



**UNIVERSITY OF EDINBURGH**  
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**COMPETITION INTERACTIONS AMONG TREES  
IN A NEOTROPICAL CLOUD FOREST:  
IMPLICATIONS FOR CLIMATE-DRIVEN RANGE  
SHIFTS**

*BY*

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## **Summary**

Tropical tree species are shifting their ranges upslope in response to increasing temperature. As they move upslope, species are also likely to encounter changes in other environmental variables, including the biotic environment. Species are likely to differ in their ability to acclimate to these novel biotic conditions, with those of lower phenotypic plasticity experiencing increased stress at their range limits. Despite this, the majority of models predicting species range-shifts in response to climate change do not account for spatial variation in biotic environment.

This study investigated how seedlings of nine locally common neotropical tree species are responding to variation in seedling-seedling and adult-seedling competition, across their elevational ranges. Linear mixed models compared the strength and direction of relationships between competition variables and plant traits to determine: (a) whether competition effects cause variation in plant traits, and (b) how these effects compare to the effect of elevation. A recommendation is made on whether competition effects should be included in range shift models.

This study found that plant traits varied in response to above- and below-ground adult-seedling competition but not seedling-seedling competition. The effects of competition were smaller than elevation for all plant traits. Variation in plant traits across elevation was found to be species specific. Physiological stress decreased with elevation in 8/9 species. It is concluded that competition effects should be incorporated into future models predicting species range shifts in order to more accurately predict species range limitations, but that competition variables remain subordinate to abiotic environmental variables in these models.

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## Abbreviations

ABERG	=	Andes Biodiversity Ecosystem Research Group
adjR <sup>2</sup>	=	Adjusted R-squared
AIC	=	Akaike Information Criterion
DBH	=	Diameter at Breast Height
F <sub>v</sub> /F <sub>m</sub>	=	Quantum efficiency of PSII
GLMM	=	Generalised Linear Mixed Model
ha	=	Hectare
ISI	=	Iterative Seedling Index
LAI	=	Leaf Area Index
LMM	=	Linear Mixed Model
m.a.s.l.	=	Metres above sea level
PAR	=	Photosynthetically Active Radiation
PSII	=	Photosystem II
R <sup>2</sup> <sub>C</sub>	=	Whole model pseudo-r-squared
R <sup>2</sup> <sub>M</sub>	=	Fixed Effect pseudo-r-squared
SD	=	Standard Deviation
SE	=	Standard Error of the mean
SPAD	=	Soil Plant Analysis Development (relative chlorophyll content)
UV-B	=	Ultraviolet light of wavelength 320-290 nm
VIF	=	Variance Inflation Factor
W <sub>i</sub>	=	Akaike weight

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# 1. Introduction

## 1.1 The Importance of understanding range shift patterns

There is consistent evidence that rapid anthropogenic climate change is causing many species, across a wide range of taxa, to shift their distributions in space (Hughes 2000, McCarty 2001, Walther et al. 2002, Parmesan 2006, Loarie et al. 2009, Chen et al. 2011). Within an ecosystem however, range shifts are not occurring equally across species, and will produce novel species assemblages in the future (Hobbs et al. 2006). Species specific range shift patterns will occur as the result of varying sensitivity to climate change caused by differences in ecology and evolutionary history (Mooney et al. 2009). The combination of novel species assemblages and novel abiotic conditions creates the potential for an increasing number of species to be less adapted to their environment. This may lead to reductions in local and regional species richness (Colwell et al. 2008), ecosystem functioning (Bellard et al. 2012), and ecosystem service provision (Dobson et al. 2011, Isbell et al. 2011). Climate induced species range shifts therefore add another mechanism by which anthropogenic change is contributing to a reduction in global diversity (Millennium Ecosystem Assessment 2005) and a homogenisation of community composition (Dornelas et al. 2014) that is comparable to previous mass extinctions (Barnosky et al. 2011). It is therefore of paramount importance for future conservation management strategies to understand how species differ in their reaction to the novel environments they encounter. Given that the Earth is committed to a changing climate regardless of the effectiveness of greenhouse gas emission mitigation (Stocker et al. 2013), the need for contingency plans is even more important.

Previous studies have demonstrated that species' success over the coming century will be largely determined by their ability to respond to changing temperatures (Colwell et al. 2008, Chen et al. 2011, Feeley et al. 2012). Responses may occur either in the form of adaptation, *i.e.* changes in phenology, physiology and morphology, or through range shifts over space as species track changing temperatures (Bellard et al. 2012). As well as the effect of temperature, previous studies have drawn attention to the biotic environment as a potential driver of species specific range-shift dynamics (Ettinger & HilleRisLambers 2013, Araújo & Luoto 2007, Meier et al. 2010, Van der Putten et al. 2010, Wisz et al. 2013).

