between the estimated parameters remains constant no matter which ways around the axes are plotted. I tested the relationship between shade and drought tolerance, shade and waterlogging tolerance, and drought and waterlogging tolerance.

3.4 Results

Of the 1532 seedlings that survived through the initial 30-day acclimation period and entered the shade and water trials, 375 individuals died in total (Figure 3.5) and 346 were removed for destructive harvesting (data not published in this thesis).

Assessing shadehouse conditions over the experiment

Temperature did not differ between the two shadehouses over the experimental period when comparing average monthly daytime (between 10:00 and 16:00) temperature (paired t-test, t = 1.39, df = 10, p-value = 0.195). However, average monthly daytime temperatures did differ among months (one-way ANOVA, F = 13.78, df = 10, p = < 0.0001). During the March to June rainy season average monthly daily temperatures ranged between 28.1^{0}C - 28.9^{0}C whereas temperatures during the dry season months September - December increased to between 29.09^{0}C – 30.11^{0}C.

To assess whether conditions inside the shadehouses were similar over the entire experimental period, I compared performance of the same species entered into the experiment at different times. Growth was compared rather than mortality as there was not sufficient data to assess mortality properly. Two cohorts of *Dicorynia guianensis* were compared, the first cohort entered the experiment in January 2017, the second in October 2017. Of the 25 individuals in the second cohort, only 12 survived, 9 of which were in the 'watered' treatment, 2 in the 'waterlogged' treatment, and 1 in the 'drought' treatment. I therefore compared growth only for the eight surviving seedlings in the 'watered' treatment with seedlings from the first cohort surviving for the same length of time in the same conditions (n = 27). I found no difference in average weekly height RGR between the two groups (one-way ANOVA, df = 1, 33, F = 0.13, p = 0.72). I also compared growth rates for three cohorts of *Sextonia rubra*. The first cohort entered the experiment in January 2017, the second in May 2017, and the third cohort entered the experiment in October 2017.

As with the *D. guianensis* seedlings, there were few seedlings in the second and third cohorts to begin with and low numbers of survivors with which to compare growth rates. I compared average weekly height RGR between cohort-1 n = 23, cohort-2 n = 7, and cohort-3 n = 11 seedlings and found no evidence of a difference in growth between the three time periods (one-way ANOVA, df = 2, 38, F = 0.06, p = 0.942). Thus I conclude that conditions over the entire experimental period were sufficiently similar to allow meaningful comparisons between species.

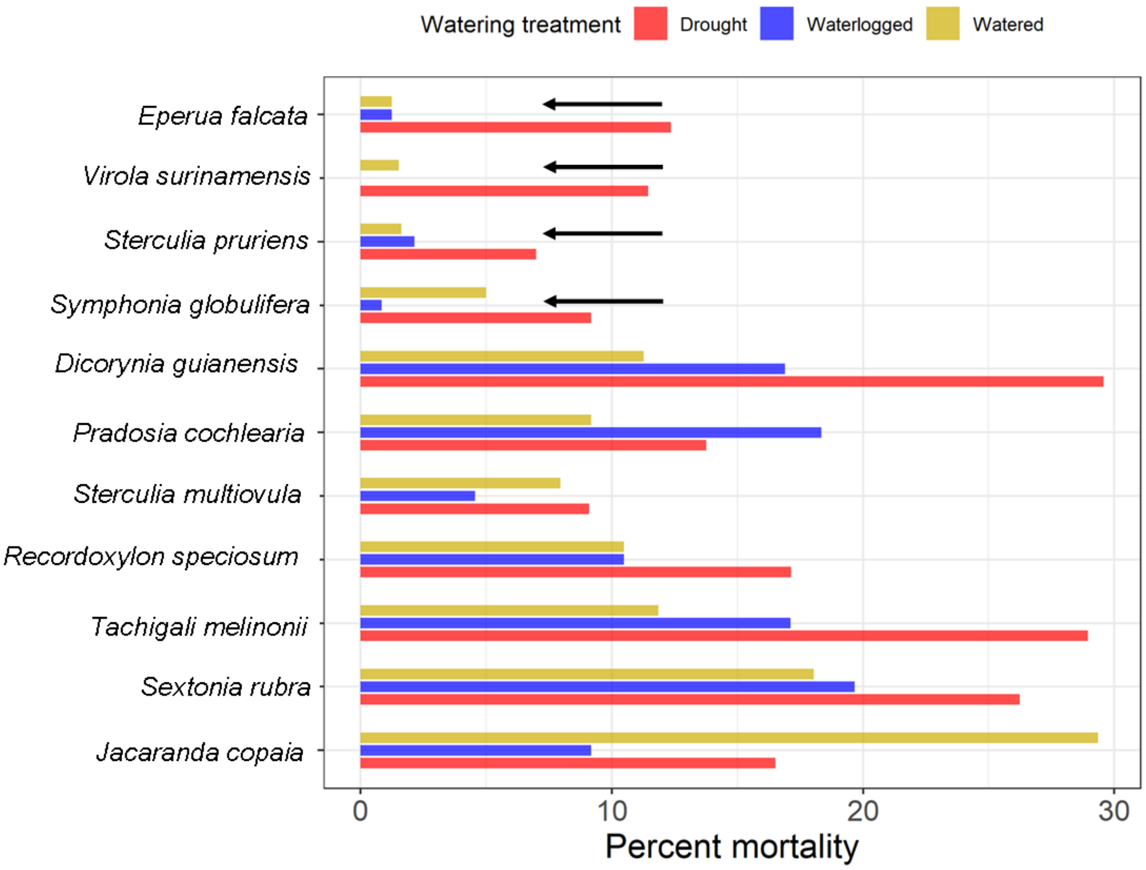

Figure 3.5. Percentage mortality experienced by each species in each of three water treatments, drought, waterlogged, and watered, across a gradient of light availability ranging <1% - 27% of full sunlight. Four species, Sterculia pruriens, Symphonia globulifera, Virola surinamensis, *and* Eperua falcata *experienced very little or no mortality in one or more treatments.Species are arranged in order of percentage mortality in the 'watered' treatment.*

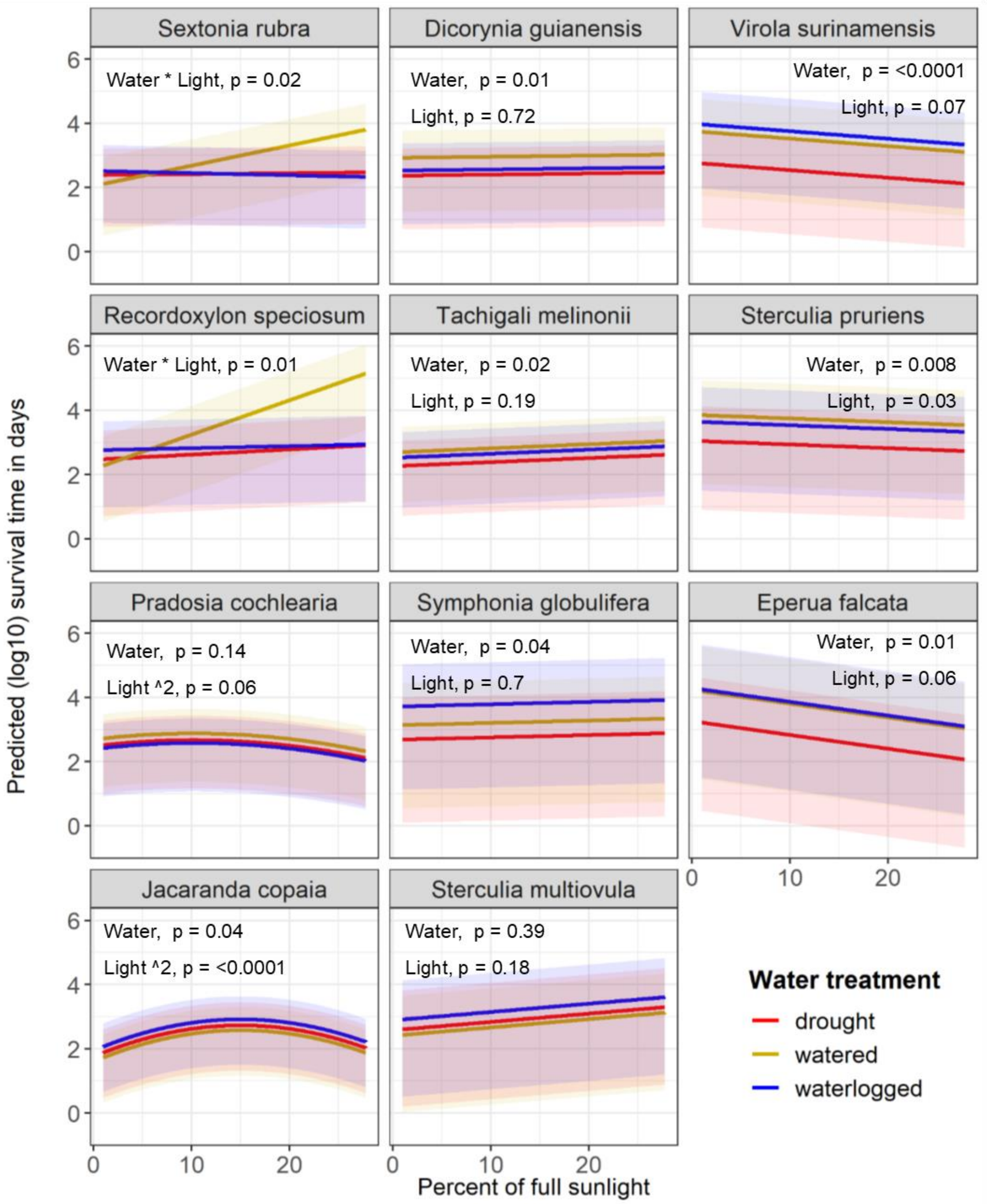

Figure 3.6. Predictions of the effect of light availability and watering treatment on seedling survival time. I predicted the median survival time for each species along a gradient of light availability spanning 1-27% of full sunlight. Bold lines represent median survival time, upper and lower shaded areas represent 95% confidence intervals. Survival time is given in days shown on a log10 scale. Predictions are based on Weibull parametric survival modelling results where the full model for each species included a linear and a quadratic light parameter, and interactions with water treatment. Interactions were retained only if the effect was significant, which was true for only Sextonia rubra *and* Recordoxylon speciosum. *Full model results given in appendices.*

Patterns of survival longevity among water treatments

Seedlings in the drought treatment had the shortest median survival times for all but three species (*P. cochlearia*, *J. copaia*, and *S. multiovula) (red lines in Figure 3.6)*. Overall, the drought treatment induced shortened survival times when compared to the watered treatment for all species (Appendix 1). The reduction survival time in the drought treatment was strongest for *T. melinonii* where seedling survival time was 0.19 times shorter compared to seedlings in the watered treatment (hazard ratio = 0.198 ± 1.737, z = -2.935, p= 0.003). Seedling survival was not significantly related to height at the start of the experiment for any species.

The longest median survival times were predicted for seedlings in the 'watered' treatment for six of eleven species (yellow lines in Figure 3.6). This was surprising given that it meant seedlings survived longer under waterlogging and/or drought conditions for the other five species. Of those species that did not conform to expectations by surviving longest in the 'watered' treatment, three species (*V. surinamensis, S. globulifera, E. falcata*) displayed the longest median survival times in the 'waterlogging' treatment, and shortest survival times under 'drought' conditions. For *S. globulifera* and *V. surinamensis*, this meant that on average seedlings located in waterlogged conditions survived for between 2-3 times longer than in 'watered' conditions.

The two other species that did not survive longest in the 'watered' treatment, *J. copaia* and *S. multiovula*, actually survived longer in the drought treatment than when receiving regular watering (Figure 3.6). For *J. copaia* this surprising result is likely because this species was strongly affected by scale insects and fungal pathogens, which appeared to be less severe for seedlings in the drought treatment (pers. obs.). Seedlings of *S. multiovula* were in the experiment for the shortest amount of time (2 months in the water treatments). If by random chance more weak seedlings were assigned to 'watered' treatment blocks compared to 'drought' treatment blocks, more seedlings would die more quickly regardless of the water treatment. This appears to be what happened with this species as the same number of seedlings died in both the ‘watered’ and ‘drought’ treatments, but those that died in the ‘watered’ treatment died more quickly.

Only two species, *S. rubra* and *R. speciosum*, experienced an interactive effect of water treatment and light availability (Figure 3.6). This meant that for seedlings of these species the effect of watering treatments on survival depended upon the level of light availability. *R. speciosum* in particular experienced an almost exponential increase in survival time at levels above 15% of full sunlight in the ‘watered’ treatment. None of the other nine species’ models returned a statistically significant interaction term for watering treatments and light availability.

Only two species, *P. cochlearia* and *J. copaia*, exhibited a non-linear response to increasing light availability (Figure 3.6). Both species’ display hump shaped responses, where at either end of the light availability gradient survival times are lower compared to survival times in the middle of the range of light values. In *J. copaia* the peak in survival time was observed at 15% of full sunlight. Whereas for *P. cochlearia* the peak survival time was at 10% of full sunlight, and median survival time was lower at the high end of the range of light availability compared to the low end.

The effect of increasing light availability was positive on seedling survival for five species, *R. speciosum*, *D. guianensis*, *T. melinonii*, *S. globulifera*, and *S. multiovula,* and negative for three species, *V. surinamensis*, *S. pruriens*, and *E. falcata,* and responses were mixed depending on water treatment conditions for *S. rubra*. Note that the effect of increasing light availability was not statistically significant in most cases.

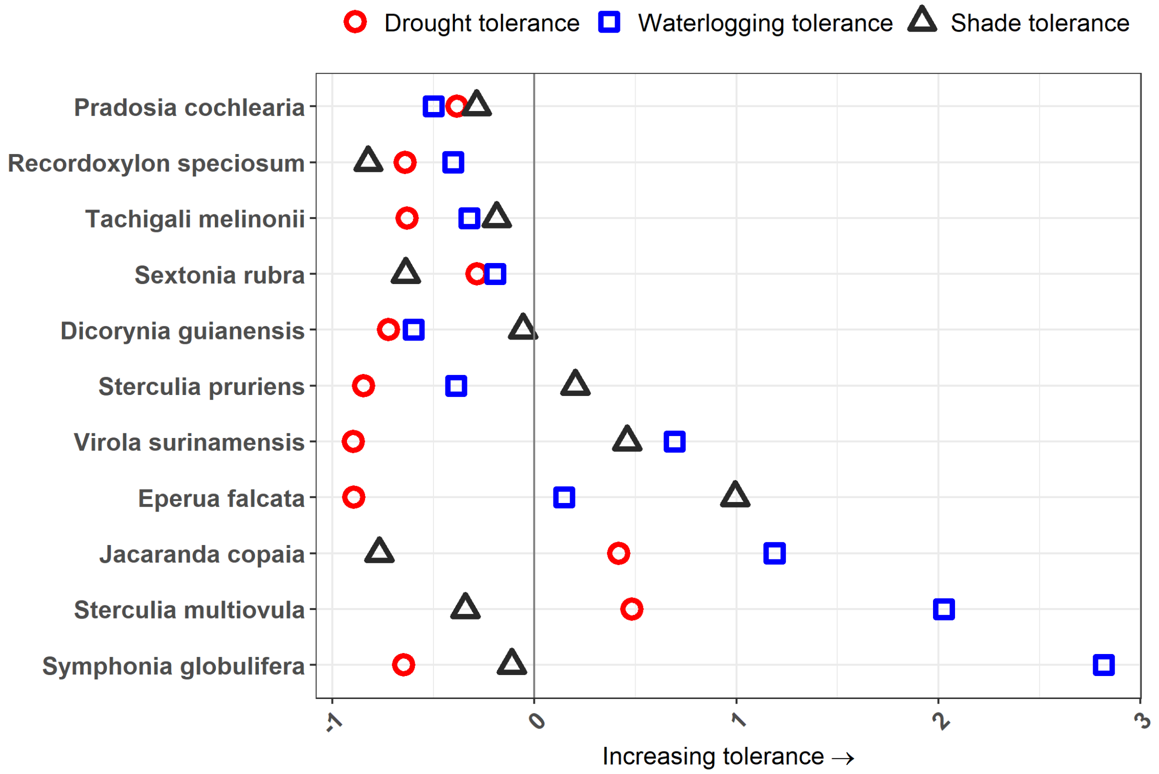

Figure 3.7. Shade, drought, and waterlogging tolerance indices of seedlings of eleven tropical tree species. Indices were calculated by taking the relative proportional difference between median survival time in watered conditions and survival time in shaded, drought, and waterlogged conditions. The reference watered treatment, drought, and waterlogged treatments were based on survival in 8% sunlight, and shade treatment survival is based on 1% sunlight. Survival times are predictions of median survival time in days based on species parametric survival modelling results. The zero line represents the reference survival time in watered / well-lit conditions and tolerance index points are deviations from that reference. A negative index means that the species performed less well in that treatment when compared to the reference treatment. Positive indices mean the species performed better in that treatment than the reference treatment. Species are arranged in order of range between tolerance indices.

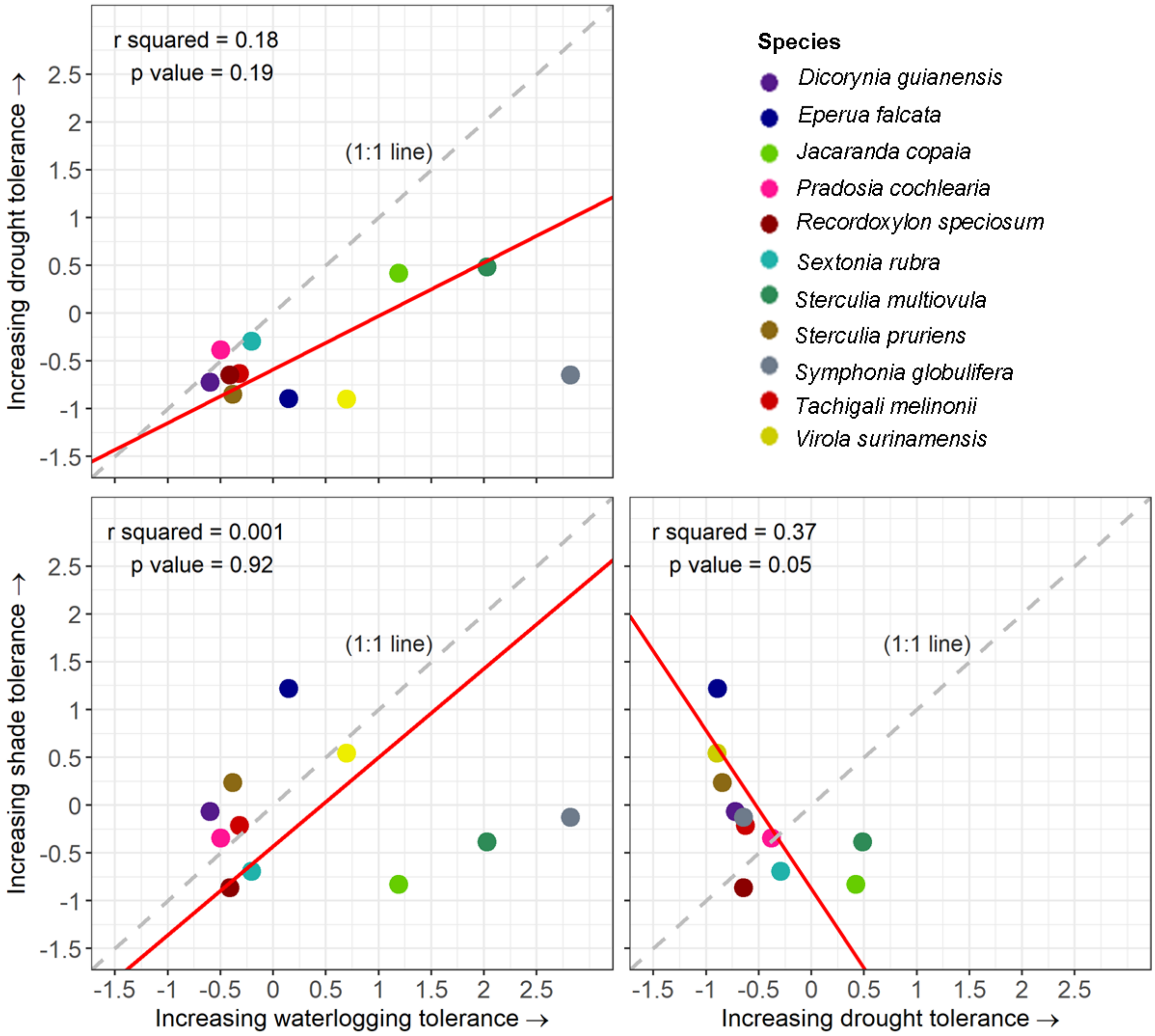

Figure 3.8. Results of standardised major axis (SMA) regression on the relationship between generated tolerance indices. The top panel shows the relationship between waterlogging and drought tolerance, the bottom-left panel shows the relationship between waterlogging and shade tolerance, and the bottom-right panel shows the relationship between drought and shade tolerance. In each case, models fit an SMA line and estimate the strength of the linear relationship between y and x.

Trade-offs between tolerance indices among species

In contrast to the predicted median survival times, which varied by orders of magnitude for some species, the tolerance indices are based on relative differences between survival times and were therefore comparable between species (Figure 3.7). The range of points representing waterlogging tolerance (blue squares in Figure 3.7) was much larger than the range for drought tolerance and shade tolerance. Three species, *S. pruriens*, *V. surinamensis*, and *E. falcata,* had positive shade tolerance indices, which mean that 8% full sunlight (the reference light level) was not the 'least-stressful' light level for these species.

An interspecific trade-off between seedling tolerance to drought and shade was observed ($r^2 = 0.37$, $p = 0.05$). There was some indication of co-tolerance to drought and waterlogging ($r^2 = 0.18$, $p = 0.19$), however tolerance to waterlogging and shade did not significantly covary ($r^2 = 0.001$, $p = 0.92$; Figure 3.8).

3.5 Discussion

I experimentally assessed survival responses to variation in light and water availability in the absence of nutrient limitation and root competition in seedlings from 11 co-occurring tree species in a seasonal lowland tropical forest in French Guiana. I found that contrary to expectation most species' survival response in different water treatments did not depend on variation in light availability i.e. there was no significant interaction between water and light availability. However, positive, negative, and non-linear survival responses to variation in light availability common to drought, waterlogging and water treatments were observed. Evidence was found to suggest a potential negative relationship between species' tolerances of drought and shade, but no evidence of an association between waterlogging tolerance and either shade or drought tolerance (Figure 3.8). Overall, these results point towards a potential turnover of species in drier forests that would lead to more drought tolerant and fewer shade tolerant species under scenarios of increasingly dry weather (Fauset et al. 2012, Kupers et al. 2019), whereas wetter forests may maintain diverse assemblages of drought, waterlogging, and shade tolerant species.

It is important to highlight that results from this shadehouse study where seedlings were grown alone in large pots in the absence of root competition and non-limiting nutrient availability may not be directly comparable to responses of naturally occurring seedlings where strong competition from adult trees for water and nutrients is likely. For this reason, caution must be used when relating experimental inferences to seedling responses in the field. In the field, competition from adult trees would likely draw down water availability much more quickly than occurred in this experiment (Comita and Engelbrecht 2014), particularly under the lower-light levels where lower soil evapotranspiration combined with high humidity likely provided respite from water limitation. Direct measurements of soil water availability and plant water status would have provided important context to improve inferences for seedlings growing in the forest based on these results. However, accurately measuring soil water availability is notoriously difficult, as availability will differ with soil depth, compaction, small scale soil compositional variation, plant size and environment (Poorter et al. 2012b). Further, seedlings growing in field conditions can increase their root foraging area and depth especially during wet seasons which would increase water foraging opportunities during drier seasons (Amissah et al. 2015). In comparison, seedlings in this experiment would have experienced impacted root growth by being removed from the forest and then planted into pots of limited volume.

However, it was only in the shadehouse that I was able to easily obtain all factorial combinations necessary to fully evaluate the roles of water and light availability on plant survival in order to answer the stated research questions. Further, it was important to isolate seedlings from sources of potential interaction such as competition, herbivores, disease, and variation in nutrient availability that could interact with the plant responses under investigation (Kraft et al. 2015, Cadotte and Tucker 2017).

How did survival time vary in water treatments over the light gradient?

Key assumptions of this study were that light and water availability would interact to impact survival responses in seedlings depending on the levels of light and water availability. For example, it was expected that survival responses under drought conditions may display facilitative, trade-off or non-linear responses along the light gradient which would be different under conditions of regular watering (Sack and Grubb 2002, Quero et al. 2006, Holmgren et al. 2012). However, modelling survival time responses demonstrated that for nine of eleven species, positive, negative, or non-linear survival responses in relation to light availability were the same in all watering treatments even though the actual survival time varied among watering treatments. Overall these results suggest a strong role for light availability in determining species survival and dynamics across habitats.

For the only two species that experienced an interactive effect of water and light, increasing light availability increased survival in the regularly watered treatment while survival in both drought and waterlogging treatments remained similar across the light gradient (Figure 3.6). Neither of these species, *R. speciosum* or *S. rubra*, had particularly high tolerance to either drought, waterlogging, or shade (Figure 3.7), which suggests that these species may only become strong competitors when water and light conditions are favourable,

Results from four of eleven species (*V. surinamensis, S. pruriens, E. falcata*, and *P. cochlearia*) demonstrated a weakened effect of low-light compared to high-light on seedling survival in all water treatments. Given that the effect of light availability was the same in all water treatments these results do not support the facilitative hypothesis (Holmgren et al. 1997). The facilitative effect of low light has been demonstrated previously in tropical seedlings in a shadehouse experiment in Ghana when increased survival in drought at low irradiance was linked to slower soil evaporation rates, lower transpiration rates, and smaller seedlings (Amissah et al. 2015). Therefore it was surprising that no interactive effect of drought and light was found for most species in this study. These results instead may point to an ability for these species to become relatively dormant under very low-light conditions which may assist survival under a wide range of water availability conditions.

Three of the four species that demonstrated greater survival in low-light conditions were the three most shade-tolerant and three most drought-intolerant species (Figure 3.7). This result agrees with findings from a meta-analysis of field and greenhouse studies evaluating the effects of drought and light that found shade tolerant and drought intolerant species were more sensitive to drought conditions and more commonly facilitated by low-light over a wide gradient of shade levels (Holmgren et al. 2012). These results suggest that for some species the risk of mortality under drought can be reduced under closed canopies, whereas in more open forests seedlings are likely to be impacted more strongly during drought events.

Higher survival in low-light conditions in the waterlogging treatment may be possible due to reduced transpiration caused by reduced photosynthesis in low-light. This would allow seedlings to reduce their water intake, reducing the build-up of toxic compounds produced during anaerobic respiration and reducing uptake of toxins from the soil (Ferreira *et al*, 2009). Seedlings in low-light may therefore remain relatively dormant during waterlogging, allocating carbohydrate reserves to new shoots or adaptations to shade (Lucas et al. 2013). Dormancy may also explain the long median survival times in the waterlogging treatment in this experiment for five of eleven species (*S. globulifera, S. multiovula, V. surinamensis*, *S. pruriens*, and *E. falcata*, Figure 3.6). Similarly, no negative effect on seedling survival was found as a result of increasing flood duration of between 3-6 months in a common garden experiment in the Amazon floodplains (Lucas et al. 2013). These results suggest that these species may experience enhanced survival compared to other species in the seasonally flooded bottomlands of Paracou where microsites are particularly shaded even if flooding events become more prolonged.

Lower survival in low-light compared to high-light conditions for five of eleven species was found in all water treatments and therefore cannot strictly support the intraspecific trade-off hypothesis (Smith and Huston 1989, Sack 2004, Niinemets and Valladares 2006). However, this result still suggests that for some species shaded forest understories will impact survival especially strongly as shaded seedlings are at greater risk of mortality in both dry and wet soils (Smith and Huston 1989, Sack 2004). The stronger impact of both drought and waterlogging in low-light conditions may be due to ecophysiological constraints on biomass allocation (Sack 2004), or because seedlings are unable to capture enough energy to sustain growth when faced with an additional stress (Parolin et al. 2010).

Seedlings of other species may be constrained to relatively narrow ranges of understory light availability conditions. For example, in this study two species displayed non-linear effects of light availability in all water treatments (*P. cochlearia* and *J. copaia*, Figure 3.6) where the positive effect of irradiance on survival was restricted to between 1-5% and 20% of full sunlight.

Interspecific trade-offs between tolerance indices

A negative relationship between species' tolerances of drought and shade was observed, however no evidence was found for an association between waterlogging and shade (Figure 3.8). The trade-off between drought and shade tolerance was mainly driven by the fact that those species that performed particularly well under low-light conditions performed poorly under drought conditions, whereas those that performed poorly under low-light conditions spanned a wider range of drought tolerance values (Figure 3.8). The lack of a relationship between waterlogging and shade tolerance was driven by the fact that the five most waterlogging tolerant species included the most and least shade tolerant species (Figure 3.8).

A trade-off between drought and shade tolerance would be expected as adaptations to both resource limitations are opposed (Smith and Huston 1989), Greater allocation to above-ground structures to increase light capture convey greater success in light limited conditions whereas allocation to below-ground structures to increase water uptake assist survival during drought. This drought-shade trade-off has recently been demonstrated in naturally regenerating tropical seedlings in Panama (Kupers et al. 2019) and may point towards a potential turnover of species in drier forests that may lead to more drought tolerant and fewer shade tolerant species under increasingly dry weather (Fauset et al. 2012, Kupers et al. 2019). However, the trade-off relationship was not absolute and species responses deviated from the trade-off relationship, which was also apparent in this study with only 11 species. Further studies of the drought-shade trade-off in tropical seedlings should incorporate functional trait analyses to find out which traits convey concordance with and deviations from the trade-off relationship.

No statistically significant relationship was found to support a relationship between tolerance of drought and waterlogging. However, the results suggest a potential co-tolerant relationship between these two variables for at least some species. The slight positive trend was driven mainly by the ability of *J. copaia* and *S. multiovula* to tolerate both drought and waterlogging (Figure 3.8). Co-tolerance of both drought and waterlogging is thought to be uncommon, but can be achieved as the functional adaptations required to survive in both can be complimentary (Parolin et al. 2010, Grubb 2016). If this were a common phenomenon among tropical seedlings, co-tolerant species may be favoured over more specialist species in rainforests predicted to increase in both droughts and flooding.

Most of the species included in this experiment have been classified with respect to habitat associations at the adult stage to either dry hilltops or wet bottomland habitats in Paracou (Table 2.3). Three species, *D. guianensis*, *P. cochlearia*, and *S. rubra* were associated with the drier hilltop habitat, whereas six species *E. falcata*, *J. copaia*, *R. speciosum*, *S. pruriens*, *S. globulifera*, and *V. surinamensis* were associated with wetter bottomland habitat, as well, *T. melinonii* was found to have no association to either habitat and *S. multiovula* was unknown.

The uneven distribution of species across adult habitat association classes (Table 2.3) may have contributed to higher waterlogging tolerance values compared to drought and shade tolerance values (Figure 3.7). This may have ultimately affected the results of the correlations between tolerance values. However, it is important to note that habitat associations at the adult stages may not reflect associations at the seedling stage. Further, associations to wetter or drier habitats are likely to be confounded with many factors including nutrient availability, pest pressure, and competition and therefore may not reflect tolerance of water availability. Here, *R. speciosum* and *S. pruriens* had relatively low waterlogging tolerance values, which may suggest that association to wetter habitat occurs at later life stages or, that it may not be something other than the waterlogged status of the bottomland habitat that determined the association.

The species in this study have also been classified with respect to adult shade tolerance (Table 2.3). Five species were classified as medium tolerant, four species as heliophilic, with only one species classified as tolerant and a further species was unknown. A lack of 'tolerant' may have biased the results with respect to shade tolerance. However, the shade tolerance results were mixed with respect to the adult classifications. For example, the one tolerant species, *P. cochlearia* was found to have relatively low shade tolerance, while *S. pruriens*, one of the species classified as heliophilc had one of the highest shade tolerances (Figure 3.7).

3.6 Conclusions

Given that climate projections predict increasing frequency and severity of both droughts and flooding for tropical regions, the relationships between seedling survival in water and light conditions explored in this study may have profound implications for species compositional changes in the tropical forest of Paracou, French Guiana. The observed trade-off between drought and shade tolerance point towards a potential turnover of species in drier forests that may lead to more drought tolerant and fewer shade tolerant species under increasingly dry weather (Fauset et al. 2012, Kupers et al. 2019), whereas wetter forests may maintain diverse assemblages of drought, waterlogging, and shade tolerant species. In particular two species, *J. copaia* and *S. multiovula* may be increasingly selected for if climate predictions of increased drought occurrence and solar radiation occur in this forest as is predicted to occur more widely in tropical forest regions. Further, as these two species also had high tolerance of waterlogging conditions they may be expected to become increasingly dominant throughout Paracou's contrasting drier hilltop and floodplain bottomland topographic habitats.

CHAPTER 4

4. The relative importance of drought, waterlogging, and light availability in driving sapling spatial patterns across habitats in French Guiana rainforests

4.1 Abstract

In tropical forests, variation in water availability between topographic habitats or soil-types is linked to local turnover in species composition. I evaluated the roles of water and light availability in governing sapling survival, and how variation in survival contributes to species turnover between topographic habitats that vary in water availability in the tropical rainforest of French Guiana. I used data on the survival of 5374 individual saplings of 25 species and frequency of drought and waterlogging over a period of 24 years, and detailed data on understory light availability. Results suggest that drought was the relatively more important factor determining differential species survival, as well as a likely important role of long-term soil instability associated with topographical water availability. Differential survival among wet habitat associated species may filter these species from drier hilltop habitats, whereas drier habitat associated species survive better than wet associated species in the driest habitats. Differences in survival related to drought and waterlogging therefore likely contribute to the observed species turnover between habitats. Further work would benefit from evaluating to what extent confounding variables such as soil nutrient status and pest pressure affect survival along the water and light availability gradients.

4.2 Introduction

Tree species distributions vary along environmental gradients where individual demographic performance scales-up to control distributional patterns (Silvertown 2004). This sorting of species along environmental gradients may make it possible for greater numbers of species to coexist in heterogeneous habitats, and may therefore be an important component in the maintenance of biodiversity (Chesson 2000).

In tropical forests, variation in water availability between topographic habitats or soil-types is linked to local turnover in species composition (Wright 2002). Lower elevation habitats are often wetter than higher elevation habitats because they are closer to the water table and receive lateral flow from uphill sites (Balvanera et al. 2011). Seasonality in rainfall can induce further drying in upland habitats during dry seasons, and waterlogging in bottomland habitats during wet seasons. Drought and waterlogging are at opposite ends of the water availability spectrum and characterise two distinctly different potentially stressful environments for plants (Parolin et al. 2010). Water deficiencies can induce hydraulic failure and carbon starvation (McDowell et al. 2008), while inundation may cause oxygen depletion leading to root death, reduced nutrient intake, and increased vulnerability due to unstable soils (Ferry et al. 2010). At local scales, individuals of the same species often have to cope with different levels of water scarcity or inundation at regular seasonal intervals, during inter-seasonal cycles, and as a result of changing weather patterns (Menezes-Silva et al. 2019).

Despite the importance of local habitat scale drought (Comita and Engelbrecht 2009, Paine et al. 2009) and waterlogging (Baraloto et al. 2007, Lucas et al. 2013) in structuring tropical tree communities, we currently do not have a good understanding of the relative importance of each, or if the relative importance changes when we consider the interacting effect of light (Sánchez-Gómez et al. 2006, Gómez-Aparicio et al. 2008, Brenes-Arguedas et al. 2011). Lower species diversity and monodominance in seasonally inundated tropical forest swamps has been linked with limited species-specific tolerance of flooding (Lopez and Kursar 2007). Although species generally perform worse during periods of low water availability, there is nevertheless large variation between species in tolerance of severity and length of adverse conditions (Condit et al. 2013). This variation may mean drought intolerant species are unable to survive and grow in drier habitats thereby contributing to species distributions (Engelbrecht et al. 2007). As climate change in the tropics is predicted to alter the frequency and intensity of drought and flooding (Cochrane and Barber 2009), and in turn their co-occurrence status with shade (Wright and Calderon 2005), determining the relative importance of each in driving distributions is of pressing concern.

The relationship between water availability and shade in wet and dry forests is complex. For example, drier forests can be associated with greater light availability as a consequence of leaf abscission to conserve water during dry seasons (Condit et al. 2000), and increased solar radiation during dry seasons due to reduced cloud cover (Brenes-Arguedas et al. 2011). Whereas wetter forests can be associated with greater leaf production and therefore less light (Niinemets and Valladares 2006). Interactions between water, light, and temperature can increase evapotranspiration in drier forests leading to even drier conditions, while in wetter forests interactions resulting in greater leaf production may lead to even wetter conditions (Niinemets and Valladares 2006). Interactions can also occur with tree demography. Higher tree mortality rates on waterlogged soils can induce a light availability gradient (Ferry et al. 2010). At the same time, logging, which increases light availability but also reduces competition for both light and water, can reduce mortality rates of adult trees (Fargeon et al. 2016).

Many tropical trees exhibit habitat associations, identified by differences in abundance among habitats (Harms et al. 2001, Gunatilleke et al. 2006, Fortunel et al. 2016). However, often little is known about the mechanisms explaining those associations (Fortunel et al. 2019), and how individual performance and dynamics vary across habitats (Yamada et al. 2007). Strong associations to topographic habitats that vary in water availability have been found for tree species at different life stages in Paracou, French Guiana (Baraloto et al, 2007; Vincent et al, 2011; Allie et al, 2015). At this site, three main topographic habitat classes have been delineated. The bottomlands are characterised by seasonal flooding, a water table that never drops below 1m during the dry season, and high soil fertility, slopes have medium to steep gradients with medium intensity waterlogging, and hilltops are flat to gently sloping with well-drained soil which can dry out during annual dry seasons (Ferry et al. 2010).

From observation alone, however, the relative importance of waterlogging and water limitation in determining the habitat association of each species cannot be unequivocally determined (Paine et al. 2018). For example, the observed differences in distributions may be because bottomland associated species are intolerant of the drier conditions in the hilltops, or because hilltop associated species are intolerant of the wetter conditions of the bottomlands. Moreover, the same species distribution patterns can occur as a result of both biotic and abiotic factors (Cadotte and Tucker 2017).

Studies based on compositional data alone are unable to distinguish whether species absence in a particular habitat is due to the environmental conditions or due to biotic factors such as dispersal limitation or competition (Kraft et al. 2015). However, observational studies that correlate community structure components such as mortality or abundance with measures of environmental variability remain valuable tools to infer the importance of the environment in species persistence (Cadotte and Tucker 2017). In this chapter, I bring to bear lots of detailed information on the spatial and temporal effects of waterlogging and drought as well as light availability, to help explain species habitat associations.

This study attempted to measure the relative importance of indices of drought, waterlogging, and shade in governing the survival of saplings with contrasting habitat associations. I focussed on saplings as it is the early life stages where most ecological sorting takes place which therefore determines future forest composition (Green et al. 2014). I analysed performance across a landscape of locally contrasting topography, which varies in water availability, and linked with spatial and temporal measures of drought and waterlogging frequency, and spatially variable light availability. I answered two broad questions:

1) What is the relative importance of drought, waterlogging, and shade in driving sapling survival?

2) To what extent does sapling survival predicted by drought, waterlogging, and shade corroborate habitat associations?

I predicted that species will have a higher probability of survival in the topographic habitat with which they are most strongly associated (Comita and Engelbrecht 2009). Further, I predicted that if soil water availability were an important driver of species survival, drought would be the most important predictor governing survival in drier habitats for species more closely associated with bottomland habitat, and that waterlogging would be the most important predictor governing survival in the wet bottomlands for those species more closely associated with drier hilltop habitats. Regarding understorey light-availability, I predicted that lower light levels would decrease survival for all species. Moreover, I predicted that drought and increasing light would interact to decrease survival, and that the effect would be stronger for bottomland-associated species located in the hilltops.

4.3 Methods

Study site

A general description of the site and environmental conditions can be found in Chapter 2. The study reported here was conducted in the Paracou experimental forest, a lowland tropical rainforest near Sinnamary, French Guiana (5°18'N, 52°55'W: 0 – 45 m elevation) (Figure 4.1). The wet season extends from March to June and the dry season from August to November, with annual precipitation of around 3040 mm (Wagner *et al*, 2011). Mean air temperature and daily minimum relative humidity range from 25.7°C and 70% in the wet season to 26.7°C and 58% in the dry season (Epron et al. 2006).

The patchwork of hills that characterise Paracou are approximately 100-300m diameter with slopes between 25%-45% and separated by narrow streams (Vincent *et al.*, 2011). This hilly landscape has been categorised with respect to topographical position of hilltops, slopes, and bottomlands (Ferry et al. 2010). These broad categories refer to a gradient of soil-water conditions, hilltops are generally drier than slopes, while slopes are not as wet as the bottomlands (Table 4.2) (Ferry et al. 2010), but also broadly describe variation in slope, angle, and soil-type.

Study species

The study species include common, woody species that were easy to identify at the sapling stage (Table 4.1). Each of the twenty-five species co-occurs locally as adults across the Paracou site. The species span a range of life-history strategies, from light-loving pioneer species to strongly shade-tolerant species (Favrichon 1994), and exhibit contrasting distributions in wet vs dry habitat in Paracou.

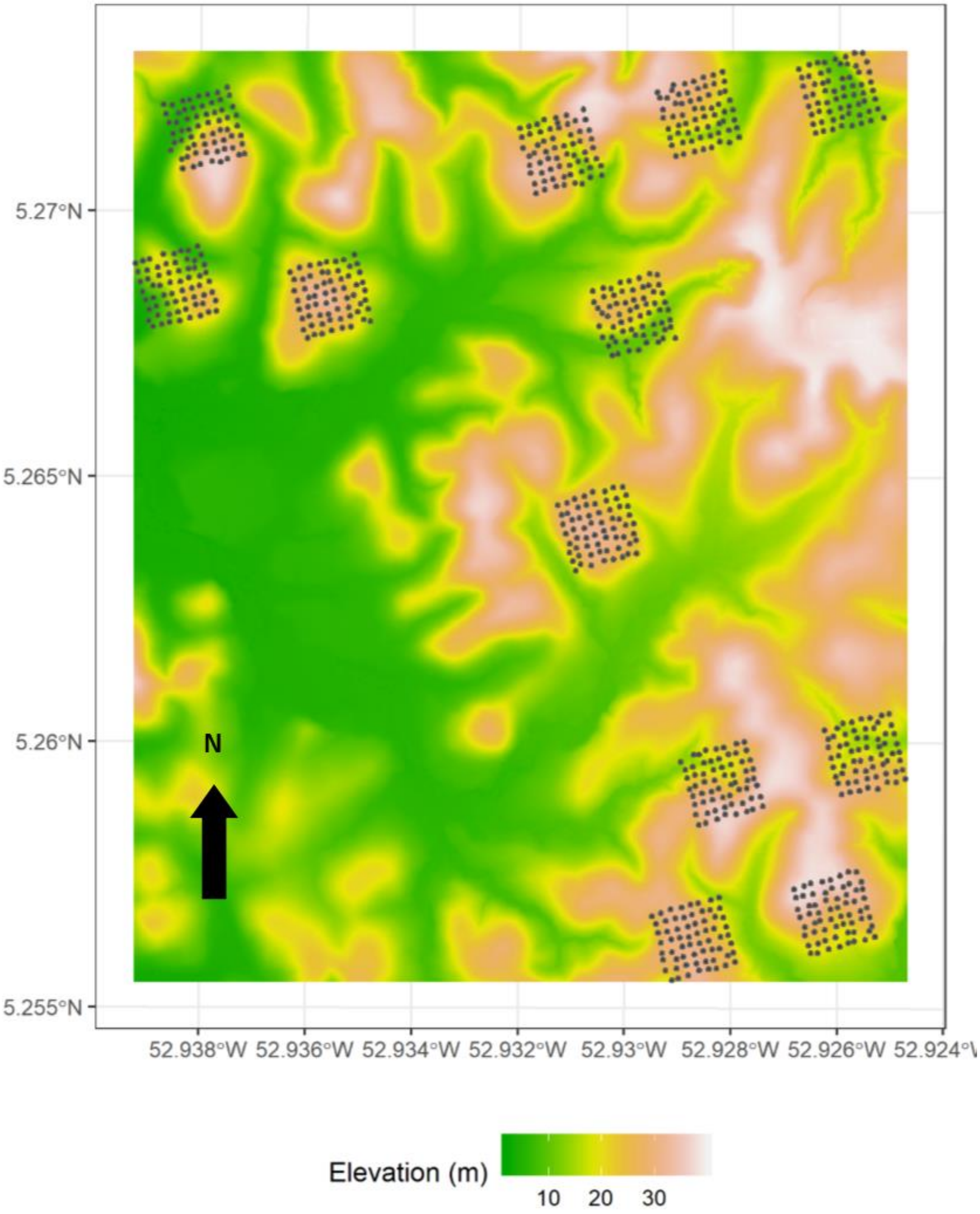

Figure 0.1. Permanent forest regeneration plots at Paracou Research Station, French Guiana, South America. Within each of 12 square plots there are sixty-four 4m radius (50.2 m2) small circular plots laid out in a grid, indicated by black dots on the map. The 768 small circular plots are used to monitor forest regeneration by monitoring abundance, growth, and survival of 25 common tree species at the sapling stage. Shown with elevation map created from a digital terrain model derived from LiDAR data acquired across the Paracou site in 2013.

Table 0.1. Table of information on the 25 five species used in this study. Included are life history strategies in terms of shade tolerance (Favrichon 1994)*, (where ST = strongly shade tolerant; T = shade tolerant; MT = mid shade tolerant; and H = heliophilous), and the total number of stems per hectare for each species in each of the three topographical designations of hilltops, slopes, and bottomlands, with the highest density highlighted for each species.*

Species name	**Family**	**Life History Strategy**	**Density of stems per hectare**		
			Hilltops	**Slopes**	**Bottomlands**
Andira coriacea (ac)	Fabaceae	MT	***24.2***	10.2	7.9
Bocoa prouacensis (bp)	Fabaceae	ST	81.3	***89.2***	36.4
Carapa surinamensis (cs)	Meliaceae	H	13.7	22.3	***31.8***
Dicorynia guianensis (dg)	Fabaceae	MT	***38.7***	33.2	25
Eperua falcata (ef)	Fabaceae	MT	55.6	104.9	***145.5***
Eperua grandiflora (eg)	Fabaceae	MT	***124***	60.3	42.1
Goupia glabra (gg)	Goupiaceae	H	***166.7***	70.5	73.9
Iryanthera hostmannii (ih)	Myristicaceae	ST	45.1	101.3	***179.6***
Iryanthera sagotiana (is)	Myristicaceae	ST	176.4	***185.7***	78.4
Jacaranda copaia (jc)	Bignoniaceae	H	***73.3***	53.6	26.1
Moronobea coccinea (mc)	Clusiaceae	MT	***59.6***	41	18.2
Platonia insignis (pi)	Clusiaceae	MT	***4***	2.4	0
Pradosia cochlearia (pc)	Sapotaceae	T	***95***	70.5	51.2
Qualea rosea (qr)	Vochysiaceae	MT	***226.3***	119.4	71.6
Recordoxylon speciosum (rs)	Fabaceae	MT	27.4	27.1	***31.8***
Schefflera decaphylla (sd)	Araliaceae	H	***54***	45.2	15.9
Sextonia rubra (sr)	Lauraceae	MT	20.1	***20.5***	10.2
Sterculia pruriens (sp)	Malvaceae	H	87.4	73.3	***106.9***
Sterculia multiovula (sm)	Malvaceae	H	1.6	4.2	***9.1***
Symphonia globulifera (sg)	Clusiaceae	MT	3.2	9	***61.4***
Symphonia sp. 1 (s1)	Clusiaceae	MT	165.1	***185.7***	127.3
Tachigali melinonii (tm)	Fabaceae	H	33	63.9	***108***
Virola michelii (vm)	Myristicaceae	H	***191***	174.8	60.2
Virola surinamensis (vs)	Myristicaceae	Unknown	11.3	13.3	***14.8***
Vouacapoua americana (va)	Fabaceae	T	***34.6***	30.7	15.9

Habitat associations

In this study, I have categorised each species as associated with hilltops, slopes, or bottomlands based on the density of stems per hectare in each habitat (abundance data from the 2016 Paracou regeneration survey) (Table 4.1). These simple categorisations broadly agree with previous studies of habitat associations for these species and these habitats in Paracou (Baraloto et al. 2007, Allie et al. 2015). I use these categorisations as a basis to assess whether species survival over time related to soil water and light availability fits what would be expected of species that occur more frequently in wet or dry habitats.

Regeneration inventories

Across Paracou, a network of permanent forest plots have been established and monitored for more than 20 years (Figure 4.1). Within each of twelve 6.25ha square plots, sixty-four small circular subplots of 50.2m^2 (4m diameter) are located on a systematic grid (Figure 4.1). The total of 768 regeneration plots cover an area of 3.84ha spread out over an area of approximately 400ha of typical hilly terrain with superficial drainage representative of the Kourou-Sinnamary region (Gourlet-Fleury et al. 2004) (Figure 4.1).

Since 1992, eight systematic inventories of the natural regeneration dynamics of the twenty-five study species have been carried out. Inside each regeneration plot, each sapling of the 25 focal species was identified, given an individual identification tag, recorded as a recruit that census or as surviving /died since previous census, and precise location mapped by recording azimuth bearing and distance from the centre of each plot to each sapling. Saplings were defined as stems taller than 1.3m with diameter at breast height between 1-10cm. Inventories were carried out in 1992, 1993, 1995, 2002, 2005, 2008, 2013, and 2016. For this study, I use data from 5374 individual saplings, observed at least twice, for a total of 26,140 observations (Montpied 1992; Jounieaux 2016).

Table 0.2. Paracou regeneration plots, topographic designation characteristics summary. Adapted from Ferry et al. 2010.

Topographic designation	Slope angle	Soil water availability	Percentage of total regeneration plots	Total area (ha)
Hilltops	Flat to gentle	Waterlogging very rare	32.2%	1.27
Slopes	Medium to steep	Low-intensity waterlogging	43%	1.68
Floodplains	Flat	High-intensity waterlogging	22.8%	0.9

Table 0.3. Paracou soil types and characteristics.

Soil Type	Soil characteristics	% of regeneration plots of different topographic designation	
Alt	Red alloterite. Water circulation is slow and always vertical. Found at the top of low slopes	Hilltops	13%
		Slopes	3%
		Bottomlands	0%
DhS	Downhill hydromorphic system. Found at the base of slopes near the permanent water table	Hilltops	3.3%
		Slopes	20.2%
		Bottomlands	5.2%
HS	Lowland hydromorphic soils. Corresponds closely to floodplains	Hilltops	0%
		Slopes	1.3%
		Bottomlands	17.6%
SLD	Superficial lateral drainage	Hilltops	11.3%
		Slopes	12.4%
		Bottomlands	0.3%
UhS	Uphill hydromorphic system. Top layer promotes accumulation of water, inducing hydromorphic conditions	Hilltops	5%
		Slopes	6.8%
		Bottomlands	0.4%

Calculation of drought and waterlogging indices

In Paracou, soils have been mapped using a classification system developed in French Guiana (Sabatier et al. 1997). Soils were defined according to the evolutionary stages in a ferralitic soil, which is related to the soil's hydromorphic functioning and chemical properties (Sabatier *et al*, 1997; Wagner *et al*, 2011). The sapling plots cover five soil categories, referred to as Alt (red alloterite at a depth of less than 1.2m), SLD (superficial lateral drainage), UhS (uphill system), DhS (downhill system), and HS (hydromorphic soil) (Sabatier et al. 1997). Soil types are associated with topographic categories, but do not completely overlap any particular one (Table 4.3).

For this study I developed indices of drought and waterlogging for the regeneration plots using a water balance model which was developed based on the soil types of Paracou (Wagner et al, 2011). The water balance model uses input variables of daily rainfall, potential evapotranspiration, and solar radiation, and produces estimates of relative extractable water (REW) per soil type, per day (see Wagner et al. 2011 for full model details). REW refers to the amount of water present in the soil that is available to plants and is a common variable used by ecophysiologists to describe drought intensity (Granier et al. 1999). REW is calculated as the actual extractable soil water divided by the difference in soil water content at maximum and minimum water content (Bréda et al. 2006). It is expressed as a dimensionless number between 0-1, where 1 is soil water at field capacity (the maximum amount of water a soil can hold against gravity) and 0 is soil water content at permanent wilting point (the point beyond which plants can no longer extract water). A REW of 0.4 is considered to be the threshold at which water becomes limiting for transpiration in tropical and temperate trees (Granier et al. 1999; Wagner et al. 2011). The model was parameterised and calibrated to the soil types of the Paracou forest study site, and was demonstrated to accurately predict extractable water for each soil type (Wagner et al. 2012). The model included the soil types Alt, SLD, Uhs, and DhS, but not HS,

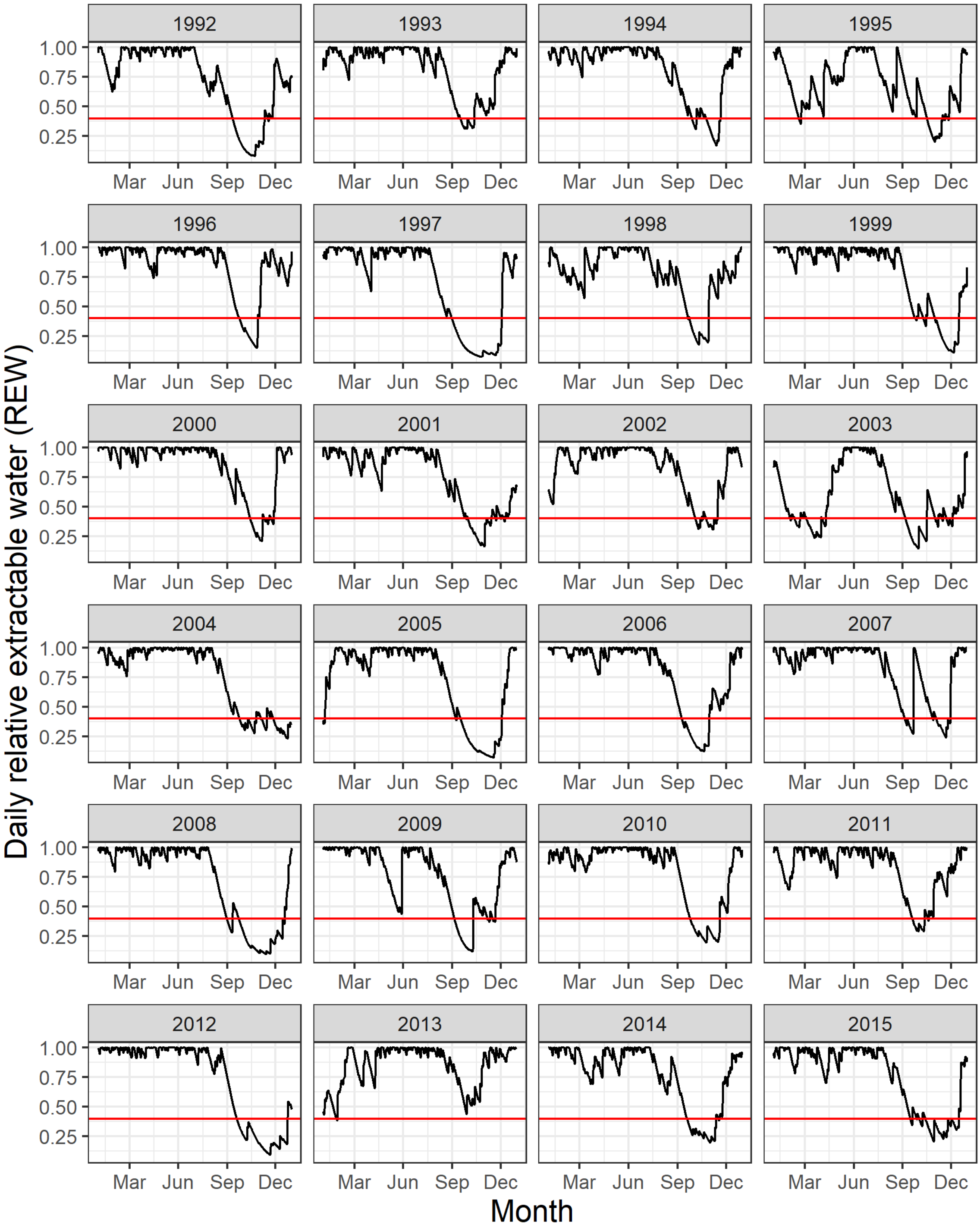

Figure 0.2. Daily relative extractable water (REW) averaged for all soil types at the Paracou experimental forest (data courtesy of Fabian Wagner (Wagner et al. *2011). The red horizontal line is shown at REW = 0.4, the level at which water becomes limiting for plants.*

To calculate the spatio-temporal drought and waterlogging indices, I computed the proportion of days REW in each soil-type dropped to or below 0.4 (hydrologic stress), or reached 1 and had excess water availability (saturation) during each census period (Figure 4.2). The sapling regeneration plots cover five soil categories, four of which were directly included in the water balance model of Wagner et al. (2011). The fifth soil type not included in the model was the hydromorphic soil type (HS soil type) associated with the wet bottomlands at Paracou. This soil type has been classified as having a water table that never drops below 1m below ground during the dry season (Baraloto et al. 2007). To include this soil type in the sapling survival models, I generated the drought index for this soil type by taking the minimum drought index value of the other soil types, and subtracting the median absolute deviation for each census. To generate the waterlogging index for this soil type, I took the maximum value of waterlogging index of all soil types and added the median absolute deviation for each census. This provided drought and waterlogging indices that classified the hydromorphic soil associated with the bottomlands as the least dry and most wet, respectively, during each census. The two indices represent two separate axes of water-stress, which do not covary ($r = -0.08$, $n = 40$, $p = 0.6$) (Figure 4.3).

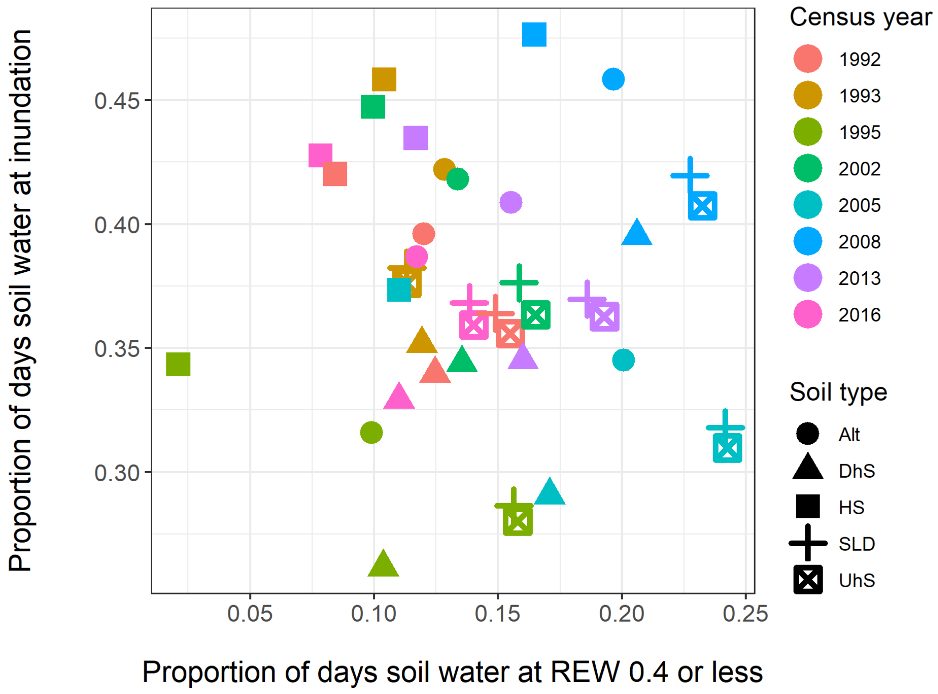

Figure 0.3. Relationship between waterlogging and drought indices based on the relative extractable water (REW) in each soil type in each census period. Where the x axis is the proportion of days soil-water availability was at or below the hydrologically stressful value of REW = 0.4, and the y axis is the proportion of days at saturation (REW = 1) during each census interval. See Methods text for further details.

Light availability

To assess the relationship between sapling survival and light, I developed a light availability index based on LiDAR generated light transmittance in three-dimensional space for each of the Paracou regeneration plots. Airborne LiDAR is able to generate 3D maps of canopy and understory optical density by analysing emitted and returned laser pulses. Airborne laser scanning works via an on-board laser which emits short infrared pulses towards the ground. As each emitted laser pulse hits successive objects along its downward path, backscattered energy is recorded by an on-board sensor, and the timing of the round-trip of the laser pulse allows calculation of the distance between the laser scanner and the object that generated the backscattered echo (Wagner et al. 2006).

The light index was generated from data that were available in the form of post-processed LiDAR returns data from a campaign over the Paracou forest site in 2013 (data provided courtesy of Gregoire Vincent of l'UMR AMAP, 2018). The LiDAR data was acquired by the private company Altoa, flying at 550m above ground level, operating a Riegl LMS-Q560 (wavelength 1550nm) with scanning angle between +/- 20^0, average pulse density of 15 pulses m^{-2}, and average footprint diameter at ground level of 25cm (Vincent et al. 2017). The post-processed LiDAR data consisted of files of local transmittance in $1m^3$ 3D grid cells (voxels) for each of the twelve square plots within which the regeneration plots are located (Figure 4.1). Local transmittance for each voxel was estimated as the ratio between inbound energy and outbound energy for every LiDAR beam crossing the voxel (estimation routines and calculation of local voxel transmittance are detailed in Vincent et al. (2017)). Due to difficulties in sampling below the canopy, many emitted pulses 'died out' before reaching the ground, resulting in one third of all undercanopy voxels being left unsampled (Vincent et al. 2017). Improved estimates of transmittance values was achieved by assigning neighbourhood values to unsampled and poorly sampled voxels (Vincent et al. 2017).

To generate the light index, I first calculated the coordinates of each of the 768 regeneration plots, then, using a 50cm buffer around each plot, I selected all voxel cubes located between 1m – 5m above the ground. I chose to extract light transmission at this height as a representative level that would be most relevant for most saplings regardless of height. For example, if there was high light transmission at 1m above the ground, there was very likely high light transmission for the whole of the vertical area above the plot and therefore available for saplings regardless of height. However, the reverse is less likely to be true. If there was high light transmission at 15m above the ground, it does not mean that there was relatively higher light transmission at 1m above the ground than a plot with lower light transmission at 15m. This compromise in representativeness in light availability for all saplings had to made because models with individual level light transmission (voxels extracted at crown height for each sapling) did not converge.

The voxel coordinates, voxel data, and airborne platform trajectory data were input into a software program, AMAPvox, which was designed for analysing LiDAR pulse interactions with vegetation (freely available from: https://amapdev.cirad.fr/projects/ voxelidar/wiki/, detailed in Vincent et al. 2017). The AMAPvox software generates a light transmittance map by calculating the transmitted light through each voxel space, taking into account solar position and clearness index (a measure of clearness of the atmosphere) for particular periods of time (Tymen et al. 2017). For this study, I integrated solar position over a year and used a clearness index of 0.5 (Vincent. G. pers. comm. 2018). The resulting transmittance values range from 0 to 1 and represent the proportion of total transmitted energy. I took the mean value of all voxels between 1-5m above ground to represent the understorey light-transmission value for that particular plot. The mean transmittance value for 274 plots was zero. Zero light penetration is unlikely in the forest and more likely to be the result of sampling difficulties in dense forest. To adjust for this, I added a very small amount of light transmission (equal to the lowest level) to these plots to adjust for the difficulty in achieving LiDAR returns in the dense canopy. The resulting mean light transmission index values ranged between 0.00000009 – 0.05, with a mean of 0.03 (Figures 8.1. to 8.12 in the Appendices show average light transmission index values between 0-30m above ground in 1m steps, for all 768 regeneration plots).

Statistical analyses

Species-specific binomial regressions were used to estimate parameters that describe the relationships between sapling survival and indices of drought, waterlogging, and light availability. Data were used from the 5,374 individual saplings observed in at least two of eight inventories between 1992 and 2016, for a total of 26,140 individual observations.

Separate models were built for each of the twenty-five species, which tested the hypotheses that sapling survival is related to drought frequency, waterlogging frequency, understory light availability, and topographic location. In each model I included as fixed factors the location of each sapling in one of the three categorical levels of topography, and the continuous measures of drought, waterlogging, and light indices. I included interaction terms involving light index to test the hypotheses that the effects of drought, waterlogging, or topography on sapling survival depend on light availability. Each plot is included in the model multiple times due to multiple censuses, therefore I have included plot as a random variable in models to account for the non-independence. All numerical predictors were scaled and centred prior to analyses by subtracting the mean and dividing by the standard deviation to allow direct comparison of the relative importance of each predictor on sapling performance (Schielzeth 2010). The survival response was aggregated at the plot level, using a two vector response of *n lived*, *n died* per plot, per census, as modelling at the individual level produced models that did not converge (Crawley 2007).

For each species, I followed a model simplification procedure which sequentially removed the least significant second-order terms and re-ran models until all remaining interaction terms were significant, as adjudicated by likelihood ratio tests (Crawley 2007). This procedure minimises the risk of overfitting while providing good contrasts of main effects across species. Model assumptions were verified by plotting residuals vs fitted values for each covariate, and spatial independence was verified by mapping residuals against the physical location of each plot (F. Dormann et al. 2007). To visualise model results, I calculated predictions of survival probability for all significant predictors across the observed range. All data analyses and graphics were produced in the software R (R Core Team, 2019).

Binomial regression results were successful for 23 out of 25 species. Models did not converge for two rare species, *Andira coriacea* and *Platonia insignis* (Table 4.1), and are therefore not considered further.

4.4 Results

Effect of location on sapling survival

The effect of sapling location was a significant predictor of sapling survival in the field for five species (Figure 4.4). For each of these species survival was highest in the dry hilltop habitat and lowest in the wet bottomlands habitat, although the differences in survival probability between habitats were small. The largest difference was observed for *T. melinonii*, which had a 10% difference in survival probability between saplings located in the hilltops and those located in the bottomlands.

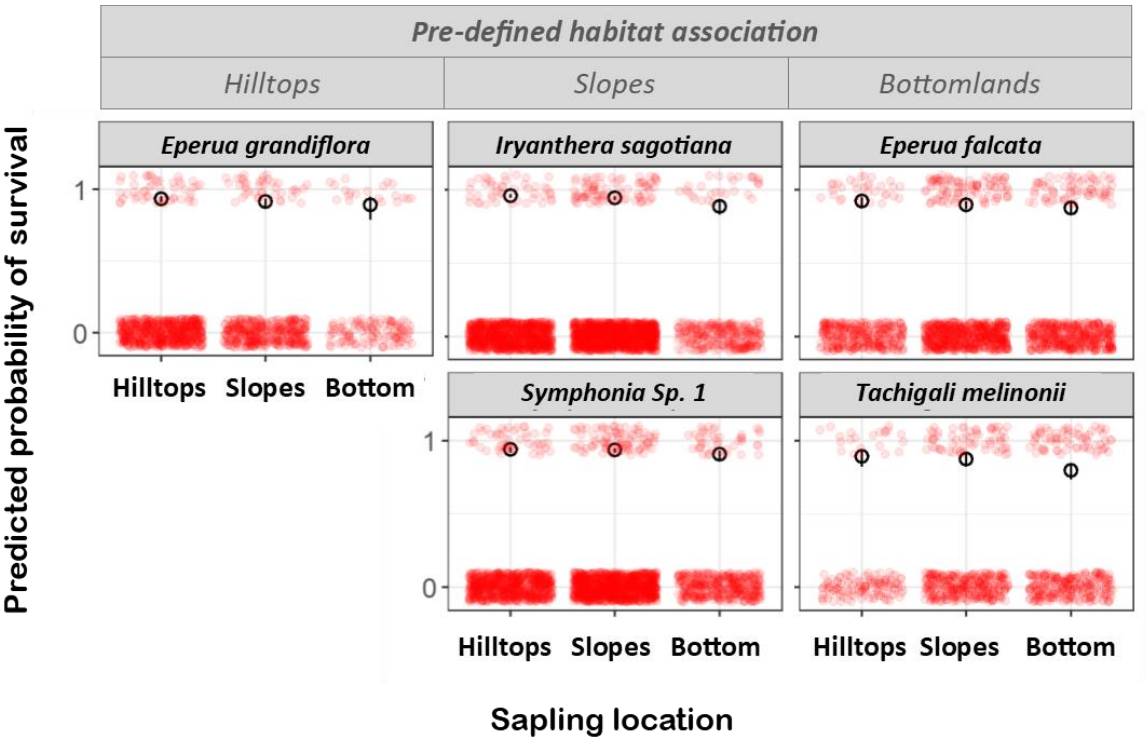

Figure 0.4. Modelled predictions of survival as a function of sapling location (when controlling for all other variables). Black open circles represent the predicted probability of survival and black lines show estimated upper and lower 95% confidence intervals around the predictions. Individual sapling survival (0) or mortality (1) in each location are plotted as red filled circles. Predictions are shown only for species for which the categorical predictor 'topography' was significant in binomial regression models. Panels are arranged in columns according to the habitat association of each species, which was defined as the topographic habitat within which density of stems ha^{-1} was greatest (Table 4.1).

Effect of drought on sapling survival

The relationship between drought index and sapling survival was significant for 5 of 23 species (*S. decaphylla, I. sagotiana, S. rubra, S. multiovula, S. globulifera*) (Figure 4.5). Increasing drought index reduced the probability of survival for all species, and the effect was strongest for the two species associated with the wet bottomlands (right-most panels on Figure 4.5). For *S. multiovula* the probability of survival decreased by 50%, and for *S. globulifera* the probability of survival decreased by 20%.

Interaction between drought index and sapling location

The effect of the drought index on sapling survival varied with sapling location for three species, *P. cochlearia*, *V. michelii*, and *B. prouacensis* (Figure 4.6). At low drought index values, the probability of survival was lower for *P. cochlearia* saplings located in the hilltop habitat compared to the slopes and bottomlands. As the drought index increased this relationship was reversed and saplings located in hilltop habitats had a higher probability of survival than saplings located in slopes and bottomlands.

For saplings of *B. prouacensis* at low drought index values the probability of survival was the same regardless of the location of the sapling, but as the drought index increased, the probability of survival was lower for individuals located in the slopes or wet bottomlands and was slightly higher for those located in the hilltops.

In contrast, saplings of *V. michelii* displayed a lower probability of survival at low levels of the drought index when located in the bottomlands, but when the drought index increased, the probability of survival for saplings in the bottomlands was higher.

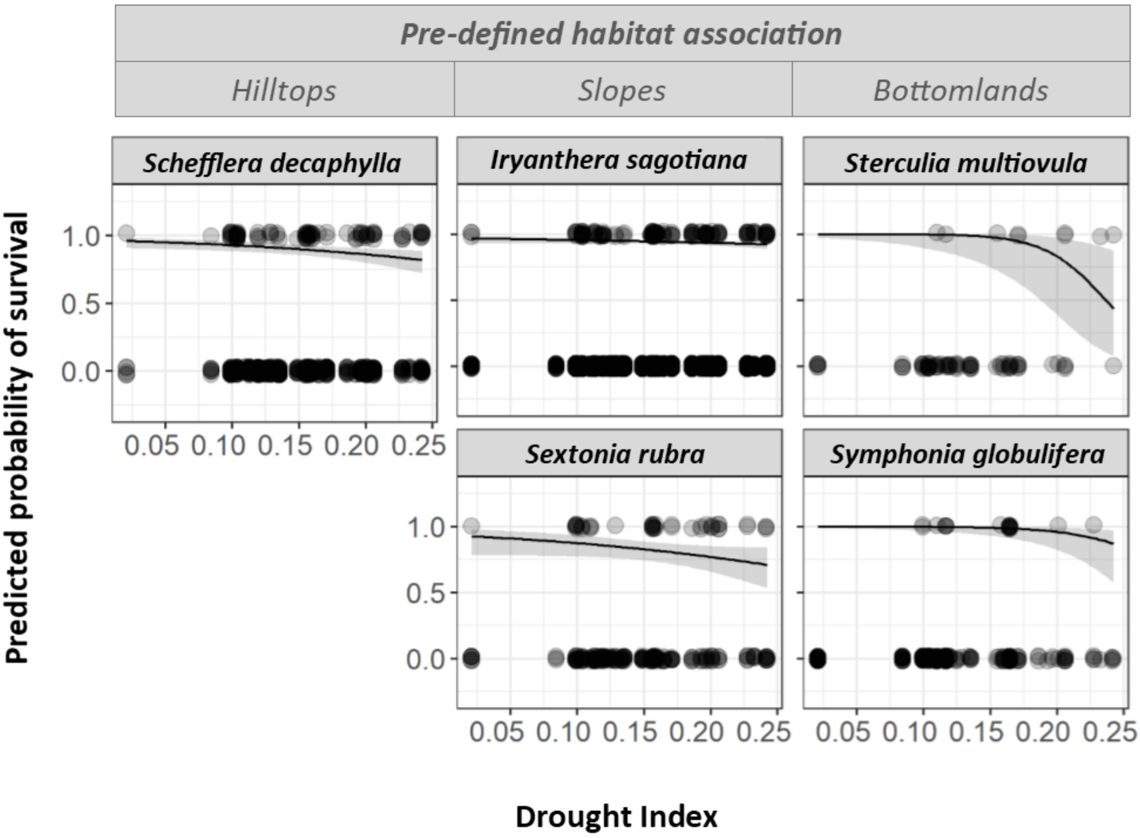

Figure 0.5. Modelled predictions of survival as a function of the Drought Index values (when controlling for all other variables). The Drought Index refers to the proportion of days soil water availability dropped below a threshold of REW ≤ 0.4 per census interval (see Methods for details). Black lines are the predicted probability of survival and grey shading shows estimated upper and lower 95% confidence intervals. Individual sapling survival (0) or mortality (1) are plotted as black filled circles. Predictions are shown only for species for which the continuous predictor 'Drought Index' was significant in binomial regression models. Panels are arranged in columns according to the habitat association of each species, which was defined as the topographic habitat within which density of stems ha^{-1} was greatest (Table 4.1).

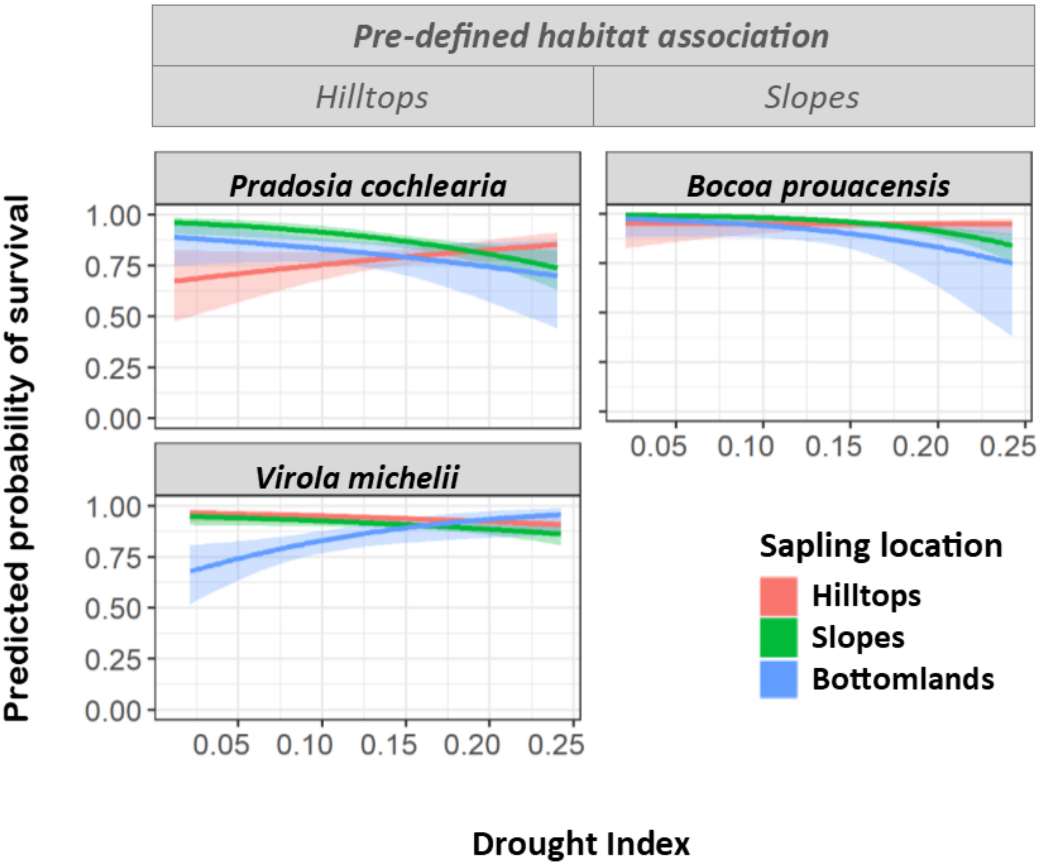

Figure 0.6. Modelled predictions of sapling survival as a function of the interactive effect of Drought Index and sapling location in three contrasting topographic habitats (when controlling for all other variables). The Drought Index refers to the proportion of days soil water availability dropped below a threshold of REW ≤ 0.4 per census interval (see Methods for details). Coloured lines represent the predicted probability of survival in each of the habitats and coloured shading shows estimated upper and lower 95% confidence intervals. Predictions are shown only for species for which the interaction between categorical predictor 'Sapling Location' and continuous predictor 'Drought Index' was significant in binomial regression models. Panels are arranged in columns according to the habitat association of each species, which was defined as the topographic habitat within which density of stems ha^{-1} was greatest (see Table 4.1).

Effect of waterlogging index on sapling survival

The main effect of waterlogging on sapling survival was significant for 9 of 23 species (Figure 4.7). Increasing waterlogging index increased the probability of survival for all species, and the effect was strongest effect for *G. glabra* which had an increase in survival probability of 27% between the lowest and highest values of the waterlogging index. More species that were associated with the hilltops than species associated with the slopes or bottomlands were significantly affected by the waterlogging index.

Interaction between waterlogging index and sapling location

The main effect of waterlogging on sapling survival varied with sapling location for four species, *S. decaphylla*, *D. guianensis*, *S. rubra*, *S. pruriens* (Figure 4.8). For the two species associated with the hilltop habitat, *S. decaphylla* and *D. guianensis*, as the waterlogging index increased the probability of survival was lower for those saplings located in the wet bottomlands, and were higher for saplings located on the slopes, but had a variable effect for saplings located in the hilltops. For the other two species, increasing waterlogging frequency was related to higher survival probability whether saplings were located in hilltops, slopes, or bottomlands. For *S. rubra*, the increase in survival probability was very pronounced for individuals located in hilltop habitats (an increase of 41%) and bottomland habitats (an increase of 55%).

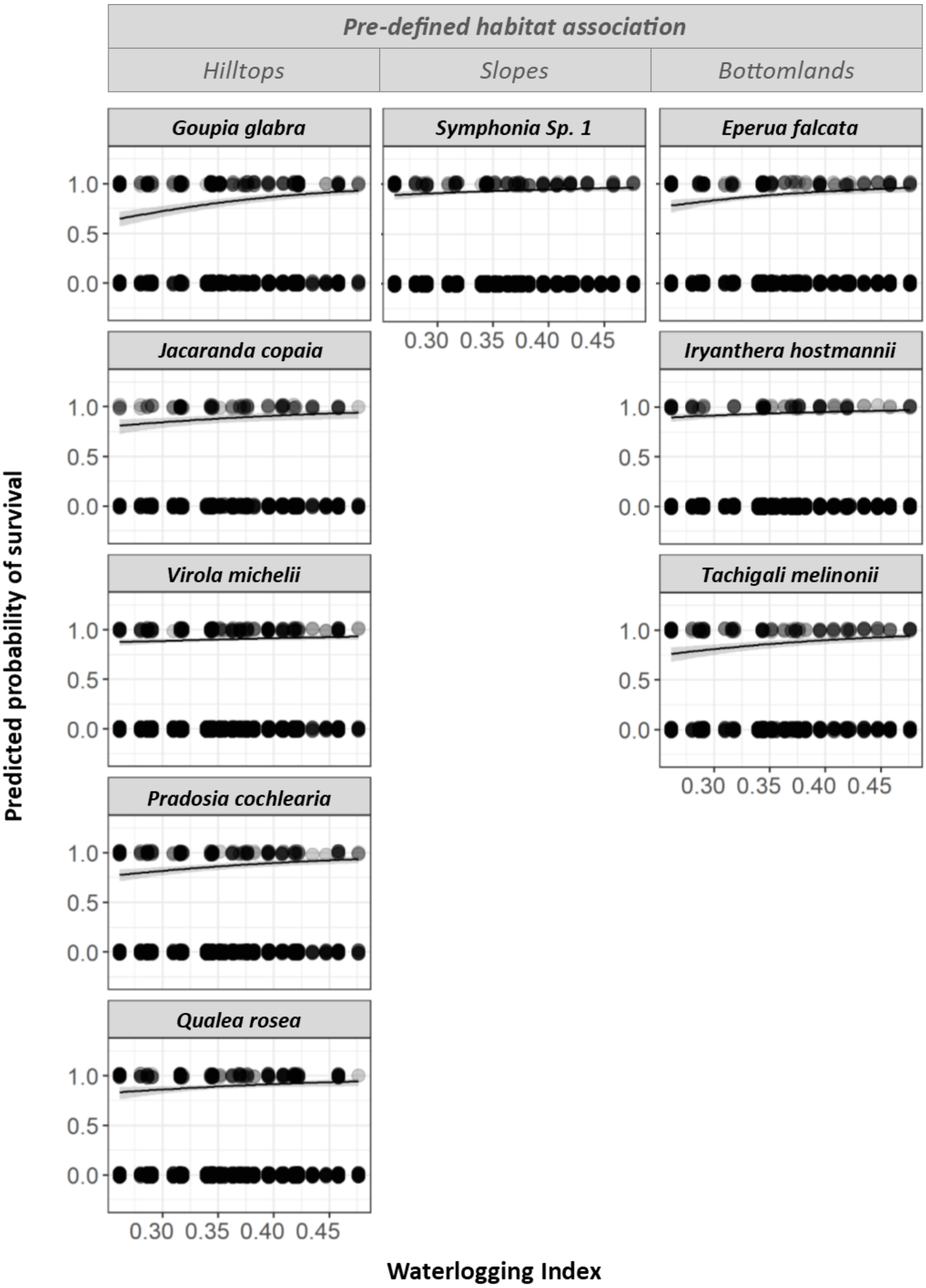

Figure 0.7. Modelled predictions of sapling survival as a function of the Waterlogging Index (when controlling for all other variables). The Waterlogging Index refers to the proportion of days when soil water availability increased above saturation, measured as REW = 1 + excess water (see Methods for details). Black lines represent the predicted probability of survival and grey shading show estimated upper and lower 95% confidence intervals. Individual sapling survival (0) or mortality (1) are plotted as black filled circles. Predictions are shown only for species for which the continuous predictor 'Waterlogging Index' was significant in binomial regression models. Panels are arranged in columns according to the habitat association of each species, which

was defined as the topographic habitat within which density of stems ha^{-1} was greatest (Table 4.1).

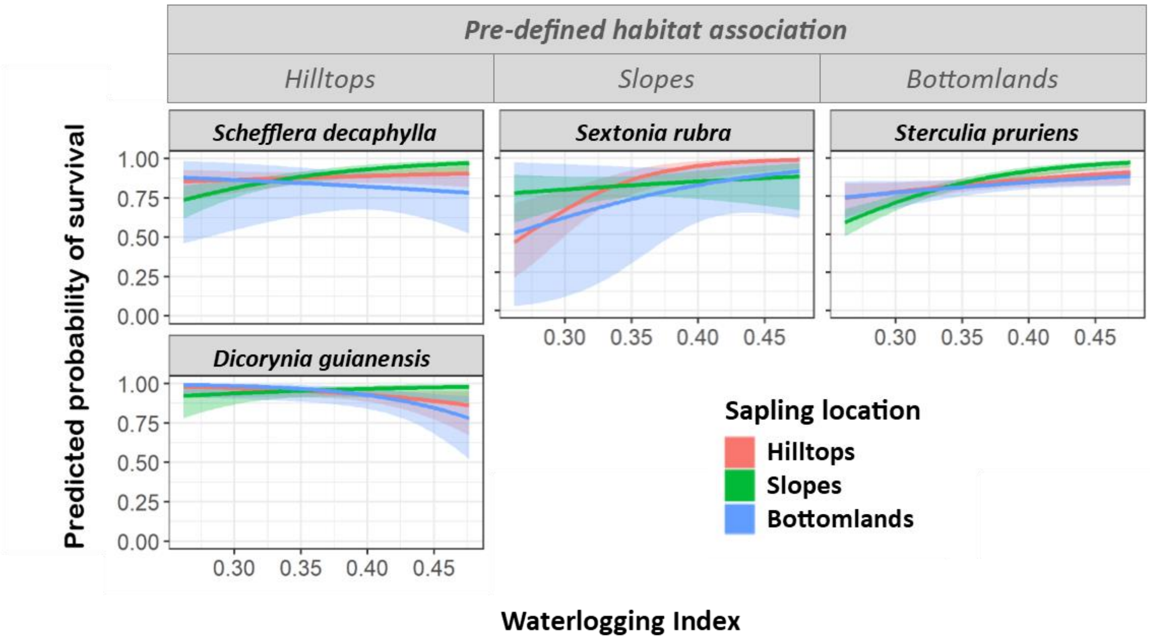

Figure 0.8. Modelled predictions of sapling survival as a function of the interactive effect of Waterlogging Index and sapling location in three contrasting topographic habitats (when controlling for all other variables). The Waterlogging Index refers to the proportion of days when soil water availability increased above saturation, measured as REW = 1 + excess water (see Methods for details). Coloured lines represent the predicted probability of survival in each of the habitats and coloured shading shows estimated upper and lower 95% confidence intervals. Predictions are shown only for species for which the interaction between categorical predictor 'Sapling Location' and continuous predictor 'Waterlogging Index' was significant in binomial regression models. Panels are arranged in columns according to the habitat association of each species, which was defined as the topographic habitat within which density of stems ha^{-1} was greatest (Table 4.1).

Effect of light availability index on sapling survival

I found evidence for a main effect of light availability on survival for 5 of 23 species (Figure 4.9). In contrast to the effects of the drought and waterlogging indices, the effect of increasing light availability on sapling survival was varied. The two species associated with the hilltop habitat, *J. copaia* and *D. guianensis*, were positively associated with increased light, whereas the three other species experienced a negative effect of increased light availability.

The main effect of increasing light availability on survival was small, with changes in the probability of survival ranging between 1-15%, except for *I. sagotiana* which had a decrease in survival probability of 28% between the lowest and highest light availability values.

Interaction between shade index and sapling location

The main effect of light availability on survival varied with sapling location for three species, *G. glabra*, *C. surinamensis*, and *E. grandiflora* (Figure 4.10). For saplings located in the hilltops (red lines) increasing light transmission was related to lower sapling survival in all species. For saplings located in the bottomlands (blue lines) increasing light transmission was related to higher survival probability for all species. The effect of location in the slopes was varied, with *E. grandiflora* experiencing an increase in survival and *G. glabra* and *C. surinamensis* experiencing lower survival probabilities.

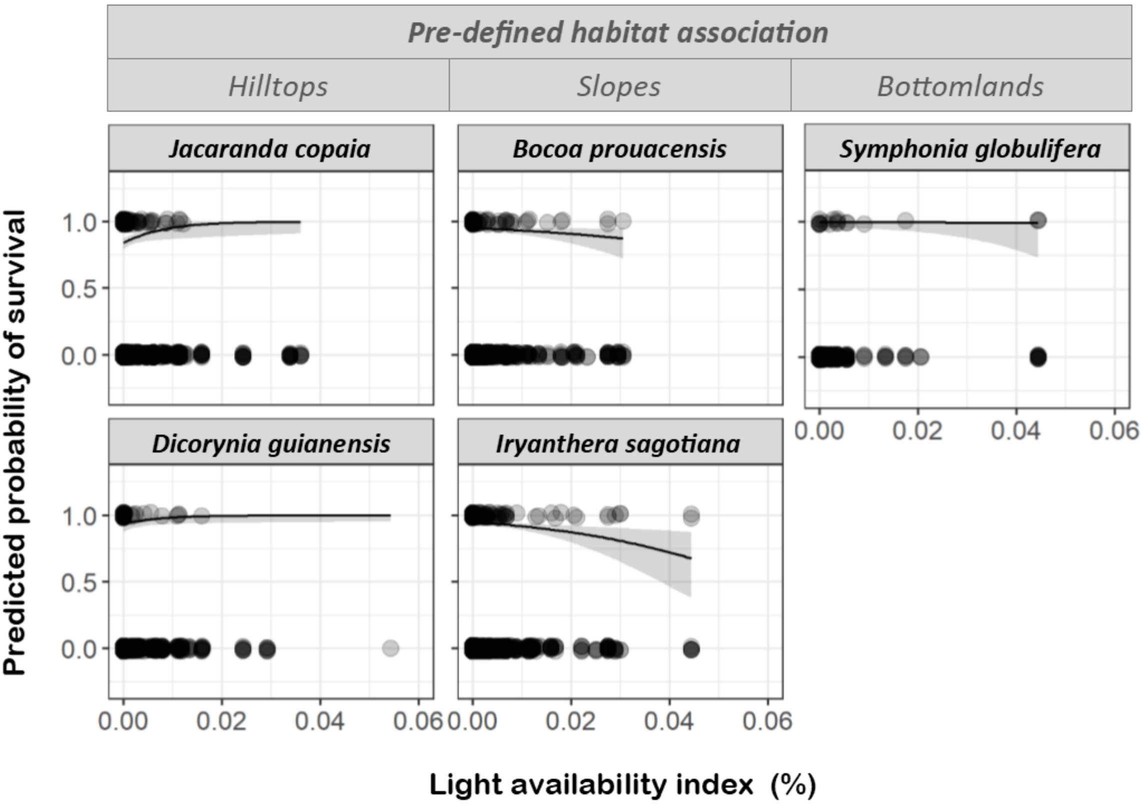

Figure 0.9. Modelled predictions of sapling survival as a function of the light availability index (when controlling for all other variables). The light availability index is the percentage of light availability between 1-5m above ground in each regeneration plot as measured by LiDAR (see Methods for details). Predictions were made across the range of observed light availability index values, which varies across species. Black lines represent the predicted probability of survival and grey shading show estimated upper and lower 95% confidence intervals. Individual sapling survival (0) or mortality (1) are plotted as black filled circles. Predictions are shown only for species for which the continuous predictor 'light availability index' was significant in binomial regression models. Panels are arranged in columns according to the habitat association of each species, which was defined as the topographic habitat within which density of stems ha^{-1} *was greatest (Table 4.1).*

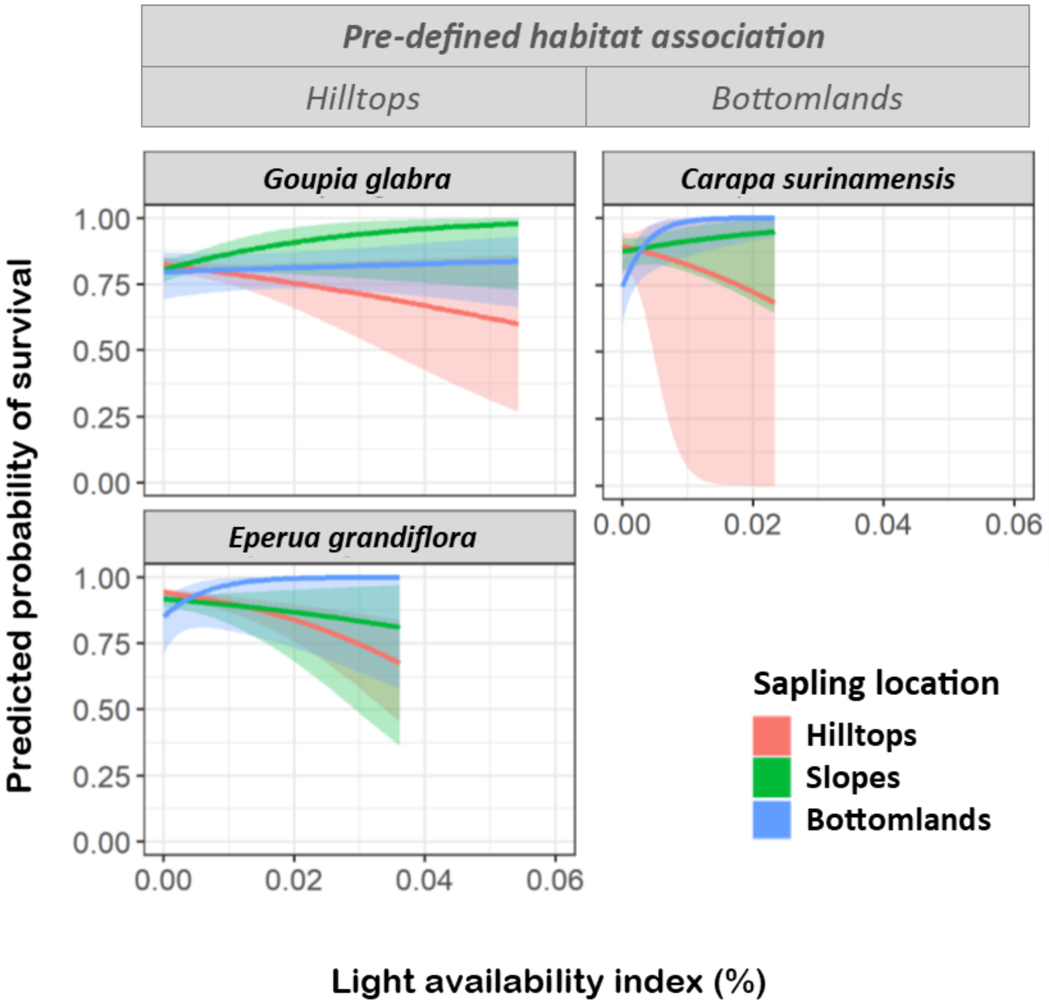

Figure 0.10. Modelled predictions of sapling survival as a function of the interactive effect of the light availability index and sapling location in three contrasting topographic habitats (when controlling for all other variables). Predictions were made across the range of observed light availability index values, which varies across species. The light availability index is the percentage of light availability between 1-5m above ground in each sapling regeneration plot as measured by LiDAR (see Methods for details). Coloured lines are the predicted probability of survival in different topographic habitats and coloured shading shows estimated upper and lower 95% confidence intervals. Predictions are shown only for species for which the interaction between continuous predictor 'light availability index' and categorical predictor 'sapling location' was significant in binomial regression models. Panels are arranged in columns according to the habitat association of each species, which was defined as the topographic habitat within which density of stems ha^{-1} was greatest (Table 4.1).

Interactions between soil water and light availability

For only 2 of 23 species the effect of drought index on sapling survival was dependent upon light availability (*T. melinonii*, and *S. pruriens*) (Figure 4.11). For both species the effect on survival response was similar. At low light availability, sapling survival probability was slightly higher at lower drought index levels (red lines in Figure 4.11). But as light availability increased, sapling survival probability was lower at low drought index levels compared to medium and high drought index levels. The negative effect of the low-level drought index was stronger for *S. pruriens*.

The effect of the waterlogging index on sapling survival depended upon light availability for three species, *D. guianensis*, *I. sagotiana*, and *C. surinamensis* (Figure 4.12). For *D. guianensis* the probability of sapling survival increased as light availability increased over all levels of the waterlogging index. For *I. sagotiana,* there was a 95% chance of survival at the low level of light availability regardless of the value of waterlogging index. As light availability increased, survival probability decreased differentially across the range of waterlogging index values. The low value of waterlogging decreased survival by 37% (red line in Figure 4.12), whereas the high value of waterlogging decreased survival probability by 13% (blue line in Figure 4.6). *C. surinamensis* had a similar survival probability across the range of waterlogging index values at low light values. However as light availability increased, survival probability decreased sharply for saplings that experienced the highest waterlogging index, whereas at low values of waterlogging the probability of survival increased.

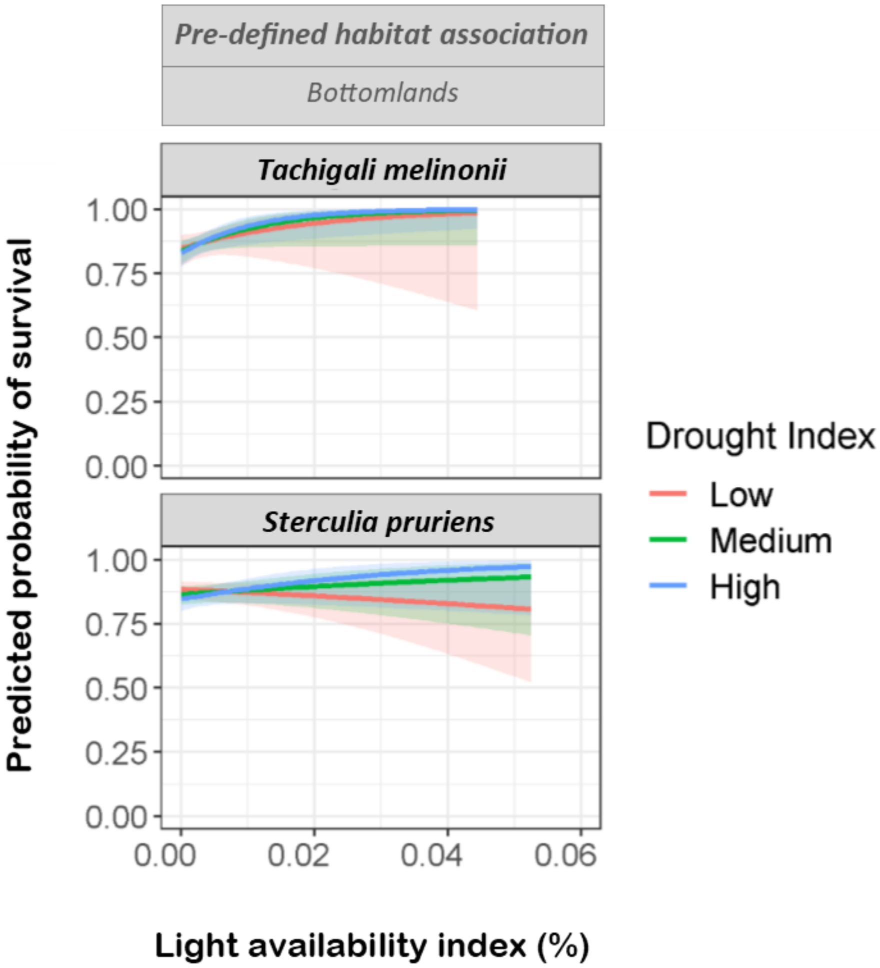

Figure 0.11.Modelled predictions of sapling survival as a function of the interactive effect of light availability index and the drought index (when controlling for all other variables). Light availability index is the percentage of light availability between 1-5m above ground in each sapling regeneration plots as measured by LiDAR (see Methods for details). The drought index refers to the proportion of days soil water availability dropped below a threshold of REW ≤ 0.4 per census interval (see Methods for details). Predictions were made at the first (low), second (medium), and third (high) quartiles of drought index values across the range of the light availability index experienced by each species, which varies across species. Coloured lines are the predicted probability of survival at each level of 'drought index' and coloured shading shows estimated upper and lower 95% confidence intervals. Predictions are shown only for species for which the interaction between continuous predictors 'light availability index' and 'drought index' was significant in binomial regression models. Panels are arranged in columns according to the habitat association of each species, which was defined as the topographic habitat within which density of stems ha^{-1} was greatest (Table 4.1).

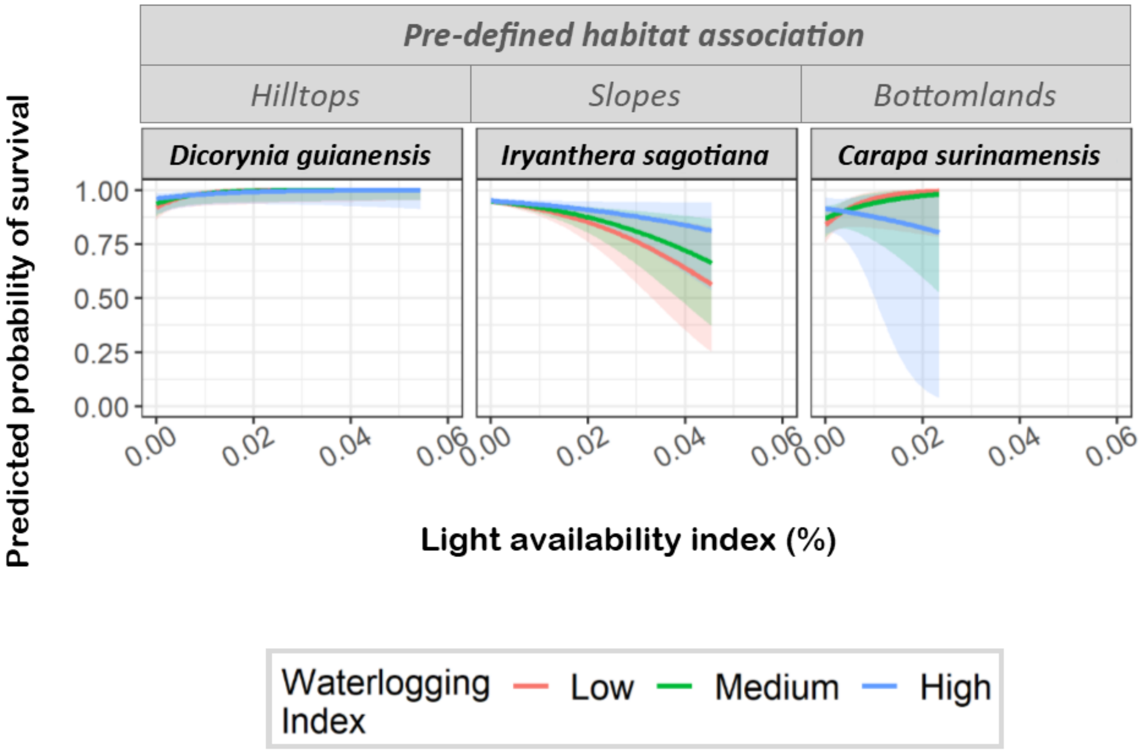

Figure 0.12. Modelled predictions of sapling survival as a function of the interactive effect of light availability index and the waterlogging index (when controlling for all other variables). The light availability index is the percentage of light availability between 1-5m above ground in each sapling regeneration plot as measured by LiDAR (see Methods for details). The waterlogging index refer to days where soil water availability increased above saturation, measured as relative extractable water (REW) = 1 + excess water (see Methods for details). Predictions were made at the first (low), second (medium), and third (high) quartiles of the waterlogging index across the range of observed light availability index values, which varies across species. Coloured lines are the predicted probability of survival at each level of 'waterlogging index' and coloured shading shows estimated upper and lower 95% confidence intervals. Predictions are shown only for species for which the interaction between continuous predictors 'light availability index' and 'waterlogging index' was significant in binomial regression models. Panels are arranged in columns according to the habitat association of each species, which was defined as the topographic habitat within which density of stems ha^{-1} was greatest (see Table 4.1).

Differential survival according to habitat association

The second aim of this study was to assess to what extent sapling survival predicted by drought, waterlogging, and light availability align with habitat associations and life history strategy. Plotting the odds ratios for the effect of drought, waterlogging, and light availability on species survival allows for visual assessment of the relationship between pairs of predictors (Figure 4.13). Here, odds ratios are interpreted as the odds of a sapling surviving a census period compared to not surviving, where an odds ratio above 1 means that survival is more likely, and an odds ratio below 1 means that mortality is more likely.

Overall, it appears that wet habitat associated species may survive better in wetter conditions. This can be seen by the positive association with increasing waterlogging index in all except one species (*S. globulifera*) associated with the wet bottomland habitat in Paracou (top left, and bottom right panels in Figure 4.13). However, the majority of dry habitat associated species also display a positive association between waterlogging index and survival. Wet associated species also had increasing mortality as the drought index increases, and increased survival as light availability increases.

Dry associated species are less distinctively grouped than wet associated species. Many dry associated species have a negative association with increasing drought index, and the size of the negative effect is similar to many of the wet associated species (distance from vertical line at odds ratio = 1 on top and bottom left panels Figure 4.13). In fact, the wet associated *E. falcata* had greater survival in increasing drought conditions than most dry associated species. When considering the known life history strategies of species at the adult tree stage, there are no readily distinguishable patterns of survival displayed by shade tolerant vs. light loving species. Whether considering patterns in relation to waterlogging, drought, or light indices, the light loving and shade tolerant species overlap.

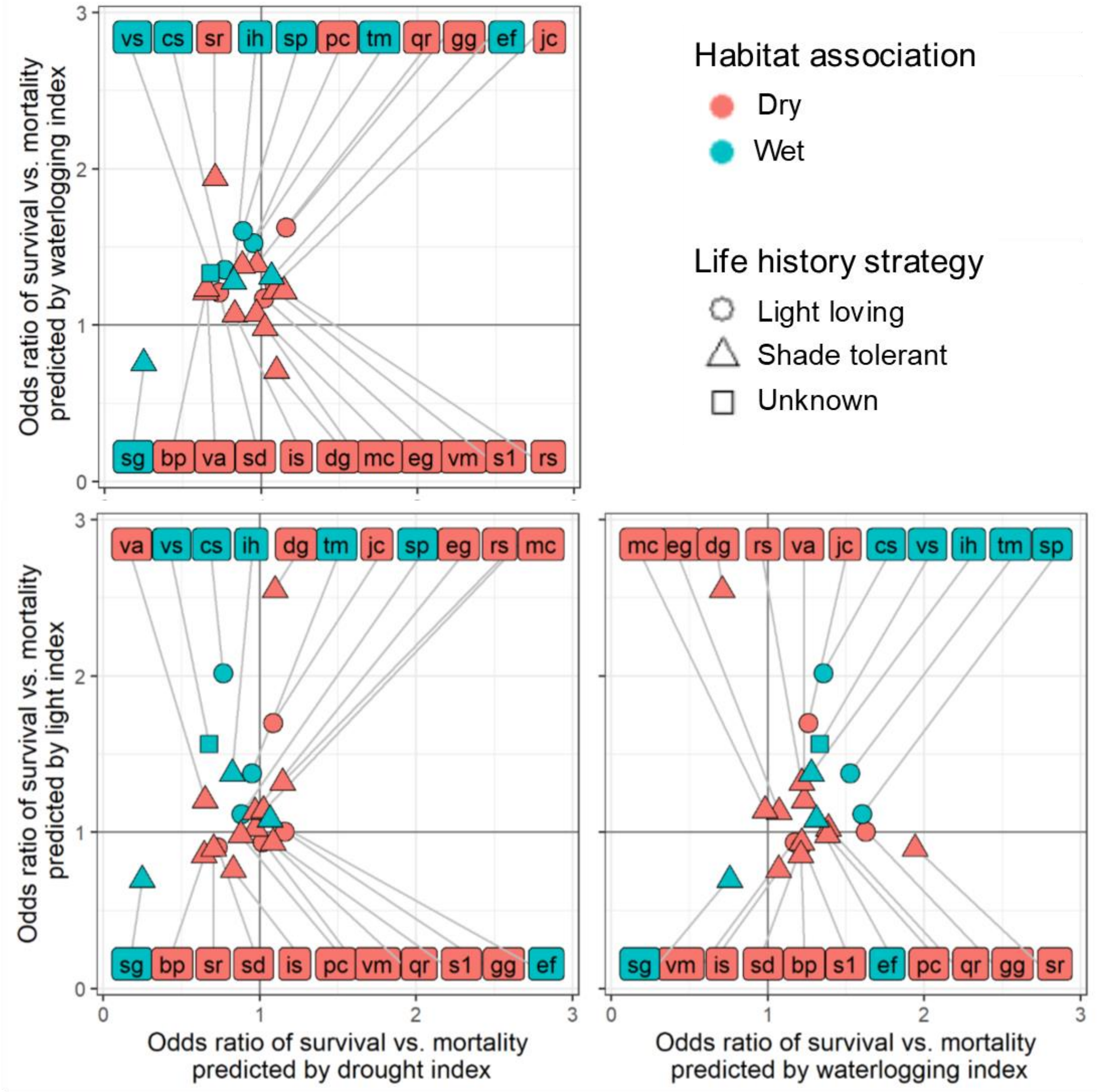

Figure 0.13. Relationship between modelled odds ratio of sapling survival predicted by drought index and waterlogging index (top left panel), drought index and light index (bottom left panel), and waterlogging index and light index (bottom right panel). Each axis represents the odds ratio of survival (vs. mortality) for every unit increase in either drought, waterlogging, or light indices (while controlling for all other variables). Odds ratios greater than 1 signify positive effects, whereas odds ratios of less than 1 signify negative effects of a particular variable. Each species is shown once on each figure (see table 4.1 for species codes). Habitat association refers to the habitat type within which the observed density of sapling stems is greatest, where 'Wet' applies to 'Bottomlands' topographic habitat, and, 'Dry', applies to both 'Hilltop', and 'Slope' topographic habitats combined (Table 4.1). Life history strategy refers to whether a species is known to be either light loving or shade tolerant as adult trees (Table 4.1).

4.5 Discussion

Relative importance of water and light availability

Sapling survival was assessed in relation to soil-water and understory light availability to evaluate their roles in determining species distribution patterns in a seasonal tropical forest. I found evidence that bottomland habitat and drought frequency was associated with reduced survival, and waterlogging frequency was associated with increased survival, whereas the effect of increasing light availability was mixed. These results suggest that although waterlogging and light are important factors governing sapling survival, drought frequency and location in bottomland habitat were the more important contributors to the separation and sorting of species as they were most consistently associated with lower probabilities of survival.

Topographic habitat

The effect of sapling location in hilltops, slopes, and bottomlands was a significant predictor of survival for 5 of 23 species (Figure 4.4). For those five species, the effect of location on survival was the same regardless of the species' pre-defined habitat association, whereby being located in the bottomlands resulted in the lowest probability of survival, and being located in the hilltops resulted in the highest probability of survival. In fact, in only four species, the probability of survival was higher in the bottomlands compared to the hilltops and slopes (albeit insignificantly) (Table 4.4). These results imply that being located in the bottomlands creates a larger inherent risk to survival than being located in the hilltops, and is consistent with a previous study at this site that found higher mortality rates for trees in the bottomlands (Ferry et al. 2010). However, in this study the majority of species did not show a significant effect of location on survival (17 out of 23 species) (Table 4.4), which suggests that survival does not differ strongly between habitats for most species. This is not uncommon, as even for species with strong habitat associations survival differences between habitats may not vary (Yamada et al. 2007).

Waterlogging frequency

Increasing waterlogging frequency had a significant effect on increasing survival for 9 of 23 species (Figure 4.2) and increased survival probability, albeit non-significantly, for a further nine species (Appendix 3). This contrasts with low survival for saplings located in the wetter bottomland habitat when compared to the drier slopes and hilltop habitats, which suggests that the negative effect of being located in the bottomlands may be independent of the frequency of waterlogging events as estimated in this study.

In previous studies at this site higher mortality rates in bottomlands compared to hilltops were caused by increased treefall deaths associated with the unstable swampy soils (Madelaine et al. 2007, Ferry et al. 2010). It is therefore possible that the waterlogging index used in this study does not adequately capture the soil-water properties that cause year-round prevalence of soil instability and swampy conditions associated with tree death in the bottomlands. For example, long-term waterlogging below the soil surface can weaken root systems (Toledo et al. 2017), which could lead to treefalls during high winds (Brokaw 1982; Denslow 1987; McDowell et al, 2018), irrespective of pulses of waterlogging measured in this study. Further, as the soil type associated with the bottomlands was not included in the original water balance model (Wagner et al. 2011), waterlogging frequency had to be estimated based on the adjacent soil type and is therefore an underestimate.

Despite low survival in the bottomlands, waterlogging frequency was significantly associated with increasing survival for many species. In fact, in only four species increasing waterlogging frequency reduced survival probability, albeit non-significantly (*D. guianensis*, *M. coccinea*, *S. globulifera*, and *S. multiovula) (*Table 4.4*)*. Enhanced survival related to waterlogging may be due to increases in the amount of nutrients in the system, particularly transient increases in phosphate concentrations due to altered soil redox status and bacterial activity (Kreuzwieser and Gessler 2010).

These results differ with those from a previous study at this site that found that temporal variability in soil saturation increased adult tree mortality (Aubry-Kientz et al. 2015). These contrasting results may reflect differences in susceptibility to waterlogged soils through ontogeny, where saplings may benefit from short and infrequent periods of waterlogging as they are protected from strong winds that may induce treefalls in the forest understory. Whereas larger adult trees suffer more frequent treefalls via a combination of unstable soils, the effects of gravity, and the greater effects of storms and strong winds.

Additionally, adult mortality as a result of waterlogging may increase the amount of light available for saplings which could in turn lead to the observed increases in survival. However, in this study the interactive effect of increasing light transmission and waterlogging frequency did not strongly support this idea. Significant interactions were obtained for only three species and the results were mixed, with both decreases and increases in survival associated with increasing light (Figure 4.12). In future studies, time varying light transmission may yield stronger evidence to support this idea.

These results suggest that for saplings in Paracou temporal waterlogging is a less important determinant of niche limitation than drought frequency and being located in the bottomlands, as increased survival does not separate and sort species, increased mortality does.

Drought frequency

Drought frequency reduced survival probability more than waterlogging frequency in all but two species (*D. guianensis*, and *M. coccinea*) (Table 4.4), underlining that sapling survival was more strongly limited by dry conditions compared to wet conditions in this site. This result directly opposes those from a previous study in the nearby Piste de Saint Elie in French Guiana, which found that spatial variation in soil saturation constrained tree zonation more than water shortage on well-draining soils (Pélissier et al. 2002). These apparently disparate results may reflect the difference between topographical variation in soil waterlogging which is long-term and associated with certain soil properties such as instability, root damage, and lack of nutrients (Kreuzwieser and Gessler 2010), and more short-term or infrequent waterlogging events that many species may be able to tolerate (Parolin 2010).

Drought frequency was related to lower survival probability, which was consistent with previous studies conducted at this site (Baraloto and Goldberg 2004, Baraloto et al. 2007, Aubry-Kientz et al. 2015, Fargeon et al. 2016), and in other seasonal tropical forests (Comita and Engelbrecht 2009, Paine et al. 2009, Baltzer and Davies 2012), and confirm the importance of water limitation in driving survival dynamics in tropical wet forests. Although the general effect of increasing drought frequency was related to lower sapling survival, a variety of responses were observed. Increasing drought frequency was related to reduced survival probability in 14 species, but had no relationship with survival for a further six species, and was related to increased survival probability for two species (Table 4.4). These results do not appear to be related to habitat preference as species with no relationship and species with increased survival were a mixture of hilltop, slope, and bottomland associated species. The positive effects of increasing drought frequency may instead reflect interactions with factors related to drought such as reduced pest and pathogen pressure (Gaviria and Engelbrecht 2015).

Light availability

High light levels were experienced by only few individual plots, and consequently few individual saplings. The unbalanced data meant that sapling survival at the higher end of the light availability range had disproportionate leverage on the estimates of the effect of light. Further, the light availability index was generated from LiDAR data collected in 2013, and therefore describes understory light transmission with regards to the spatial distribution of trees at that time. Sapling survival observations began in 1992 and went through to 2016, and therefore it is likely that vegetation growth and tree falls will have altered the availability of light in the understory over this time. As such, despite the spatial accuracy of the LiDAR generated light index, this index should be considered a coarse grain measure of understory light availability. Despite these concerns, the light transmission index was significantly related to the observed survival patterns of 5 of 23 species, and was a significant interaction parameter describing survival for a further 7 of 23 species which suggests that this predictor was measured on an ecologically relevant scale.

Interactions between water and light availability

The effect of increasing light transmission depended on drought frequency for only two species, *T. melinonii*, and *S. pruriens*, whereby increasing light was related to an increase in survival probability (Figure 4.11). The effect of increasing light transmission depended on waterlogging frequency for three species, *D guianensis, I. sagotiana*, and *C. surinamensis,* where the effect of increasing light was variable across the range of waterlogging values (Figure 4.12). Given that very low-light and high-light levels are likely to interact with drought (Smith and Huston 1989, Sack and Grubb 2002, Sack 2004, Craine and Reich 2005, Laanisto and Niinemets 2015, Grubb 2016), and waterlogging (Lopez and Kursar 2003; Niinemets and Valladares 2006; Lucas et al. 2013) to affect plant performance in different ways, it was surprising that I did not observe significant interactions in more species. However, in the shadehouse study reported in Chapter 3 there was also no evidence of an interactive effect of light and water in the majority of species. Moreover, in this study even the highest light transmission levels were still very low, and therefore it is possible that under the range of observed light values most species did not experience differential survival. Further, individuals were not evenly spread across light and drought gradients and therefore it is difficult to obtain significant interaction results.

Sapling survival and species-habitat associations

Associations to topographic habitats are common and widespread in tropical forest tree communities (Harms et al. 2001, Palmiotto et al. 2004, Gunatilleke et al. 2006, Baraloto et al. 2007, Russo et al. 2008, Guo et al. 2017), however, the underlying mechanisms are often poorly understood (Fortunel et al. 2019). One hypothesis suggests that intolerance of waterlogged conditions by dry habitat associated species is a stronger constraint on tropical tree distributions than the limitations of drier habitat for species associated with waterlogged conditions (Lopez and Kursar 2003; Baraloto et al. 2007). Here, I examined the temporal effects of waterlogging and drought frequency, as well as interactions between these factors and sapling location on survival to look for evidence that refutes or aligns with this hypothesis. The results were mixed and did not point to an irrefutable role for either waterlogging or drought in driving habitat associations through differential survival.

When considering the temporal effects of waterlogging and drought, results suggest that the limitations of drought conditions constrain the distribution of species associated with waterlogged habitat. The majority of species experienced an increase in survival probability associated with increasing waterlogging frequency regardless of habitat association, whereas drought frequency was associated with decreased survival for a higher proportion of bottomland associated species compared to drier-habitat associated species (Figure 4.13), This is not surprising given that traits associated with wet habitat associated species, such as low wood density (Chave et al. 2006), are linked to low resistance to xylem embolism and hydraulic failure which are key traits in tolerating drought (Greenwood et al. 2017, O'Brien et al. 2017, Poorter et al. 2019). It is important to note however that fewer species in this study were associated to the bottomlands which may introduce a bias to these results. It is possible that sampling more species associated with the bottomland habitat would result in a finding a greater diversity of responses to dry periods and result in different conclusions being drawn.

When considering interactions between drought and waterlogging frequency and sapling location, I considered two non-mutually exclusive hypotheses. First, if drought was an important factor limiting bottomland associated species from the hilltops, I would expect bottomland associated species to survive less well in the hilltops as a function of increasing drought frequency. Second, if waterlogging was an important factor limiting hilltop associated species from the bottomlands, I would expect hilltop associated species to survive less well in the bottomlands as a function of increasing waterlogging frequency. The interaction between drought frequency and sapling location did not align with the first hypothesis as there was no evidence of a relationship for any species associated with the bottomlands (Figure 4.5). Moreover, the interaction of drought and location in the hilltops was related to lower survival for the hilltop associated *V. michelii,* which is the opposite of what I expected. However, the hilltop associated *P. cochlearia* did have higher survival associated with increasing drought frequency in the hilltops. The interaction of waterlogging frequency and sapling location provides some evidence that agrees with the second hypothesis, as lower survival was associated with increasing waterlogging in the bottomland habitat for hilltop associated species (Figure 4.8), but this was only a significant result for two species (*D. guianensis* and *S. decaphylla*).

The mixed results for interactions between water availability and sapling location were not unexpected as effects are difficult to detect in the field because individuals are not evenly dispersed throughout habitats and environmental gradients (Metz 2012). Further, habitat associations may not necessarily be associated with large differences in performance across habitats (Yamada et al*.* 2007; Comita and Engelbrecht, 2009; but see Fortunel et al, 2016). Instead, habitat associations may be caused and maintained by small performance differences between co-occurring species (Yamada et al. 2007, Comita and Engelbrecht 2009).

Sapling habitat associations in this study were determined simply based on the density of stems per hectare in each habitat. The categorisations broadly agreed with those found in previous studies of these species in these habitats at the adult tree stage (Baraloto et al. 2007, Allie et al. 2015) (Table 2.3). However, there were some notable differences. As saplings *Goupia glabra* and *Jacaranda copaia* had higher densities of stems in the hilltop habitats of Paracou, whereas at the adult stage they were associated with the bottomlands. Both *G. glabra* and *J. copaia* are typical pioneer species associated with gaps with low to moderate wood density (Siliprandi et al. 2016, Hogan et al. 2018). This change in association suggests that these species are able to take advantage of the greater light availability in the hilltop habitats during establishment, but are unable to maintain those high densities in the throughout ontogeny which may be due to frequent drying episodes.

The results of this study suggest that differential survival among bottomland associated species filters these species from the dry hilltop habitats especially during particularly dry years. Whereas, hilltop and slope associated species may have a home advantage when water is limiting, thereby allowing these species to survive better than wet-associated species in the driest habitats, and therefore contributing to the observed habitat associations.

4.6 Conclusions

I examined the relationship between sapling survival, habitat associations, and water and light availability in the tropical rainforest of French Guiana. I used data on the frequency of drought and waterlogging over a period of 24 years, and detailed data on understory light availability. I found that i) sapling survival was commonly lower in the bottomlands compared to the slopes and hilltops, ii) the effect of increasing light was more variable than the effect of drought or waterlogging and did not depend on water availability, iii) increased drought frequency commonly reduced survival whereas increased waterlogging frequency commonly increased survival, iv) increased waterlogging reduced survival for some hilltop associated species in the bottomlands, and v) increased drought was not related to survival for bottomland associated species in the hilltops. Taken together these multiple lines of evidence suggest that drought was the relatively more important factor determining differential species survival, as well as a likely important role of long-term soil instability associated with topographical water availability over temporal waterlogging in determining differential species survival and therefore distributions. Difficulties associated with confounding variables reduced the ability of the data to provide robust answers to the question of what determines habitat associations, and further work would benefit from addressing these problems.

CHAPTER 5

5. Tolerances of drought and waterlogging but not shade predict tropical sapling performance in topographic habitats

5.1 Abstract

Modelling approaches that incorporate species tolerance of environmental gradients could improve the understanding of species distributions by providing explicit links between species performance and environmental conditions. In this study, I used experimentally assessed species tolerance of drought, waterlogging, and shade to predict sapling performance in habitats that differ in water and light availability, but also other factors such as nutrients. If field performance depended upon species tolerance, I would expect to find statistical interactions between tolerance indices and the location of saplings in wetter and drier habitats. I found evidence that abundance in topographic habitats defined by variation in water availability did depend on differential tolerance of drought, and waterlogging, but not shade. I found no evidence that sapling survival was related to any of the indices. Very low sample sizes for sapling abundances increase the uncertainty around these results, however, this study demonstrates a possible basis for tree species distributions across locally contrasting topographic habitats that differ in water availability, which has important implications for the prediction of tree distributions and dynamics in novel environments. Overall, these results suggest that both drought and waterlogging are important factors generating species turnover between wetter and drier habitats in the lowland topical forest of Paracou, French Guiana.

5.2 Introduction

In tropical forests, water and light are two of the most important resources shaping individual tree performance and therefore distributions, along environmental gradients (Valladares and Niinemets 2008, Wright et al. 2010, Comita and Engelbrecht 2014, Jones et al. 2014, Detto et al. 2018). As land managers in the tropics are confronted with having to maintain ecological processes in the face of increased habitat fragmentation (Haddad et al. 2015, Wilson et al. 2016), and changing drought frequency and intensity of rainfall (Feng et al. 2013), an understanding of the extent to which water and light availability control species distributions will be essential.

Linking distribution pattern and process using functional trait approaches is popular amongst researchers (Lavorel and Garnier 2002, Westoby and Wright 2006, Kraft et al. 2008, Poorter et al. 2008, Sterck et al. 2011, Violle et al. 2014, Yang et al. 2014, Visser et al. 2016). However, predicting distributions remains difficult as the same suite of traits may provide suitability to a number of environments, different trait combinations may be suitable for the same environment, and many functional traits are not as closely linked to performance as they are hoped to be (Paine et al. 2015, 2018, Yang et al. 2018, Swenson et al. 2020).

Modelling approaches based on whole-plant tolerance of environmental gradients could improve the understanding of species distributions by providing links between observed distributions and environmental conditions (Craine et al. 2012, Sterck et al. 2014, Paine et al. 2018). Limiting-resource tolerance models (LRTMs) are based on the relationship between species performance and environmental resources and therefore explicitly link vital rates to environmental conditions. This relationship may be used to predict performance in other environments for which we have information about the availability of the resource. In this chapter, I assess the degree to which tolerances to limited resources predict observed patterns of species distributions in the field over topographic habitats that differ in water and light availability.

The study area remains the Paracou experimental forest where the contrasting wet and dry characteristics of the undulating topography and detailed light availability data are exploited for this investigation (described in detail in Chapter 2). Species performance across the landscape has been characterised using the sapling observation data set described in Chapter 2 and explored in-depth in Chapter 4. From the sapling observation data alone I was able to quantify the relative importance of water and light in determining the distribution and relative abundance of each species (Chapter 4). However, I was unable to generate evidence to support the statement that the observed variation in species performance between bottomland and hilltop forests was because i) bottomland associated species were unable to tolerate the intensity of seasonal drought on the hilltops, or that ii) hilltop associated species may be intolerant of the flooding regime in the bottomlands.

In the field, gradients of drought, waterlogging, and light rarely occur independently from one another. This confounding of variables makes it challenging to attribute observed plant distributions to environmental variation (Dormann 2007). Therefore, to make predictive statements about where to expect different species to be located along environmental gradients it may be beneficial to incorporate information on the tolerance of species to environmental gradients (Pearson and Dawson 2003, Battaglia et al. 2004, Baltzer et al. 2008). Here, I integrate the experimentally assessed drought, waterlogging, and shade tolerance indices generated in Chapter 3 to explore the idea that the classification of species based on whole-plant performance in low resource conditions uniquely combines understanding of plant performance and environment, and therefore predictive potential.

Previous studies have linked species tolerance to environmental resources with performance and observed spatial patterns across local-scale landscapes. For example, an elegant set of studies in Panama used experimentally assessed seedling drought tolerance (Engelbrecht and Kursar 2003) to explain differences in distribution across a rainfall gradient and at local scales across a hydrologically relevant topographic gradient (Engelbrecht et al. 2007, Comita and Engelbrecht 2009). Baltzer et al. (2008) successfully linked common garden experimental data on physiological tolerances to a rainfall gradient across the Malay-Thailand border to explain differences in distributions. Shade tolerance defined as light compensation points of juvenile trees growing on two different soils in Australia were calculated by measuring growth in different light environments and found to be correlated with in-situ minimum light requirements (Sendall et al. 2015). Here, the aim was to build on these studies by investigating the effect of two separate but interlinked resources, light and water, and three separate indices of tolerance, to drought, waterlogging, and shade.

In this study, I tested the degree to which whole-plant tolerance indices predict species performance along topographic gradients defined by water availability and understory light availability. Specifically I aimed to answer whether tolerance of drought, flooding, or shade best predicts abundance and survival patterns in the field. If field performance was dependent upon species' resource tolerance I would expect to find evidence of statistical interactions between tolerance indices and topographic location in models. For example, if drought was an important mechanism generating species turnover, then I would expect elevated abundance or an increased mortality risk for drought intolerant species, but only for those individuals located in the drier hilltop habitat. This work seeks to advance the understanding of species distributions across three important environmental gradients in tropical forests.

5.3 Methods

Study site

A general description of the site and environmental conditions can be found in Chapter 2. The study reported here was conducted at the Paracou experimental forest, a lowland tropical rainforest near Sinnamary, French Guiana (5°18'N, 52°55'W: 0 – 45 m elevation), where the wet season extends from March to June with a pronounced dry season from the end of August to November, and annual precipitation of around 3040 mm (Wagner et al, 2011). Mean air temperature and daily minimum relative humidity range from 25.7°C and 70% in the wet season to 26.7°C and 58% in the dry season (Epron et al. 2006). Paracou is characterised by an undulating topography with a network of hills that have been broadly categorised as hilltops, slopes, and bottomlands, which refer to a gradient of soil-water conditions, as well as variation in slope, angle, and soil-type. Hilltops are generally drier than slopes, while slopes are not as wet as the bottomlands (Table 4.2 in Chapter 4),

Study species

The study species are the eleven species studied in Chapter 3*, Dicorynia guianensis, Eperua falcata, Symphonia globulifera, Sterculia pruriens, Sextonia rubra, Recordoxylon speciosum, Virola surinamensis, Pradosia cochlearia, Tachigali melinonii, Jacaranda copaia*, and *Sterculia multiovula*. Each of the eleven species co-exists locally as adults across the Paracou site. The species span a range of life-history strategies, from light-loving pioneer species to strongly shade-tolerant (Favrichon 1994), and exhibit contrasting distributions in wet versus dry habitat in Paracou (See Table 2.3 in Chapter 2, and Table 4.1 in Chapter 4).

Tolerance indices

Three experimentally assessed tolerance indices, for drought, waterlogging, and shade, were calculated and described in detail in Chapter 3 and are included in each model. Each index describes the relative difference within a species between survival in well-watered and medium-light conditions and survival in experimentally manipulated drought, waterlogged, or shaded conditions. Specifically, for the drought index this was the difference between survival in well-watered and watering-withheld treatments, for the waterlogging index it was the difference between survival in well-watered and flooded treatments, and for the shade index it was the difference between survival in 8% of full sunlight and survival in 1% of full sunlight conditions.

Light availability

Light availability is a continuous measure of average light availability between 1-5m above-ground inside each plot. This variable was calculated using LiDAR data collected in 2013 and was described in detail in Chapter 4. The light transmittance values range from 0 to 1 and represent the proportion of total transmitted energy in the three-dimensional space that occupies the area between 1-5m above-ground inside each plot including a 0.5m buffer around each plot. The resulting mean light transmission index values ranged between 0.00000009 – 0.05, with an overall mean of 0.03.

Measures of sapling performance and distribution

In this study, I tested two responses that represent alternate aspects of sapling performance in the field, *abundance* and *survival.* Saplings are defined as stems at least 1.3m tall and between 1-10cm dbh. The two response variables have been calculated from the Paracou sapling regeneration inventory dataset described in Chapter 2 and explored in detail in Chapter 4. The regeneration inventory focuses on saplings (≥ 1.3m in height) of twenty-five co-occurring tree species common to

Paracou (Gourlet-Fleury et al. 2004). The inventory was carried out in a network of permanent forest plots that have been established and monitored for more than 20 years (Figure 4.1, Chapter 4). Within each of twelve 6.25ha square plots, sixty-four small circular subplots of 0.005ha (4m diameter, 50.2m^2) are located on a systematic grid (each regeneration plot is shown as a black dot in Figure 4.1). Inventories were carried out in 1992, 1993, 1995, 2002, 2005, 2008, 2013, and 2016. For this analysis, the dataset has been reduced to include only the eleven species mentioned above.

Abundance

To describe species distribution across the Paracou site I generated a response variable of the number of stems per species per 0.005ha plot. The data used were from the 2013 sapling regeneration census, which was the same year the light availability data were collected. Abundance data from a total of 797 saplings (range per species 7 – 152) from the 2013 census over all 768 plots were used in this analysis.

Survival

Census level sapling survival data were used to describe species performance across the site. Counts of the number of surviving and dead stems per 0.005ha plot, per census, per species of all saplings observed in at least two of eight inventories between 1992 and 2016 were included, for a total of 7577 observations of 1848 saplings. No stems of the focal species were observed in 190 out of 768 plots.

Data analyses

I used mixed modelling methods to test the hypothesis that the effect of tolerance of drought, waterlogging, and shade on species performance in the field depends on topographic designation and light availability. I tested three responses that represent alternate aspects of sapling performance in the field, *abundance*, *survival*, and *AGB RGR*. Each of the three models had the fixed covariates *topographic habitat* (categorical with 3 levels, *hilltops*, *slopes*, and *bottomlands*, with *slopes* set as the reference level), *plot light availability* (continuous between 0-1), and *drought, waterlogging, and shade tolerance* indices (continuous).

Independence of predictors (multicollinearity) was verified by calculating the variance inflation factor (VIF), which represents the proportion of variance in one predictor explained by the other predictors, for each predictor. In each model the VIF for all predictors did not exceed the cut-off point of two which suggests no multicollinearity among predictors (Zuur 2009). The predictors of drought and shade tolerance indices were shown to be negatively correlated in Chapter 3 (Figure 3.8) but both predictors had low VIF. This situation can occur when the individual predictors are not correlated with any other predictor in the model and/or when the correlation between predictors is not strong. Thresholds of correlation coefficients between predictors when collinearity begins to compromise model estimation are of $r^2 > 0.7$ (Dormann et al. 2013). In this case the negative correlation between drought and shade tolerance was $r^2 = 0.37$. Given that it was important to assess the effect of each predictor on the response after controlling for the other, I decided to maintain both predictors in the model and accept the low risk of inflated standard errors and high variance.

I fitted interaction terms between topography and tolerance terms as well as light availability and tolerance terms. Continuous covariates were standardised and centred before any data analysis to achieve a mean of zero and standard deviation of 1 to improve interpretation of coefficients (Schielzeth 2010).

Abundance model

The abundance model was fit using a generalised linear mixed model with Poisson distributed errors and a log-link function, which ensured positive predicted values. Each plot was sampled multiple times, each time obtaining one abundance count for each species, and therefore included a random term to account for dependency among observations within plots. I also included random intercepts for species to account for potential correlated errors due to species identity. Final model fit was assessed by checking the difference between model deviance and residual degrees of freedom which indicated no problems (model deviance = 4666, residual df = 8433).

Binomial survival model

The binomial survival model was fit using a generalised mixed model with a binomial error structure and weighted by sample size using a two-vector response variable (Crawley 2007). I used the same random effects structure as the abundance model. Final model fit was assessed by checking the difference between model deviance and residual degrees of freedom which indicated a good fit (model deviance = 5098.3, residual df = 5089).

For each model I followed a model simplification procedure which sequentially removed the least significant interaction terms and re-ran models until all remaining interaction terms were significant, as adjudicated by parametric bootstrapping methods, and kept all fixed effects (Crawley 2007). The final model was refit using restricted maximum likelihood estimation (Zuur 2009). Model assumptions were verified by plotting residuals vs fitted values, vs each covariate in the model, and assessing residuals for spatial dependency by plotting residuals against the physical location of each plot and visually inspecting for signs of clumping.

To visualise model results I predicted abundance and survival probability across the range observed in our tolerance indices for each of the three topographic categories. Model predictions are provided with confidence intervals for fixed effects only, as there is no simple way to extract uncertainty when models contain random effects as the random levels observed are not generalisable.

All data analyses and graphics were produced in the software R (R Core Team, 2014). Generalised abundance and binomial survival models were carried out using the glmer() function in the R package lme4 version 1.1-21 (Bates et al. 2007).

5.4 Results

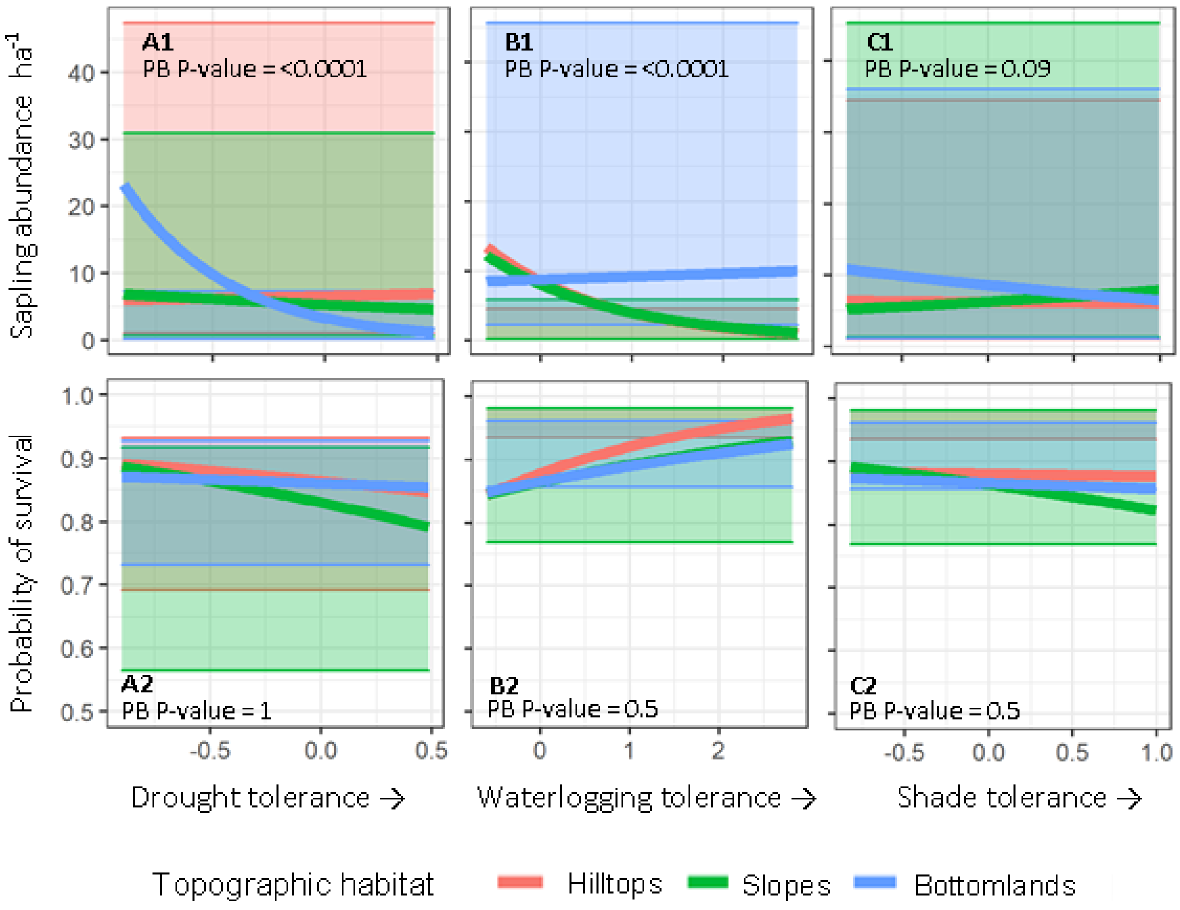

Figure 0.1. Modelled predictions of the interaction between increasing drought tolerance (panels A1 and A2) and waterlogging tolerance (panels B1 and B2), and shade tolerance (panels C1 and C2) with sapling location in three topographic habitats known to vary in water availability on two different response variables - sapling abundance (panels A1, B1, C1) and survival (panels A2, B2, C2). The predictions span the range of tolerance values observed in the focal study species. Parametric bootstrapped p-values are provided for each modelled outcome. Confidence intervals are provided for fixed effects only for estimates in each habitat at the maximum tolerance value.

Drought tolerance index

Abundance

Increasing drought tolerance was related to lower abundance for sapling individuals located in the wet bottomland habitat (estimate = -1.02 log units, parametric bootstrap p-value associated with the interaction between habitat and drought tolerance (PB p = <0.0001) (Figure 5.1, panel A1 & Table 5.1), however very wide confidence intervals, related to low sample sizes, mean these results need to be interpreted with caution. The difference in estimated levels of abundance between species with the lowest and highest drought tolerance when located in the bottomlands was a decrease of just over 20 individuals ha^{-1}. The overall mean species abundance was 16 individuals ha^{-1}, and the median abundance was zero individuals ha^{-1}.

Across the range of observed drought tolerance values the estimated abundance of saplings located in both the hilltops and slopes did not vary, with abundance estimates ranging between 5-7 individuals ha^{-1} in each class across the range (Figure 5.1, panel A1).

Survival

The results strongly suggest that drought tolerance was not related to the observed sapling survival patterns in the three topographic habitats (parametric bootstrap p-value associated with the interaction between habitat and drought tolerance (PB p = 1) (Panel A2, Figure 5.1, Table 5.2). The model predicted that increasing drought tolerance was related to lower survival estimates in all habitats, with the biggest reduction in survival probability for saplings located in the slopes (estimate = -0.13 ± 0.15 log odds per census). However, with the data available it was not possible to be confident about these relationships.

Waterlogging tolerance index

Abundance

Across the range of observed waterlogging tolerance values the model estimated the abundance of saplings located in the dry hilltop and slope habitats respond similarly with a decrease in abundance of between 12-13 individuals ha^{-1} for species with the highest waterlogging tolerance compared to species with the lowest waterlogging tolerance (PB p = <0.0001) (Panel B1, Figure 5.1, Table 5.1). However, as with the results for the drought tolerance index, very wide confidence intervals mean that these results need to be interpreted with caution.

For saplings located in the wet bottomlands increasing waterlogging tolerance was not related to changes in abundance (Panel B1, Figure 5.1). However as a result of the estimated decrease in abundance of saplings located in hilltops and slopes, highly waterlogging tolerant species in wet bottomlands were estimated to have abundances of 10 individuals ha^{-1} compared to 1 individual ha^{-1} in drier hilltops and slopes.

Survival

The results for the effect of increasing waterlogging tolerance on sapling survival were highly non-significant, which means that with the data available it is not possible to be confident about these relationships. However, model results suggest that increasing waterlogging tolerance may be related to higher survival estimates in the drier hilltop habitat (estimate = 0.39 log odds per census), and to higher survival in the wetter bottomland habitat (estimate = 0.18 log odds per census, parametric bootstrap p-value associated with the interaction between habitat and waterlogging tolerance (PB p = <0.0001) (Panel B2, Figure 5.1, Table 5.2).

Shade tolerance index

Abundance

The results for the effect of the shade tolerance index were not statistically significant, therefore any interpretation of the estimated relationships should be done with extreme caution. However, increasing shade tolerance had no effect on abundance in the drier hilltop habitat (estimate = -0.02 log units), but results suggest there may be a negative relationship with lower abundance in the wetter bottomland habitat and a positive relationship with higher abundance in slope habitats (parametric bootstrap p-value associated with the interaction between habitat and shade tolerance (PB p) = 0.09) (Panel C1, Figure 5.1, Table 5.1). Modelled estimates suggest an increase in abundance of 3 individuals ha^{-1} for the most shade tolerant species when located in the slopes and a decrease of 5 individuals ha^{-1} for the most shade tolerant species when located in the bottomlands.

Survival

The results for the effect of increasing shade tolerance on sapling survival were highly non-significant, which means that with the data available it is not possible to be confident about these relationships. However, model results suggest that increasing shade tolerance does not have an effect on survival estimates in the drier hilltop habitat or wetter bottomland habitat, but may be associated with a reduction in survival in the slopes (parametric bootstrap p-value associated with the interaction between habitat and shade tolerance (PB p) = 0.5) (Panel C2, Figure 5.1, Table 5.2).

Light transmission

Abundance

Modelled interactions between light transmission and location in the three topographic habitats were not significant in either the abundance or survival model and were therefore removed from the models to allow greater precision in estimates for the remaining predictors. The only significant interaction effect was found for drought tolerance and light transmission where there was an estimated 18% increase in the odds of survival for the most drought tolerant species (Table 5.2).

The individual effect of increasing light transmission was not significant therefore it is not possible to be confident in the model estimate, however the results suggest that there may be a very small positive relationship with abundance (estimate = 0.07 log units, parametric bootstrap p value (PB p = 0.13), equivalent to an approximate difference in abundance between the lowest and highest light transmission of 1 individual stem ha^{-1}.

Survival

Model results suggest that the interaction between increasing drought tolerance and plot light transmission may be related to an increase in sapling survival (estimate = 0.17 log odds per census, parametric bootstrap p-value associated with the interaction between habitat and shade tolerance (PB p) = 0.08) (Table 5.2). Results of interactions between waterlogging and shade tolerance were highly non-significant and were therefore removed from the model to aid more precise estimates for the remaining parameters.

Table 0.1. Abundance model estimated regression parameters in log units, standard errors, z-values, and Parametric Bootstrapped P-values. Results of a Poisson GLMM which tested for evidence of an interactive effect between experimentally assessed tolerance indices and abundance in different habitats. Abundance is based on stems counted during the 2013 regeneration census in each of the 0.005 ha plots (n plots 768).

Model predictor	**Estimate**	**SE**	**z value**	**PB P-value**
(Intercept)	-3.35	0.29	-11.76	—
Drought tolerance	-0.37	0.43	-0.84	—
Waterlogging tolerance	-0.52	0.32	-1.60	—
Shade tolerance	-0.02	0.37	-0.04	—
Hilltops	-0.12	0.08	2.97	—
Bottomlands	0.25	0.08	1.53	—
Plot light transmission	0.07	0.05	1.53	0.15
Drought tolerance * Hilltops	0.42	0.12	3.92	
Drought tolerance * Bottomlands	-0.65	0.1	-6.33	<0.0001
Waterlogging tolerance * Hilltops	-0.32	0.11	-3.02	
Waterlogging tolerance * Bottomlands	0.57	0.08	7.20	<0.0001
Shade tolerance * Hilltops	-0.002	0.08	-0.03	
Shade tolerance * Bottomlands	-0.13	0.07	-1.93	0.09
Std. dev. Individual plot	0.92			
Std. dev. Species	0.89			

Table 0.2. Survival model estimated regression parameters of the log odds of survival, standard errors, z-values, and Parametric Bootstrapped P-values. Results of a binomial GLMM which tested for evidence of an interactive effect between experimentally assessed tolerance indices and observed survival in the field. Individual stem survival was modelled as the number of stems that lived and died per census interval, aggregated at the species level.

Model predictor	**Estimate**	**SE**	**z value**	**PB P-value**
Intercept	1.91	0.1	18.72	—
Drought tolerance	-0.13	0.15	-0.83	—
Waterlogging tolerance	0.26	0.11	2.42	—
Shade tolerance	-0.08	0.14	-0.56	—
Hilltops	0.08	0.06	1.46	—
Bottomlands	-0.04	0.06	-0.66	—
Plot light transmission	0.09	0.04	2.16	—
Drought tolerance * Hilltops	0.007	0.13	0.06	
Drought tolerance * Bottomlands	0.08	0.16	0.73	1
Waterlogging tolerance * Hilltops	0.13	0.12	1.02	
Waterlogging tolerance * Bottomlands	-0.08	0.09	-0.85	0.5
Shade tolerance * Hilltops	0.06	0.1	0.587	
Shade tolerance * Bottomlands	0.04	0.09	0.4	0.5
Drought tolerance * Plot light transmission	0.08	0.05	1.64	0.08
Std. dev. Individual plot	0.28			
Std. dev. Species	0.28			

5.5 Discussion

The results of this study revealed evidence that sapling abundance but not survival in the topographic habitats of Paracou defined by variation in water availability depend on tolerance of drought, and waterlogging, but not shade. Drought tolerance displayed a negative relationship with sapling abundance in the wet bottomlands, but no relationship with abundance in the drier hilltop or slope habitat. Whereas waterlogging tolerance had a negative relationship with abundance in both the hilltop and slopes and no relationship with abundance in the bottomlands. These results support the idea that differences in tolerance of water availability among species contributes to the sorting of species along gradients of water availability (Baraloto et al. 2007, Born et al. 2015, Fortunel et al. 2016), and more specifically that both drought and waterlogging are important factors generating species turnover between wetter and drier habitats.

Drought tolerance and abundance in topographic habitats

Given that drought tolerant species are more likely to perform better than less drought tolerant species in drier habitats (Engelbrecht et al. 2007), it was expected that drought tolerant species would be present in greater abundance in hilltops compared to bottomlands. This has been demonstrated previously, for example in Panama it was found that seedling drought sensitivity correlated with performance, but only during the dry season in dry hilltop habitats and no correlation was found for drought sensitivity and seedling performance in wetter habitats (Comita and Engelbrecht 2009).

The results of this study did not corroborate this expectation; instead I found evidence that drought tolerance was negatively associated with abundance for saplings located in the wet bottomlands. This suggests a role for drought tolerance to explain differences in abundance in wet habitats where perhaps it is easier to perform well in wetter conditions for species without specific adaptations for enhanced performance under drought conditions. However this interpretation contrasts with the shadehouse results from Chapter 3, where some species performance in drought and waterlogged conditions showed some evidence of co-tolerance (Figure 3.8). Moreover, functional strategies to cope with drought and waterlogging are potentially complimentary (Parolin et al. 2010).

Previous work on the causes of differential distributions across wet and dry forested habitats suggested that slower growth rates of dry-distribution species, possibly due to trade-offs associated with greater drought tolerance, may exclude these species from wetter forests where faster growing wet-distribution species have a competitive advantage (Brenes-Arguedas et al. 2011). Indeed drought tolerance is associated with conservative life history strategies and slower growth rates, and conversely drought sensitivity is associated with acquisitive, fast-growing species (Ouédraogo et al. 2013). However seasonal flooding in tropical forests is known to cause many tree species to reduce their photosynthetic activity and growth, whereas high photosynthetic activity and fast growth is linked to more favourable non-flooded periods (Parolin et al. 1998).

The negative relationship between drought tolerance and abundance in the wettest habitat found in this study supports the assertion that more drought tolerant species may be excluded from wetter habitats. However it was not possible to judge whether this relationship was caused by differences in growth rates between drought tolerant and intolerant species. It would be expected that species with contrasting acquisitive and conservative growth strategies would respond differently to available light levels (Sterck et al. 2011) but I did not find any evidence for increasing light transmission interacting with drought tolerance or location in different habitats related to abundance. A model that included growth rates of individual saplings was attempted in this study but suffered from a lack of data and non-convergence issues. Further investigations would benefit from analysing larger datasets in order to investigate whether differences in growth rates contributed to the observed relationship.

Against expectations, drought tolerance was not related to abundance in the hilltops, as estimates were similar across the range of observed drought tolerance values. Results from the shadehouse study in Chapter 3 showed that although seedlings displayed differences in survival related to drought, the range of drought tolerance values was small when compared to the range in tolerance of waterlogging and shade (Figure 3.7). This may suggest that overall, water limitation in the hilltops of Paracou was not strong enough to impose a performance difference between drought intolerant and tolerant species that would lead to differences in abundance. Alternatively, these results could be obtained if drought intolerant species were able to continually replace individuals that were less able to reproduce, grow and survive well in the drier conditions of the hilltops.

Waterlogging tolerance and abundance in topographic habitats

Species with greater waterlogging tolerance were estimated to be relatively restricted to the bottomlands with only very few individuals estimated to be located in the slopes or hilltops (panel B1, Figure 5.1), consistent with expectations that waterlogging tolerant species are more likely to perform better than less waterlogging tolerant species in wetter habitats (Battaglia and Sharitz 2006). Whereas waterlogging intolerant species were estimated to have similar abundance in all three habitats. This suggests that for the most waterlogging tolerant species it may be difficult to consistently regenerate, grow, and survive well in drier habitats.

Previous work on distributional responses of floodplain tree species in Amazonia have reported that many species are generalists that occur across a range of soil water and soil conditions including tolerating drought (Parolin et al. 2010, Assis et al. 2015, Kurzatkowski et al. 2015). In the shadehouse study in Chapter 3, *S. globulifera* and *S. multiovula* were the two most waterlogging tolerant species and *S. multiovula* was the most drought tolerant while *S. globulifera* was in the middle of the range for drought tolerance (Figure 3.7). These results point towards agreement with the assertion that many flooding tolerant species may be able to tolerate drier conditions as well, however it does not explain the very low abundance estimates in the hilltops and slopes related to waterlogging tolerance. Three of the four most waterlogging tolerant species in this study also had the lowest density of stems per hectare at Paracou (*S. multiovula*, *S. globulifera*, and *V. surinamensis*) which further increases the uncertainty around these results (Table 4.1, Chapter 4). Further work that incorporates seedlings and/or adult trees at Paracou could increase the sample size and therefore reduce uncertainty and provide more information on what prevents these waterlogging tolerant species from being more abundant in drier habitats.

Shade tolerance and abundance in topographic habitats

Given that wetter forests can be associated with greater leaf production, lack of deciduousness and increased cloudiness and therefore less understory light availability (Smith and Huston 1989, Santiago et al. 2004, Niinemets and Valladares 2006, Brenes-Arguedas et al. 2011, Amissah et al. 2015), I expected that shade tolerance would be associated with higher abundance in the bottomlands and lower abundance in the hilltops and slopes. Against expectations, I found that increasing shade tolerance had very little effect on abundance in any of the three habitats (Panel C1, Figure 5.1). This result may indicate that for saplings in Paracou shade tolerance is a less important determinant of species differential distributions than drought and waterlogging tolerance, and points to agreement with a study in Panama that found light availability was less important than changes in water availability in influencing tree regeneration and distributions along tropical rainfall gradients (Gaviria and Engelbrecht 2015).

Despite the general agreement that wetter forests have lower light availability, a previous study at Paracou found that increased treefall rates along the gradient of hilltops to bottomlands was related to an increase in light availability as well as increased nutrient availability (Ferry et al. 2010). Overall, the evidence suggests a complex relationship between water availability and nutrients affecting forest structure and influencing light availability in the understory of Paracou which will take careful experimentation and analyses to untangle the relative importance of each in shaping species distributions in these habitats.

Tolerance indices and survival in topographic habitats

None of the tolerance indices were significantly related to the probability of survival in different habitats (Figure 5.1). This result may reflect the reality that tolerance of drought, waterlogging and shade had no effect on sapling survival, or alternatively may be because survival patterns in the different habitats were related to confounding factors such as differences in nutrient availability or pest pressure. In Chapter 4 sapling survival was significantly related to temporal trends in water availability, therefore further study of the relationship between tolerances and survival may benefit from incorporating temporal trends in drought and waterlogging. Utilising predictors more directly related to soil water availability would also reduce the problem of confounding variables related to differences between the three habitats.

Tolerance indices and survival along a light gradient

In the only significant effect of an interaction between the tolerance indices and light transmission, the effect of increasing drought tolerance and increasing light was related to an 18% increase in the chance of survival when the species was more drought tolerant (Table 5.3). This result may suggest that drought tolerant species are particularly positively affected by gap creation in forest understories. However the lack of evidence for a relationship with light transmission and any other model parameter as well the lack of relationship between shade tolerance and abundance and survival in different habitats make the interpretation of this result difficult.

Drier forests can be associated with greater light availability related to adaptations for water balance that favour small leaves and therefore lower leaf area index (Givnish 1988, Brenes-Arguedas et al. 2011), lower rainfall is associated with decreased cloudiness and therefore increased radiation (Wright and van Schaik

1994, Condit et al. 2004), and leaf abscission to conserve water during dry seasons may mean more light can penetrate the forest understory (Condit et al. 2000). However the understory of the hilltops of Paracou may be light limited as there is a higher density of stems ha^{-1}, higher basal area, higher average canopy height, and lower mortality compared to the bottomlands (Ferry et al. 2010).

In this study, there was very little variation in the available light at the measured height of between 1-5m from the forest floor in all 768 plots. Future work to disentangle the relationships between species resource tolerance, performance and light availability would benefit from calculating the available light at the appropriate height for individual trees. This was done for this study but because models with individual level light transmission (voxels extracted at crown height for each sapling) did not converge, a compromise in representativeness in light availability for all saplings was made. Incorporating temporal variation in light availability may also benefit further studies and has been achieved elsewhere using multi-temporal LiDAR data for assessing spatiotemporal patterns of understory light intensity and aspects of forest structure (Vepakomma et al. 2011, Peng et al. 2014, Calders et al. 2015, Réjou-Méchain et al. 2015, Wüest et al. 2020).

5.6 Conclusions

This study found some evidence to support the claim that species differential tolerance of resource availability can predict sapling abundance over environmental gradients. I tested the ability of tolerance of drought, waterlogging, and shade, three important aspects determining species distributions in tropical understories, to predict distributions over local landscape scales most relevant to forest managers in the tropics. Contrary to predictions that drought tolerance would influence sapling performance in drier conditions and waterlogging tolerance would influence sapling performance in wetter conditions, I instead found evidence that drought tolerance influences sapling abundance in the wet habitat and waterlogging tolerance influences sapling abundance in the drier hilltop and slope habitats. Shade tolerance did not affect abundance in any of the three habitats, suggesting that light plays a subordinate role to water availability in shaping sapling distributions in the understory of Paracou, French Guiana.

Studies based on species tolerance of limiting resources have been credited with improving the understanding of species distributions by providing mechanistic and predictive links between observed distributions and environmental conditions (Craine et al. 2012). In contrast to functional and phylogenetic ecology studies which may lack the ability to predict plant performance across different environments, studies of whole-plant tolerances directly link plant performance to variation in resource availability and therefore generate explanatory and predictive power regarding plant performance across environments (Craine et al. 2012, Paine et al. 2018). This study is a first step towards achieving this goal. Further studies would benefit from including direct measurements of temporal variation in field soil water availability, increased accuracy and temporal variation in understory light availability, as well as including measures of variation soil nutrient availability to tease apart the relative contribution of these often confounding variables.

6. Summary and Conclusions

In this thesis, I evaluated the relative roles of drought, waterlogging and light availability as drivers of differential species distributions across local scale habitats that varied in water and light availability, as well as other factors, in a seasonal wet tropical forest in French Guiana.

Despite the known importance of water and light in structuring communities, there is currently no consensus on the mechanism that drives species distributions between wet and dry habitats (Lopez and Kursar, 2003; Baraloto et al*.* 2007), or how this relationship is affected by light (Brenes-Arguedas et al. 2011). Answering these questions is particularly challenging as field gradients of drought, waterlogging, and light rarely occur independently from one another, and often co-vary with other abiotic and biotic factors. This confounding of variables, as well as uneven dispersal of plants across environmental gradients (Metz 2012), makes it challenging to attribute observed plant distributions to environmental variation (Dormann 2007).

I tackled investigating the relative roles of drought, waterlogging, and light availability in structuring the regenerative community of Paracou in three related lines of investigation. First, I experimentally assessed seedling survival across gradients of water and light availability to test theories of responses to combinations of multiple stresses and to test for evidence of trade-offs between tolerances of drought, waterlogging and shade. I then evaluated the roles of water and light in governing sapling survival in the field using indices of drought, waterlogging, and understory light availability. Finally, I tested the ability of experimentally derived species tolerance indices of drought, waterlogging and shade to predict observed species abundance and survival patterns over the contrasting wet and dry topographic habitats of Paracou. In this final section of my thesis, I will provide an overall summary of the results and limitations of the work presented herein.

Relationship between tolerance of drought, waterlogging, and shade in tropical seedlings

Currently the relationship between seedling tolerance of drought, waterlogging, and light availability is unclear. Acclimation or adaptation to any one stress is energetically costly and may lead to a reduced ability to survive in another, and tolerance to any one stress is typically reduced by the presence of other co-occurring stresses (Niinemets and Valladares 2006). Moreover, the combined effects of drought and light, and waterlogging and light on plant performance and the implications for species interactions are debated in tropical and temperate plant ecology (Battaglia and Sharitz, 2006; Holmgre*n* et al. 2012).

To address these knowledge gaps, I designed and implemented an experimental protocol that isolated the effects of drought, waterlogging, and light on seedling survival. I chose to undertake this investigation in the shadehouse as it was only under these conditions that I was able to easily obtain all factorial combinations necessary to fully evaluate the roles of water and light availability on plant survival. Moreover, it was necessary to isolate seedlings from sources of potential interaction such as competition, herbivores, disease, and variation in nutrient availability that could interact with the plant responses under investigation in order to assess the effects of water and light directly (Kraft et al. 2015, Cadotte and Tucker 2017).

As well as the benefits the pot experimental approach provides there are important caveats to consider when drawing inferences between the results of this study and seedling responses in the field. Seedlings in this study were grown alone in large pots in the absence of root competition and limiting nutrient availability, as well as safeguarded from large herbivores and many of the natural enemies found in the forest. Whereas seedlings growing in the forest suffer from intense competition, disease, natural enemies, and are often nutrient limited. A valuable follow-up study would be to repeat the experiment in the field to compare the isolated responses to water and light with responses to water and light under natural conditions.

I examined survival times of 1532 seedlings of eleven species using 20,000 individual observations. I used survival modelling techniques to investigate within and between species variation in survival time along an experimental irradiance gradient and in three contrasting water availability regimes, drought, waterlogged, and regularly watered. I carried out a multi-step data analysis whereby individual survival models were built for each species, then based on those models I predicted survival times in different treatments and assessed them for evidence of intraspecific trade-offs and interactions between water and light. I calculated tolerance indices based on survival time predictions, then assessed indices for evidence of interspecific trade-offs.

The first question I answered was, in the absence of root competition and when nutrient availability is not limiting, to what extent does species' survival in the shadehouse under drought, waterlogged and watered conditions vary over a gradient of light availability? A key assumption underpinning my expectations of seedling responses were that light and water availability would interact to impact survival responses depending on the levels of light and water availability. For example, I expected that survival responses under drought conditions may display facilitative, trade-off or non-linear responses along the light gradient which would be different under conditions of regular watering (Sack and Grubb 2002, Quero et al. 2006, Holmgren et al. 2012). Contrary to expectations, I found that most species did not experience an interactive effect of water and light. Instead, I found that most species responded either positively, negatively or non-linearly to light availability regardless of watering treatment. Moreover, I found evidence that many species can withstand waterlogged and very low-light conditions for long periods suggesting that the ability to undergo dormancy and allocating carbohydrate reserves to new shoots or adaptations to shade may be key to survival under these conditions (Lucas et al. 2013).

The second question I answered was, in the absence of root competition and when nutrient availability is not limiting, to what extent do experimentally assessed species' tolerance of drought, waterlogging, and light trade-off? Given that seedling survival strategies under combinations of drought, waterlogging, and light availability were likely to be influenced by trade-offs related to selection for particular biomass allocation patterns (Smith and Huston 1989, Sack 2004), I predicted that a species which exhibits greater tolerance of drought or waterlogging does so at the expense of lower tolerance of low-light. For example, species with greater tolerance of low-light may be particularly vulnerable to drought compared to light demanding species as a result of selection for allocation to stems and leaves rather than roots (Sack 2004). Whereas species may exhibit co-tolerance of both drought and waterlogging as functional trade-offs to both conditions may support survival in the presence of both conditions. For example, some of the same functional and anatomical characteristics that allow plants to cope with drought conditions also alleviate the stress of waterlogged conditions, such as increased root allocation (Parolin et al. 2010, Grubb 2016).

Correlative tests of species tolerance indices revealed a negative relationship between drought and shade tolerance, but no evidence of an association between waterlogging and shade tolerance, and some suggestion of an association between drought and waterlogging tolerance for some species. If these relationships held for seedlings in natural forest conditions, under scenarios of increasingly dry weather forests may undergo a turnover of species that would lead to more drought tolerant and fewer shade tolerant species (Fauset et al. 2012, Kupers et al. 2019). Whereas wetter forests may maintain more diverse assemblages of drought, waterlogging, and shade tolerant species.

The relationships between seedling survival in different water and light conditions explored in this study may have profound implications for species compositional changes in the contrasting wet and dry topographic habitats of Paracou. In particular two species, *J. copaia* and *S. multiovula* may be increasingly selected for if climate predictions of increased drought occurrence and solar radiation occur in Paracou as is predicted to occur more widely in tropical forest regions. Further, as these two species also had high tolerance of waterlogging conditions they may be expected to become increasingly dominant throughout Paracou's contrasting drier hilltop and floodplain bottomland topographic habitats.

Relative importance of drought, waterlogging, and light for sapling field survival

In tropical forests, variation in water availability between topographic habitats or soil-types is linked to local turnover in species composition (Wright 2002). However, despite the importance of local habitat scale drought (Comita and Engelbrecht 2009, Paine et al. 2009), and waterlogging (Baraloto et al. 2007, Lucas et al. 2013) in structuring tropical tree communities, we currently do not have a good understanding of the relative importance of each, or if the relative importance changes when we consider the interacting effect of light (Sánchez-Gómez et al. 2006, Gómez-Aparicio et al. 2008, Brenes-Arguedas et al. 2011).

In Paracou, three main topographic habitat classes have been delineated. The bottomlands are characterised by seasonal flooding, a water table that never drops below 1m during the dry season and high soil fertility, whereas slopes have medium to steep gradients with medium intensity waterlogging, and hilltops are flat to gently sloping with well-drained soil which can dry out during annual dry seasons (Ferry et al. 2010). Systematic inventories of the natural regeneration dynamics of saplings of twenty-five study species in Paracou have revealed contrasting abundances among these topographic habitats, and associations to a particular topographic habitat have been found for some of these species as adults *(*Baraloto et al. 2007; Vincent et al. 2011; Allie et al. 2015).

From observation alone, the relative importance of waterlogging and water limitation in determining the habitat association of each species cannot be unequivocally determined (Paine et al. 2018). For example, the observed differences in distributions may be because bottomland associated species are intolerant of the drier conditions in the hilltops, or because hilltop associated species are intolerant of the wetter conditions of the bottomlands. Moreover, the same species distribution patterns can occur as a result of both biotic and abiotic factors (Cadotte and Tucker 2017). In this chapter, I brought to bear lots of detailed information on the spatial and temporal effects of waterlogging and drought as well as light availability, to explore the relationship between sapling field survival and field measures of drought and waterlogging frequency, and light availability, and assessed if these relationships could help explain observed habitat associations.

Data were used from 5,374 individual saplings observed in at least two of eight inventories between 1992 and 2016, for a total of 26,140 individual observations. Species-specific binomial regressions were used to estimate parameters that described the relationships between sapling survival and indices of drought, waterlogging, and light availability. Separate models were built for each of the twenty-five species, which tested the hypotheses that sapling survival is related to drought frequency, waterlogging frequency, understory light availability, and topographic location.

I found that sapling survival was often lower in the wetter bottomlands compared to the drier slopes and hilltops which confirmed findings from a previous study at Paracou that found increased adult mortality in the bottomlands due to treefalls (Ferry et al. 2010). In contrast, I found that increased waterlogging frequency was associated with increased survival, which suggests that the negative effect of being located in the bottomlands may be independent of the frequency of waterlogging events as quantified by the waterlogging index. Enhanced survival related to waterlogging may be because saplings benefit from short and infrequent periods of waterlogging as they are protected from strong winds in the forest understory that may induce treefalls in adults, or may be due to periods of inundation increasing the amount of nutrients in the system. This result underlines one of the key limitations in this study; that variables of soil nutrient availability and other chemical changes associated with drought and waterlogging were not measured. Next steps to untangle the role of contrasting water availability in determining habitat distributions in this system would benefit from including measurements of these important aspects of habitat differentiation.

I also found that increased drought frequency commonly reduced survival, and the effect of increasing light was more variable than the effect of drought or waterlogging and did not depend on water availability. Taken together these results suggest that although waterlogging and light are important factors governing sapling survival, drought frequency and location in bottomland habitat were the more important contributors to the separation and sorting of species as they were most consistently associated with lower probabilities of survival.

I also considered if sapling survival related to water and light availability could help explain observed habitat associations. One hypothesis suggests that intolerance of waterlogged conditions by dry habitat associated species is a stronger constraint on tropical tree distributions than the limitations of drier habitat for species associated with waterlogged conditions (Lopez and Kursar, 2003; Baraloto et al*.* 2007). I examined the temporal effects of waterlogging and drought frequency, as well as interactions between these factors and sapling location on survival to look for evidence that refutes or aligns with this hypothesis. The results were mixed and did not point to an irrefutable role for either waterlogging or drought in driving habitat associations through differential survival.

Taken together these multiple lines of evidence suggest that drought was the relatively more important factor determining differential species survival, as well as a likely important role of long-term soil instability associated with topographical water availability over temporal waterlogging in determining differential species survival and therefore distributions among habitats. Difficulties associated with confounding variables reduced the ability of the data to provide robust answers to the question of what determines habitat associations, and further work would benefit from addressing these problems.

Tolerance of drought, waterlogging, and shade predict sapling performance in the field

Modelling approaches that incorporate species physiological tolerance of environmental gradients may improve the prediction and understanding of species distributions by providing explicit links between species performance and environmental conditions (Craine et al. 2012, Sterck et al. 2014, Paine et al. 2018). Models based on the relationship between species performance and environmental resources explicitly link vital rates to environmental conditions, and this relationship may be used to predict performance in other environments for which we have information about the availability of the resource. In this chapter, I took a first step along the road to achieving this goal by using the experimentally assessed species tolerance indices of drought, waterlogging, and shade, generated in Chapter 3 to predict observed sapling performance in contrasting wetter and drier habitats in Paracou.

In Chapter 4, I quantified the relative importance of drought, waterlogging, and light indices in determining survival of each species. However, I was unable to generate evidence to support the statement that the observed variation in species performance between bottomland and hilltop forests was because i) bottomland associated species were unable to tolerate the intensity of seasonal drought on the hilltops, or that ii) hilltop associated species may be intolerant of the flooding regime in the bottomlands.

One of the difficulties in attributing the observed sapling distributions to variation in water and light availability was the fact that gradients of drought, waterlogging, and light often covary with multiple other sources of abiotic and biotic variation. This confounding of variables makes it challenging to attribute observed plant distributions to particular aspects of environmental variation (Dormann 2007). To address this problem, I integrated the experimentally assessed drought, waterlogging, and shade tolerance indices generated in Chapter 3. If field performance did indeed depend upon species tolerance of drought, waterlogging or shade, I would expect to find statistical interactions between tolerance indices and the location of saplings in wetter and drier habitats.

I found evidence that sapling abundance but not survival in the topographic habitats of Paracou defined by variation in water availability depend on tolerance of drought, and waterlogging, but not shade. Contrary to predictions that drought tolerance would influence sapling performance in drier conditions and waterlogging tolerance would influence sapling performance in wetter conditions, I instead found evidence that drought tolerance influences sapling abundance in the wet bottomland habitat and waterlogging tolerance influences sapling abundance in the drier hilltop and slope habitats. Shade tolerance did not affect abundance in any of the three habitats, suggesting that light plays a subordinate role to water availability in shaping sapling distributions in the understory of Paracou. Overall, these results support the idea that differences in tolerance of water availability among species contributes to the sorting of species along gradients of water availability. More specifically, these results indicate that both drought and waterlogging are important factors generating species turnover between wetter and drier habitats in the lowland topical forest of Paracou, French Guiana.

In contrast to functional and phylogenetic ecology studies which may lack the ability to predict plant performance across different environments, studies of whole-plant tolerances directly link plant performance to variation in resource availability and therefore generate explanatory and predictive power regarding plant performance across environments (Craine et al. 2012, Paine et al. 2018). This study provided some evidence that experimentally assessed tolerance indices of drought and waterlogging can predict variation in sapling abundances in contrasting wet and dry habitats. Future studies to explore this idea further would benefit from quantifying tolerances of a greater number of carefully selected species with a wide range of distributional variation in wetter and drier habitats, as very low sample sizes for tolerance indices as well as sapling abundances in the field caused a large amount of uncertainty around the results presented in this chapter, Additionally, advances in overcoming spatial autocorrelation problems were not utilised in this chapter and any future work would need to consider this aspect more carefully. Further, tolerance indices were calculated for seedlings and then used to infer variation in performance among habitats at the sapling stage. Future studies would benefit from assessing this relationship using data from the same life stage if possible, as tolerance of environmental factors may change through ontogeny.

Implications for species distributions in a changing climate

Understanding ecological responses to rapid environmental change is an urgent necessity, and is especially important in tropical forests as these ecosystems are predicted to be among those most affected by fluctuating climate patterns (Sheldon 2019). In tropical regions, climate change scenarios forecast intensification of the seasons, where dry and wet seasons will become increasingly unstable in length and intensity (Neelin et al. 2006, Fu 2015). Therefore, future tropical tree distributions are likely to alter along lines delimiting wet and dry habitats and studies that explicitly consider how species sort along local hydrological gradients are of paramount importance.

The results presented in this thesis strongly suggest that both water limitation and waterlogging are important factors limiting species performance and therefore structuring communities along environmental gradients. Given these results, I can infer that, under a scenario of increasingly dry weather, the Paracou experimental forest may see a turnover in species composition that would lead to more drought tolerant and fewer waterlogging tolerant species in drier habitats such as hilltops, as fewer waterlogging tolerant species would be likely to survive the dry conditions.

Further, given that interspecific trade-offs appear to separate drought tolerant and shade tolerant species, drier forests may experience a turnover of species towards more drought tolerant and fewer shade tolerant species. In this thesis I have focussed on plant responses to locally contrasting soil-moisture availability. However, as plant responses at this scale are ultimately responsible for distributions at large as well as finer spatial scales (Silvertown et al. 2015), these results may be applicable more widely among neotropical and other tropical forests.

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8. Appendices

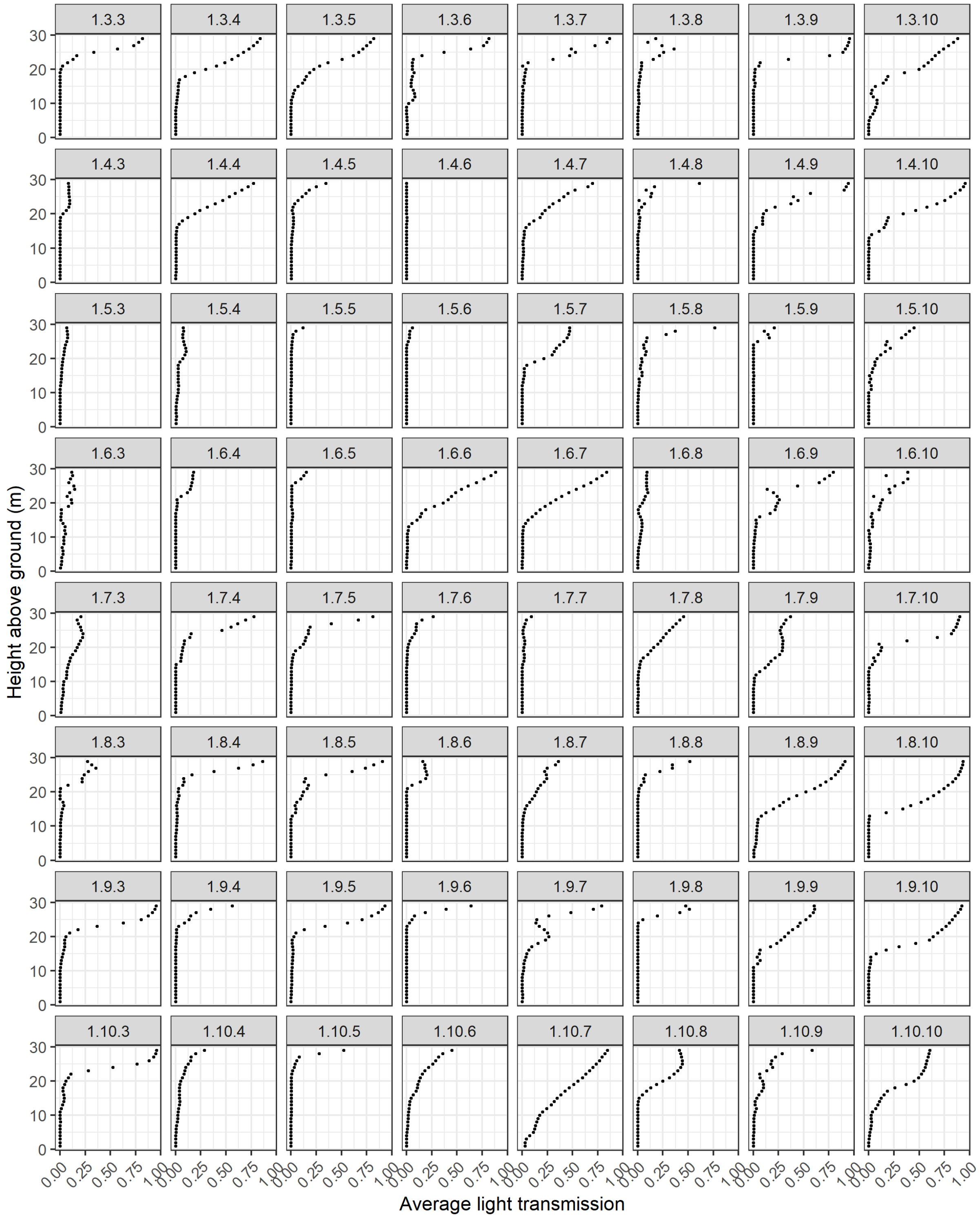
Appendix 1 – Table of results of survival models in Chapter 3

Results of mixed-effect parametric survival models which tested for evidence of the strength of light and watering treatment on the number of days before seedling mortality. The three watering treatments were – drought, waterlogging, and watered to field capacity, where watered to field capacity was the reference category against which drought and waterlogging treatments were compared. Light availability was a gradient ranging from 0.2 – 27% of full sunlight. Parameters were included that tested for a nonlinear effect of light availability, and interactive effect of watering treatment and light availability on seedling survival time. Model parsimony was achieved via sequential removal of terms starting with interactions and nonlinear terms adjudicated by Likelihood Ratio Tests. Each species was modelled separately. Intercept represents the estimated survival time in the watered to field capacity treatment when light availability was at zero. Coefficient estimates > 1 indicate an increase in survival time compared to the baseline survival, and estimates < 0 indicate a decrease in survival time compared to the baseline survival (survival in watered treatment).

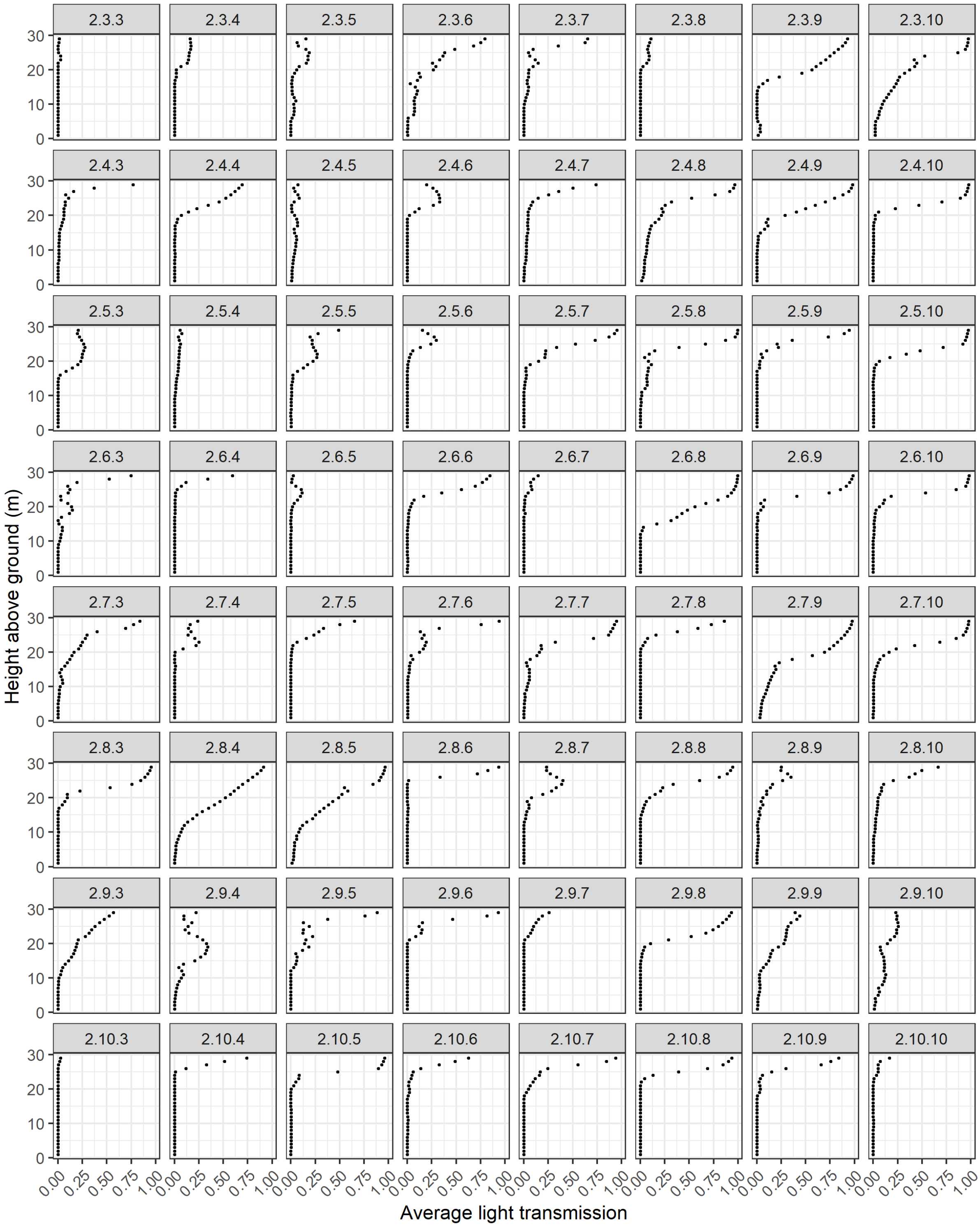
Species	Term	Estimate	std.error	z statistic	p.value
Tachigali melinonii	Intercept	981.49	1.632	14.072	<0.0001
	Drought	0.198	1.737	-2.935	0.003
	Waterlogged	1.913	2.001	0.936	0.35
	Light	1.03	1.023	1.303	0.193
Dicorynia guianensis	Intercept	666.74	1.258	28.319	<0.0001
	Drought	0.577	1.272	-2.283	0.022
	Waterlogged	0.834	1.282	-0.734	0.463
	Light	1.008	1.023	0.357	0.721
Pradosia cochlearia	Intercept	751.1	1.293	25.746	<0.0001
	Drought	0.913	1.22	-0.458	0.647
	Waterlogged	0.742	1.212	-1.553	0.12
	Light^2	0.996	1.002	-1.888	0.059
Sextonia rubra	Intercept	497.811	1.231	29.911	<0.0001
	Drought:Light	0.962	1.031	-1.285	0.199
	Waterlogged:Light	0.941	1.033	-1.856	0.063
Jacaranda copaia	Intercept	630.013	1.278	26.25	<0.0001
	Drought	0.973	1.201	-0.151	0.88
	Waterlogged	1.5	1.231	1.952	0.051
	Light^2	0.99	1.002	-4.696	<0.0001
Recordoxylon speciosum	Intercept	1269.547	1.389	21.757	<0.0001
	Drought:Light	0.94	1.04	-1.576	0.115
	Waterlogged:Light	0.919	1.046	-1.883	0.06
Sterculia multiovula	Intercept	1427.038	1.766	12.778	<0.0001

	Drought	0.899	1.576	-0.234	0.815
	Waterlogged	1.835	1.691	1.155	0.248
	Light	1.062	1.046	1.333	0.183
Sterculia pruriens	Intercept	4774.348	2.139	11.144	<0.0001
	Drought	0.339	1.516	-2.601	0.009
	Waterlogged	1.345	1.618	0.616	0.538
	Light	0.93	1.034	-2.19	0.029
Symphonia globulifera	Intercept	3451.256	2.112	10.897	<0.0001
	Drought	0.32	1.699	-2.15	0.032
	Waterlogged	3.454	1.998	1.791	0.073
	Light	1.017	1.048	0.359	0.72
Virola surinamensis	Intercept	6359.117	2.206	11.072	<0.0001
	Drought	0.185	1.607	-3.56	<0.0001
	Waterlogged	3.027	1.84	1.816	0.069
	Light	0.947	1.03	-1.82	0.069
Eperua falcata	Intercept	6204.522	2.419	9.886	<0.0001
	Drought	0.214	1.881	-2.438	0.015
	Waterlogged	2.312	2.115	1.119	0.263
	Light	0.906	1.054	-1.891	0.059

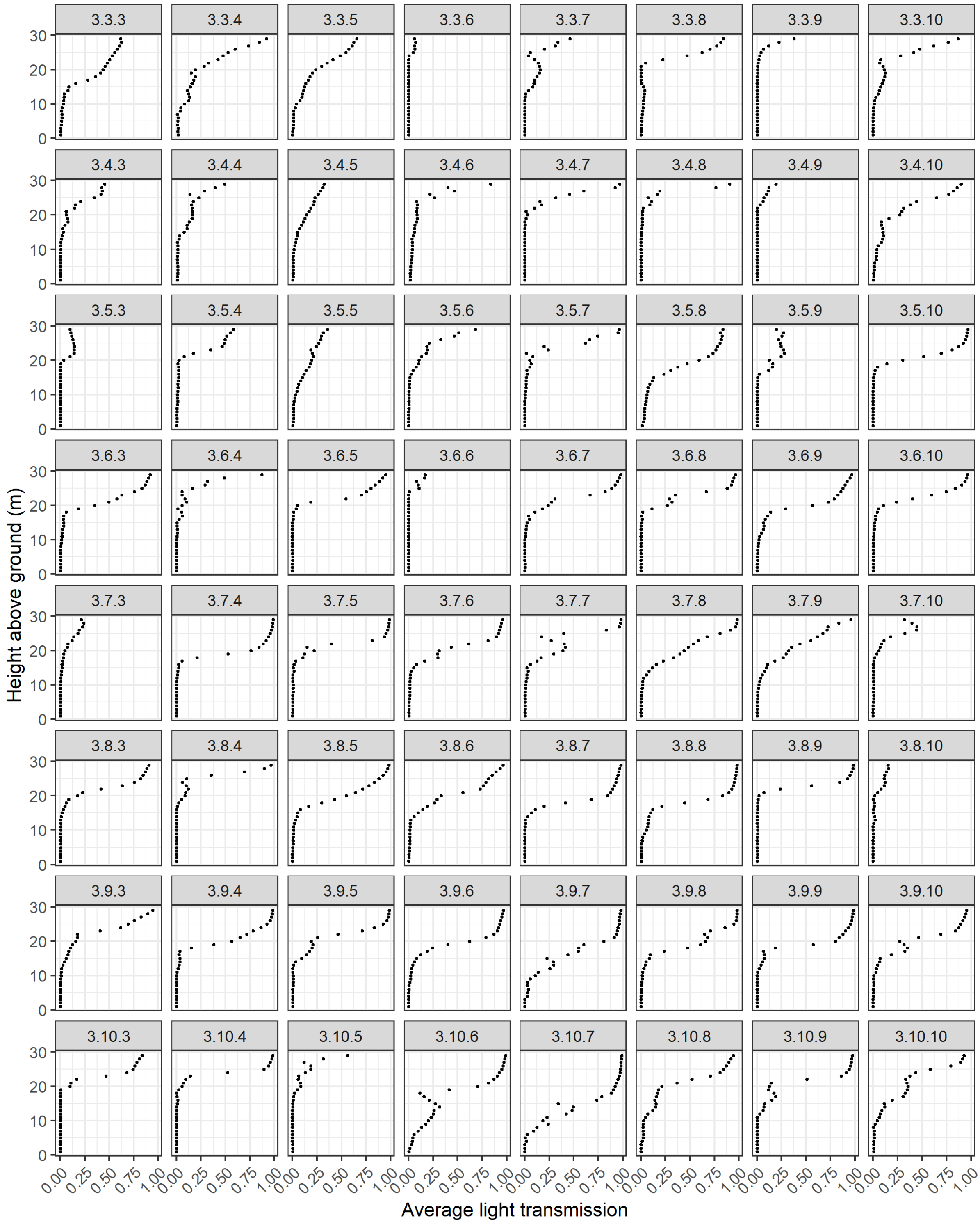
Appendix 2 – Average LIDAR generated light transmission values – Plots 1-12



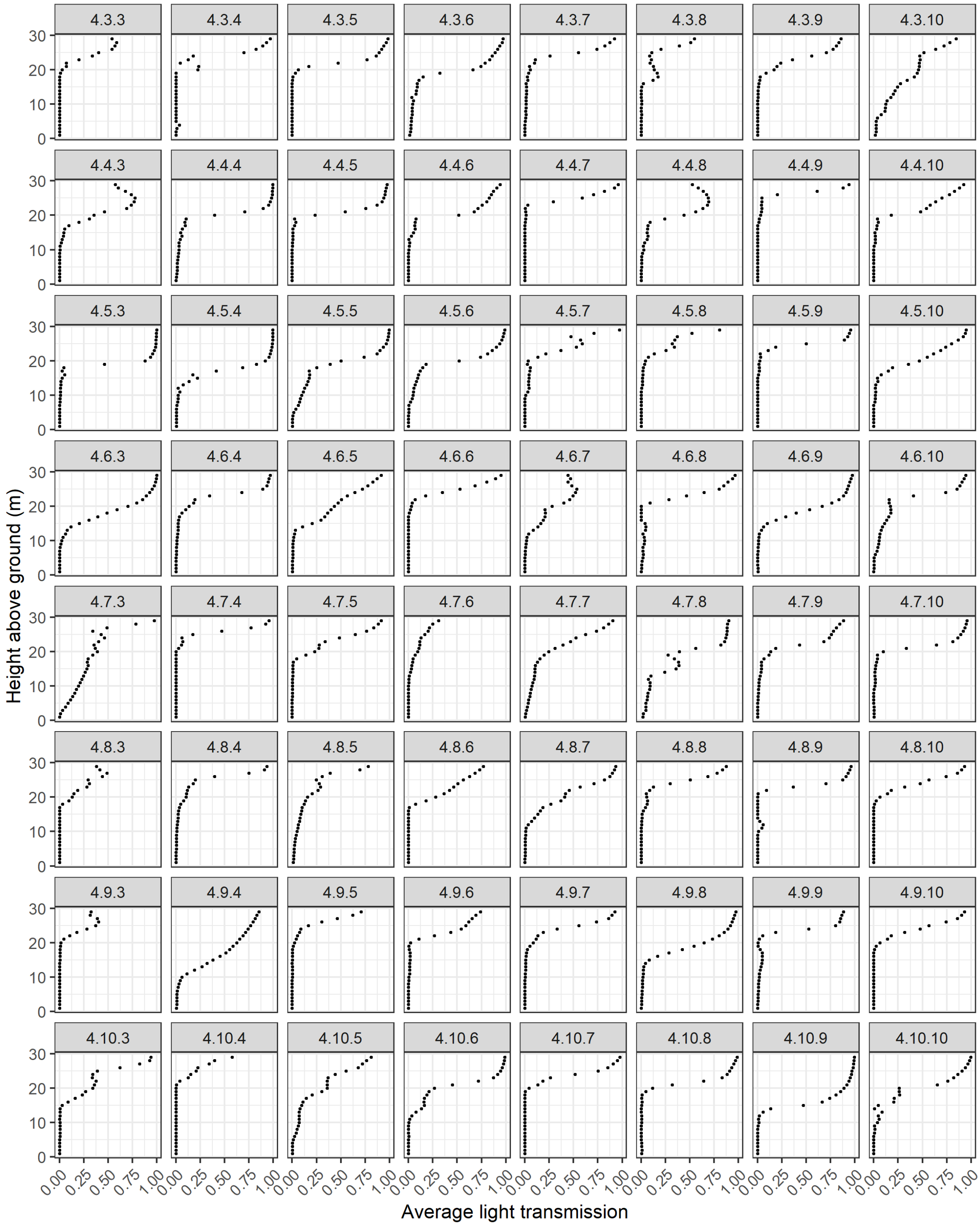
Plot 1 - Average LiDAR generated light transmission index values between 0-30m above ground in 1m steps, for all 64 regeneration plots nested within larger Plot 1 (See map in Figure 4.1).



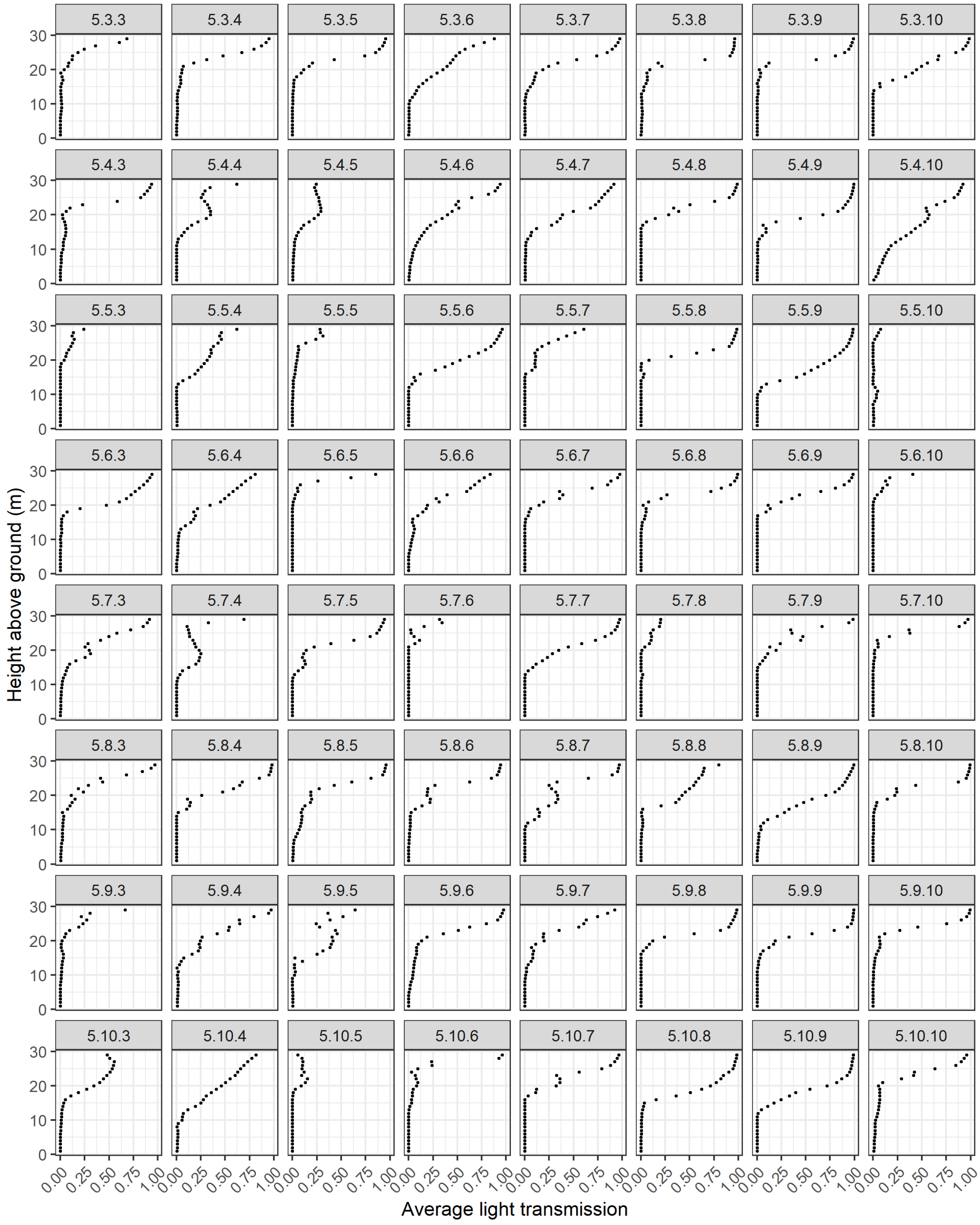
Plot 2 - Average LiDAR generated light transmission index values between 0-30m above ground in 1m steps, for all 64 regeneration plots nested within larger Plot 2 (See map in Figure 4.1).



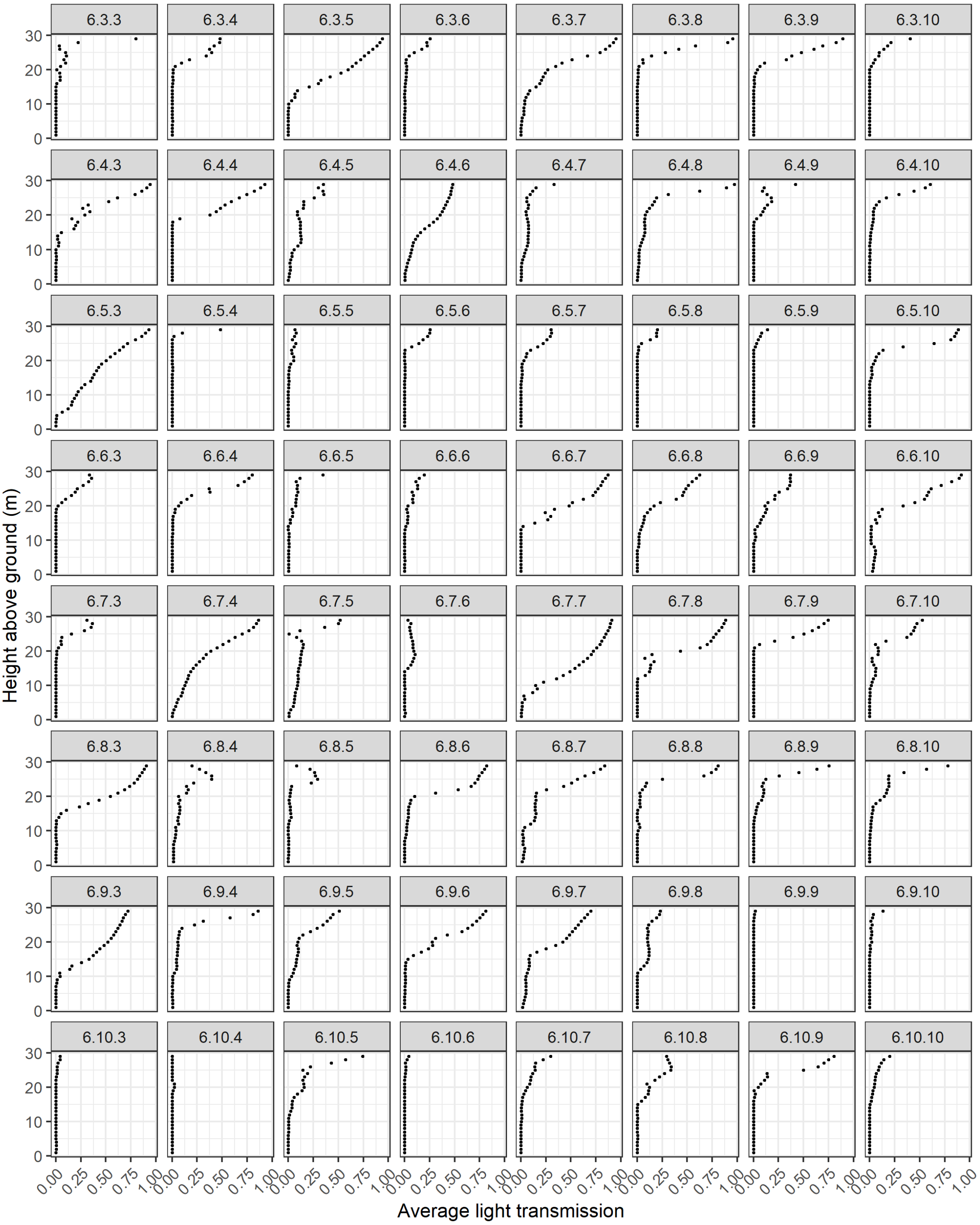
Plot 3 - Average LiDAR generated light transmission index values between 0-30m above ground in 1m steps, for all 64 regeneration plots nested within larger Plot 3 (See map in Figure 4.1).



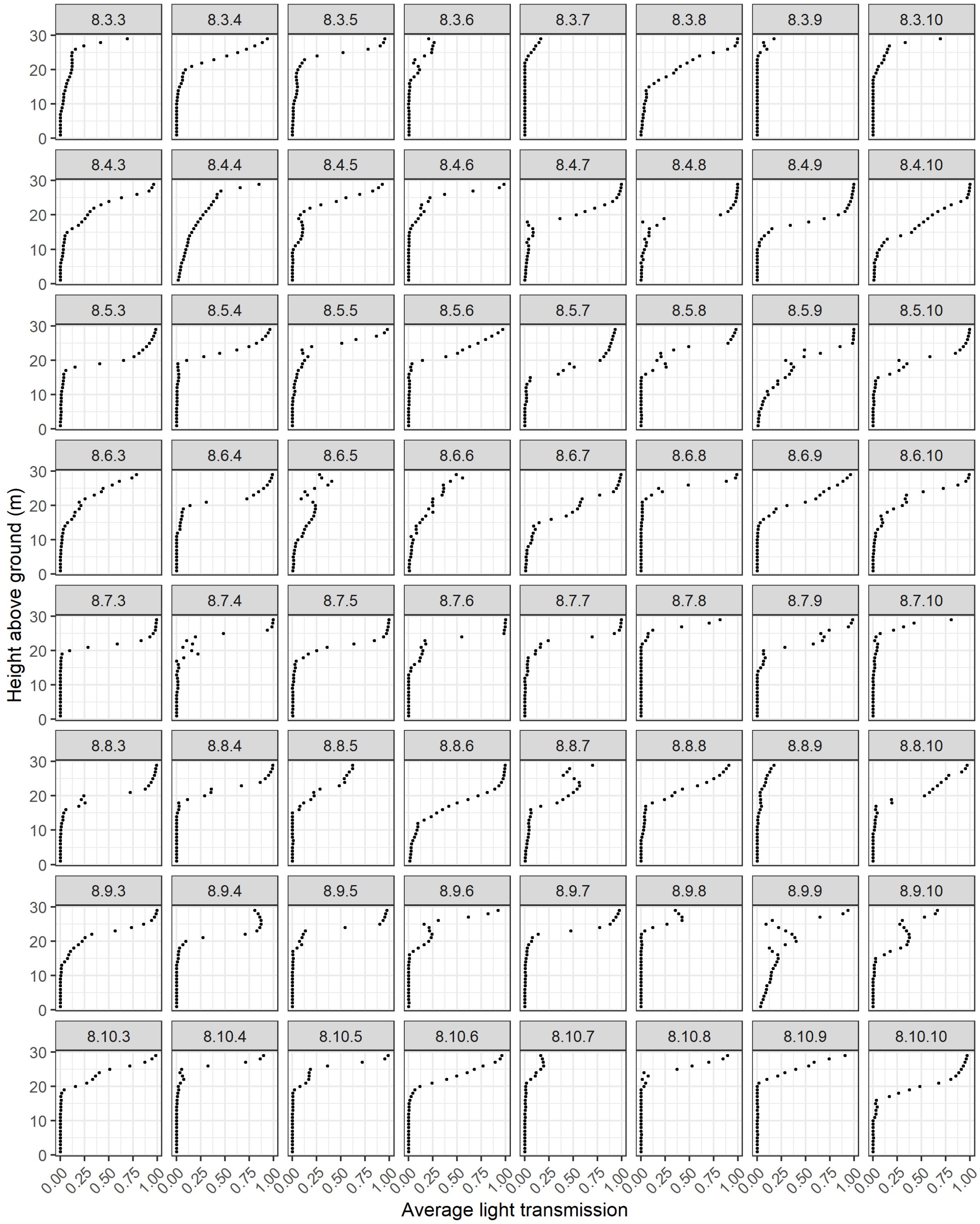
Plot 4 - Average LiDAR generated light transmission index values between 0-30m above ground in 1m steps, for all 64 regeneration plots nested within larger Plot 4 (See map in Figure 4.1).



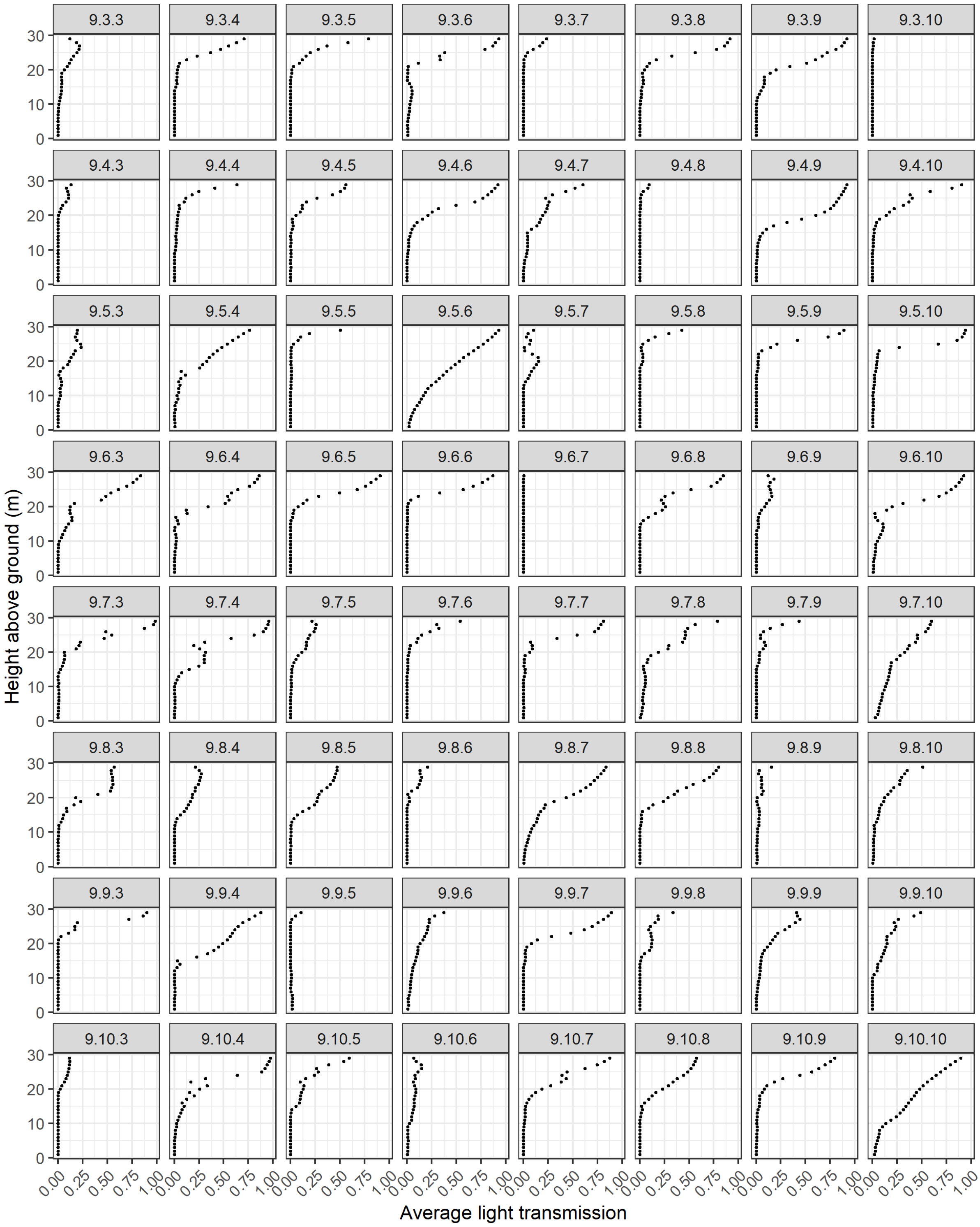
Plot 5 - Average LiDAR generated light transmission index values between 0-30m above ground in 1m steps, for all 64 regeneration plots nested within larger Plot 5 (See map in Figure 4.1).



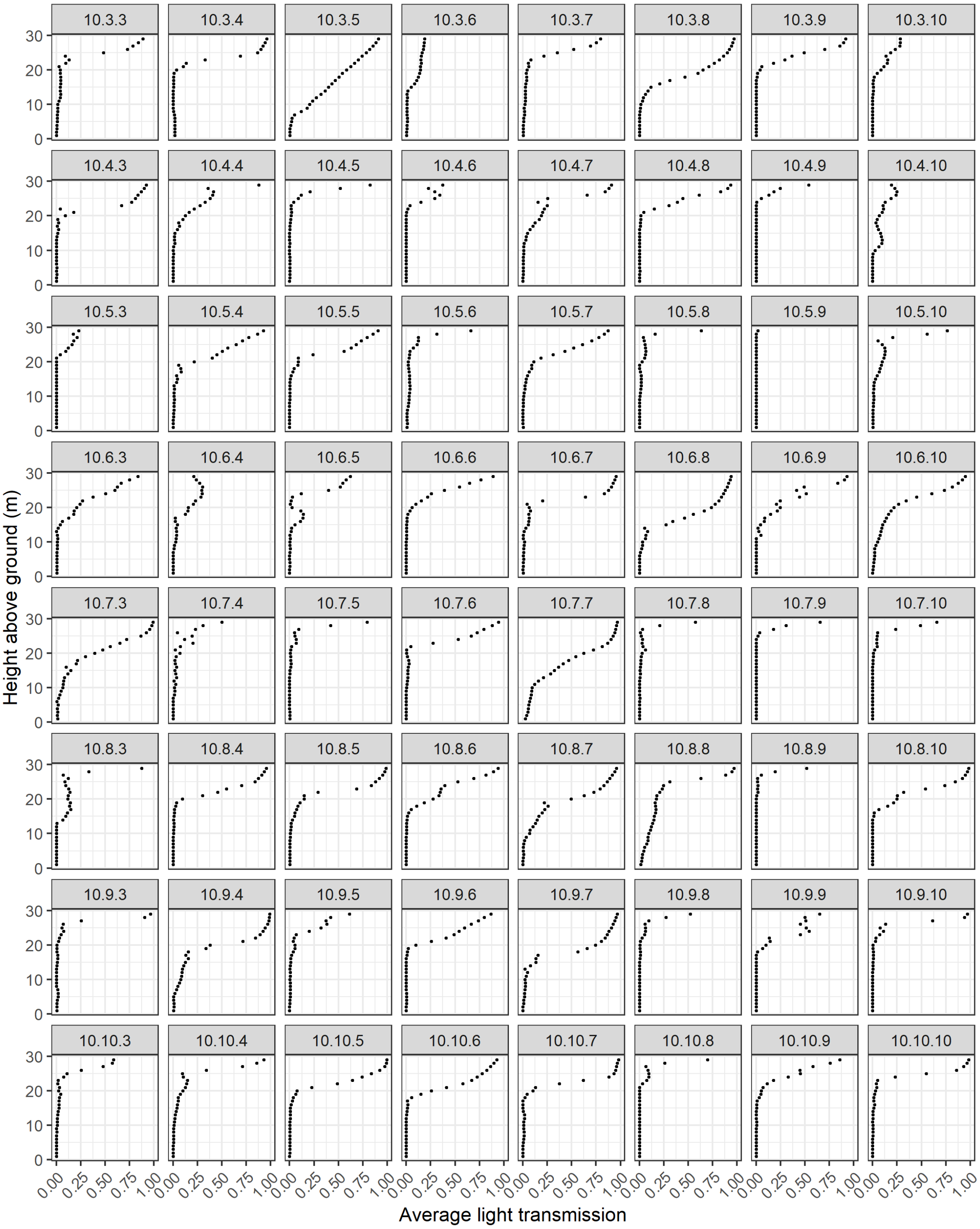
Plot 6 - Average LiDAR generated light transmission index values between 0-30m above ground in 1m steps, for all 64 regeneration plots nested within larger Plot 6 (See map in Figure 4.1).



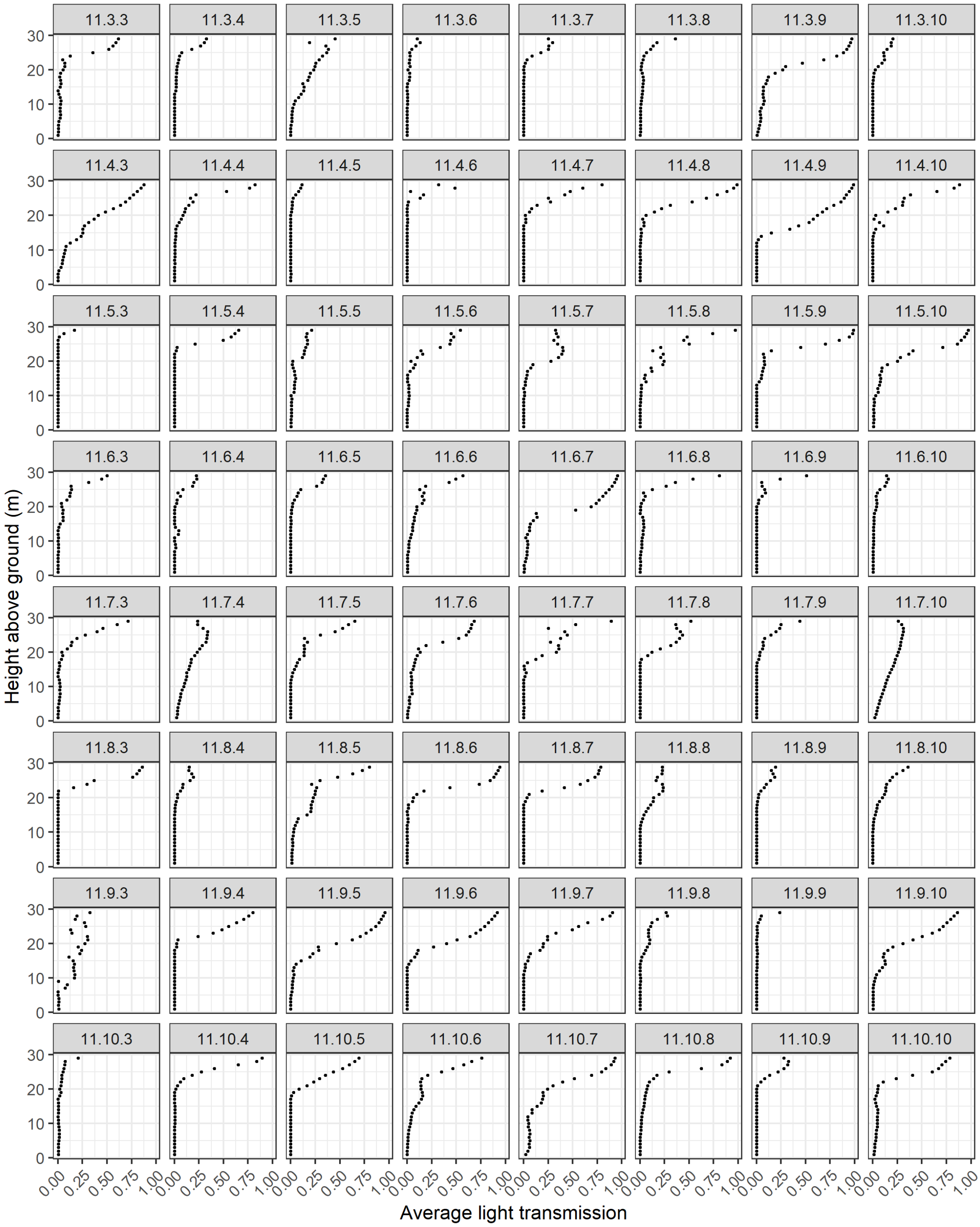
Plot 7 - Average LiDAR generated light transmission index values between 0-30m above ground in 1m steps, for all 64 regeneration plots nested within larger Plot 7 (See map in Figure 4.1).



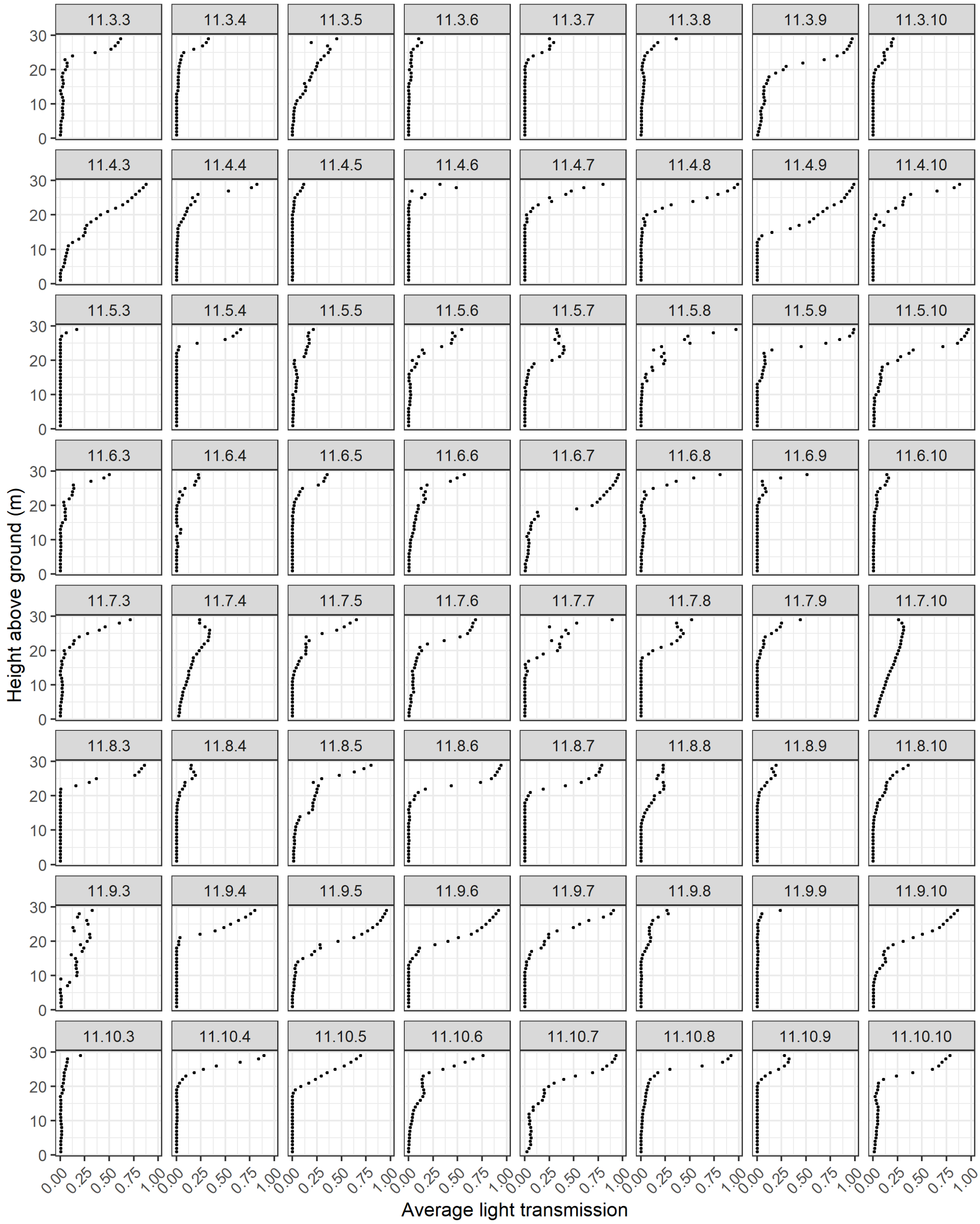
Plot 8 - Average LiDAR generated light transmission index values between 0-30m above ground in 1m steps, for all 64 regeneration plots nested within larger Plot 8 (See map in Figure 4.1).



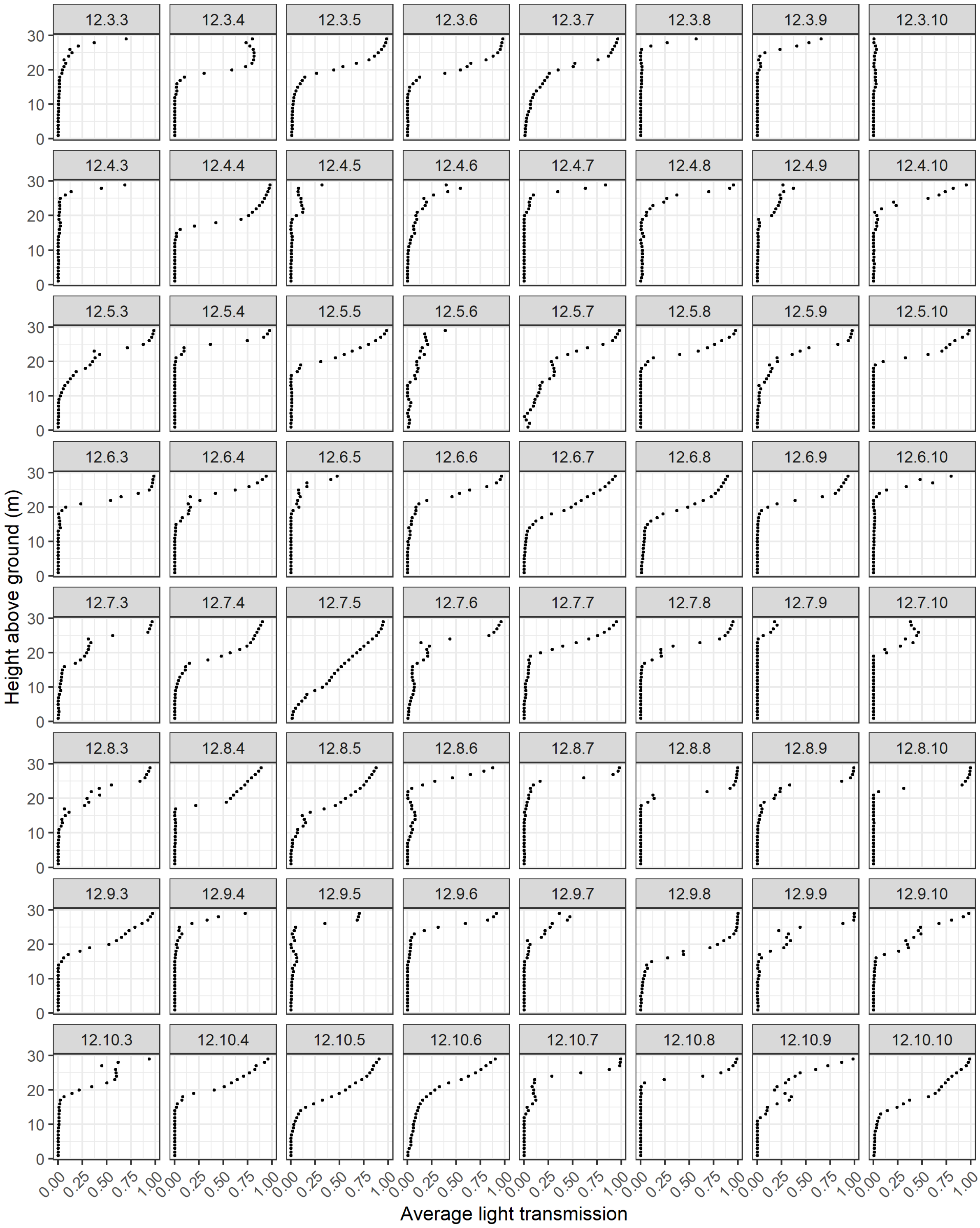
Plot 9 - Average LiDAR generated light transmission index values between 0-30m above ground in 1m steps, for all 64 regeneration plots nested within larger Plot 9 (See map in Figure 4.1).



Plot 10 - Average LiDAR generated light transmission index values between 0-30m above ground in 1m steps, for all 64 regeneration plots nested within larger Plot 10 (See map in Figure 4.1).



Plot 11 - Average LiDAR generated light transmission index values between 0-30m above ground in 1m steps, for all 64 regeneration plots nested within larger Plot 11 (See map in Figure 4.1).



Plot 12 - Average LiDAR generated light transmission index values between 0-30m above ground in 1m steps, for all 64 regeneration plots nested within larger Plot 12 (See map in Figure 4.1).

Appendix 3 – Table of results of logistic regression models – from Chapter 4

Results of mixed-effect logistic regression models which tested for evidence of the strength of light transmission, drought frequency, waterlogging frequency, and sapling location on the probability of survival. Parameters were included that tested for an interactive effect of drought and light, waterlogging and light, drought and sapling location, waterlogging and sapling location, and light and sapling location. Model parsimony was achieved via sequential removal of terms starting with interactions adjudicated by Likelihood Ratio Tests. Each species was modelled separately. Coefficient odds ratio estimates > 1 indicate an increase in the odds of survival compared to the baseline survival, and estimates < 0 indicate a decrease in the odds of survival compared to the baseline survival (survival in slope habitat).

Species	Term	Estimate	Std. Error	z statistic	P value
Virola michelii	Intercept	10.735	0.119	20.017	<0.001
	Waterlogging freq.	1.162	0.068	2.219	0.026
	Drought freq.	1.018	0.079	0.226	0.822
	Light	0.936	0.075	-0.885	0.376
	Hilltops	1.391	0.141	2.346	0.019
	Bottomlands	0.79	0.221	-1.069	0.285
	Hilltops*Drought freq.	0.806	0.104	-2.075	0.038
	Bottomlands*Drought freq.	1.558	0.13	3.407	0.001
Goupia glabra	Intercept	4.134	0.079	17.875	<0.001
	Waterlogging freq.	1.615	0.07	6.878	<0.001
	Drought freq.	1.155	0.079	1.813	0.07
	Light	1.006	0.064	0.087	0.931
	Hilltops	1	0.093	0	1
	Bottomlands	0.928	0.136	-0.547	0.584
Jacaranda copaia	Intercept	9.169	0.141	15.678	<0.001
	Waterlogging freq.	1.244	0.104	2.091	0.037
	Drought freq.	1.08	0.1	0.767	0.443
	Light	1.693	0.197	2.674	0.007
	Hilltops	1.219	0.17	1.167	0.243
	Bottomlands	1.038	0.238	0.155	0.877
Schefflera decaphylla	Intercept	7.187	0.192	10.285	<0.001
	Waterlogging freq.	1.198	0.143	1.264	0.206
	Drought freq.	0.736	0.11	-2.784	0.005
	Light	0.903	0.108	-0.949	0.343
	Hilltops	1.052	0.216	0.237	0.813
	Bottomlands	0.74	0.355	-0.848	0.397
	Waterlogging freq.*Hilltops	0.938	0.171	-0.371	0.71
	Waterlogging freq.*Bottomlands	0.707	0.247	-1.403	0.16
Tachigali	Intercept	5.781	0.115	15.2	<0.001

melinonii	Waterlogging freq.	1.497	0.09	4.501	<0.001
	Drought freq.	0.947	0.102	-0.539	0.59
	Light	1.343	0.171	1.722	0.085
	Hilltops	1.282	0.178	1.399	0.162
	Bottomlands	0.666	0.151	-2.694	0.007
	Drought freq.*Light	1.312	0.116	2.338	0.019
Sterculia pruriens	Intercept	5.473	0.089	19.088	<0.001
	Waterlogging freq.	1.57	0.079	5.699	<0.001
	Drought freq.	0.887	0.081	-1.48	0.139
	Light	1.109	0.107	0.963	0.335
	Hilltops	0.954	0.122	-0.383	0.701
	Bottomlands	0.853	0.134	-1.191	0.234
	Waterlogging freq.*Hilltops	0.868	0.116	-1.222	0.222
	Waterlogging freq.*Bottomlands	0.809	0.108	-1.975	0.048
	Drought freq.*Light	1.235	0.072	2.927	0.003
Carapa surinamensis	Intercept	7.975	0.207	10.029	<0.001
	Waterlogging freq.	1.353	0.166	1.82	0.069
	Drought freq.	0.778	0.177	-1.419	0.156
	Light	1.995	0.355	1.947	0.052
	Hilltops	1.353	0.27	1.118	0.263
	Bottomlands	0.653	0.258	-1.654	0.098
	Waterlogging freq.*Light	0.592	0.219	-2.39	0.017
	Drought freq.*Light	0.635	0.22	-2.057	0.04
Sterculia multiovula	Intercept	49.415	1.169	3.337	0.001
	Waterlogging freq.	0.309	1.03	-1.139	0.254
	Drought freq.	0.129	0.694	-2.951	0.003
	Light	9.653	2.062	1.1	0.271
	Hilltops	4.857	1.242	1.272	0.203
	Bottomlands	0.122	1.208	-1.744	0.081
	Waterlogging freq.*Hilltops	0.241	1.092	-1.305	0.192
	Waterlogging freq.*Bottomlands	2.824	0.965	1.075	0.282
	Waterlogging freq.*Light	0.024	2.5	-1.484	0.138
Qualea rosea	Intercept	9.014	0.088	24.944	<0.001
	Waterlogging freq.	1.364	0.069	4.512	<0.001
	Drought freq.	0.974	0.069	-0.382	0.703
	Light	1.023	0.079	0.294	0.769
	Hilltops	0.934	0.105	-0.651	0.515
	Bottomlands	1.046	0.152	0.294	0.769
Symphonia sp. 1	Intercept	12.313	0.082	30.566	<0.001
	Waterlogging freq.	1.204	0.077	2.392	0.017
	Drought freq.	1.081	0.082	0.948	0.343
	Light	0.932	0.082	-0.856	0.392
	Hilltops	1.222	0.123	1.625	0.104
	Bottomlands	0.745	0.142	-2.073	0.038

Iryanthera sagotiana	Intercept	14.954	0.093	29.203	<0.001
	Waterlogging freq.	1.067	0.079	0.819	0.413
	Drought freq.	0.837	0.084	-2.105	0.035
	Light	0.756	0.065	-4.286	<0.001
	Hilltops	1.589	0.131	3.521	<0.001
	Bottomlands	0.56	0.162	-3.576	<0.001
	Waterlogging freq.*Light	1.119	0.062	1.826	0.068
Eperua grandiflora	Intercept	9.519	0.12	18.772	<0.001
	Waterlogging freq.	1.068	0.102	0.649	0.516
	Drought freq.	0.971	0.109	-0.273	0.785
	Light	1.132	0.225	0.55	0.582
	Hilltops	1.52	0.159	2.635	0.008
	Bottomlands	0.638	0.234	-1.921	0.055
	Hilltops*Light	0.628	0.229	-2.024	0.043
	Bottomlands*Light	2.167	0.438	1.765	0.077
Bocoa prouacensis	Intercept	15.719	0.151	18.247	<0.001
	Waterlogging freq.	1.197	0.118	1.525	0.127
	Drought freq.	0.655	0.138	-3.07	0.002
	Light	0.855	0.09	-1.744	0.081
	Hilltops	1.222	0.196	1.021	0.307
	Bottomlands	0.555	0.253	-2.325	0.02
	Hilltops*Drought freq.	1.505	0.183	2.23	0.026
	Bottomlands*Drought freq.	0.899	0.225	-0.47	0.638
Pradosia cochlearia	Intercept	4.709	0.091	17.104	<0.001
	Waterlogging freq.	1.359	0.08	3.824	<0.001
	Drought freq.	0.885	0.082	-1.485	0.138
	Light	0.984	0.095	-0.173	0.862
	Hilltops	0.843	0.116	-1.472	0.141
	Bottomlands	0.899	0.159	-0.674	0.5
Moronobea coccinea	Intercept	6.015	0.138	12.957	<0.001
	Waterlogging freq.	0.983	0.118	-0.149	0.881
	Drought freq.	1.024	0.121	0.199	0.842
	Light	1.142	0.151	0.88	0.379
	Hilltops	1.266	0.181	1.303	0.192
	Bottomlands	0.683	0.258	-1.478	0.139
Dicorynia guianensis	Intercept	21.61	0.281	10.941	<0.001
	Waterlogging freq.	0.716	0.209	-1.597	0.11
	Drought freq.	1.045	0.187	0.233	0.815
	Light	2.442	0.441	2.023	0.043
	Hilltops	0.864	0.297	-0.492	0.623
	Bottomlands	1.084	0.424	0.19	0.849
	Waterlogging freq.*Hilltops	0.857	0.246	-0.624	0.533
	Waterlogging freq.*Bottomlands	0.601	0.292	-1.746	0.081
	Waterlogging freq.*Light	0.607	0.278	-1.796	0.073
Vouacapoua	Intercept	31.245	0.284	12.131	<0.001

americana	Waterlogging freq.	1.219	0.229	0.864	0.387
	Drought freq.	0.663	0.248	-1.658	0.097
	Light	1.219	0.36	0.551	0.581
	Hilltops	0.829	0.341	-0.549	0.583
	Bottomlands	0.681	0.469	-0.819	0.413
Recordoxylon speciosum	Intercept	7.793	0.166	12.348	<0.001
	Waterlogging freq.	1.203	0.171	1.08	0.28
	Drought freq.	1.136	0.168	0.758	0.449
	Light	1.316	0.239	1.147	0.251
	Hilltops	1.05	0.248	0.198	0.843
	Bottomlands	0.826	0.293	-0.652	0.514
Sextonia rubra	Intercept	5.313	0.288	5.806	<0.001
	Waterlogging freq.	1.861	0.242	2.565	0.01
	Drought freq.	0.717	0.181	-1.84	0.066
	Light	0.888	0.208	-0.572	0.568
	Hilltops	1.701	0.382	1.389	0.165
	Bottomlands	0.625	0.571	-0.824	0.41
	Waterlogging freq.*Hilltops	1.677	0.307	1.686	0.092
	Waterlogging freq.*Bottomlands	0.926	0.406	-0.188	0.851
Iryanthera hostmannii	Intercept	17.968	0.127	22.821	<0.001
	Waterlogging freq.	1.262	0.101	2.307	0.021
	Drought freq.	0.83	0.108	-1.733	0.083
	Light	1.373	0.169	1.877	0.06
	Hilltops	1.173	0.193	0.827	0.408
	Bottomlands	1	0.167	-0.003	0.998
Eperua falcata	Intercept	8.053	0.086	24.211	<0.001
	Waterlogging freq.	1.3	0.079	3.316	0.001
	Drought freq.	1.063	0.085	0.721	0.471
	Light	1.085	0.087	0.93	0.352
	Hilltops	1.363	0.147	2.113	0.035
	Bottomlands	0.778	0.135	-1.857	0.063
Symphonia globulifera	Intercept	54.531	0.697	5.735	<0.001
	Waterlogging freq.	0.771	0.369	-0.706	0.48
	Drought freq.	0.274	0.418	-3.099	0.002
	Light	0.702	0.153	-2.319	0.02
	Hilltops	0.817	0.792	-0.255	0.799
	Bottomlands	0.346	0.732	-1.449	0.147
Virola surinamensis	Intercept	7.219	0.231	8.569	<0.001
	Waterlogging freq.	1.317	0.211	1.307	0.191
	Drought freq.	0.684	0.224	-1.697	0.09
	Light	1.562	0.395	1.129	0.259
	Hilltops	0.836	0.298	-0.601	0.548
	Bottomlands	1.025	0.368	0.066	0.947