The effects of biotic interactions have been largely ignored in previous range shift models, in the belief that they play a small role in limiting species ranges compared to abiotic environmental change (Pearson & Dawson 2003, and references therein). There is little evidence to specifically suggest this is the case however (Araújo & Luoto 2007). There is robust evidence of the importance of various aspects of the biotic environment on population dynamics, including soil biota effects (Wardle 2004, van Grunsven et al. 2010), predation (Hillyer & Silman 2010), competitive interactions (Freckleton et al. 2009), and mutualisms (Meier et al. 2010). However, little of this knowledge has been included in providing a mechanistic understanding of how biotic interactions may influence range shifts under climate change (Araújo & Luoto 2007). By understanding how species are affected physiologically by the biotic environment and how species adapt their morphology, more accurate and precise predictions of future range shifts can be made (Feeley & Silman 2010, Feeley et al. 2012). This study aims to partly fill this knowledge gap by measuring plant trait responses to competitive interactions, in order to assess whether models predicting range shifts should include such parameters.

## 1.2 The role of biotic interactions

Species ranges shift at different rates in response to climate change (Walther et al. 2002). As such, the relative overlap of different species' ranges is likely to change as climate change progresses, producing novel species assemblages. In forests, biotic interactions are often strong and species turnover occurs over short distances, primarily due to dispersal limitation and vertical stratification of forest habitat (Condit 2002). Thus, the creation of novel species assemblages will lead to marked changes in competition

among plants for resources such as light, nutrients, water and space (Schweiger et al. 2008). Trees are some of the slowest taxa to migrate in response to climate change due to their long life-span and sessile nature. Thus, trees will be affected by biotic interactions more than other taxa as they fail to track changes in climate at a suitable rate (Wisz et al. 2013).

Araújo & Luoto (2007) compared the results of >600 studies and found that the inclusion of biotic interactions significantly increased the explanatory power of species range shift models. This trend was seen even at large scales where biotic interactions are expected to play a minor role compared to climate (Davis et al. 1998). Similarly, Gilman et al. (2010) found that biotic interactions affect communities at a range of spatial scales. Biotic interactions caused changes in individual fitness at the local scale, while at the regional scale they found changes in community structure. Unsurprisingly, range shift models that only include direct abiotic drivers of range shifts have often produced inaccurate predictions, with many becoming significantly better when biotic interactions are included (Heikkinen et al. 2007).

### 1.3 Bioclimatic envelope models

The majority of attempts to predict the spatial response of species to climate change have relied on bioclimatic envelope modelling (Pearson & Dawson 2003). Bioclimatic envelopes are constructed from correlations between present species spatial boundaries and observed environmental conditions within those boundaries, then projected into the future under different climate change scenarios to predict how species boundaries will change (e.g. Berry et al. 2002, Peterson et al. 2002, Thuiller et al. 2005, Araújo et al. 2006) (Sinclair et al. 2010). These models make a number of over-simplifications and assumptions however, leading to criticisms over their accuracy (Pearson & Dawson 2003).

Basic bioclimatic envelope models assume that the breadth of the realised niche (observed spatial range) equals that of the fundamental (bioclimatic envelope) niche (Jump & Peñuelas 2005, Hoffmann & Sgrò 2011). This assumption is challenged by studies which demonstrate that the realised niche is often smaller than the fundamental niche, owing to biotic interactions with other species (Davis et al. 1998, Van der Putten et al. 2010, Ettinger et al. 2011). Furthermore, bioclimatic envelope models assume that species respond instantaneously to climate change and that this change is equal in across all individuals of a species. This ignores potential lag effects caused by dispersal limitation, adaptive capacity limits, and intra/interspecific variation of these constraints (Jackson & Sax 2010, McLaughlin & Zavaleta 2012).

Currently, the accuracy of bioclimatic envelope models is limited by a paucity of data regarding the effects of non-climatic range shift rate controls on individuals and populations (Wiens 2011). Furthermore, it is inadequate to add biotic range shift controls as a simple exponent or constant to be added to range shift models, as biotic effects interact with each other in complex ways and species respond heterogeneously to them (Parmesan 2006, Moritz et al. 2008, Doak & Morris 2010, Feeley et al. 2011). By adding biotic interactions such as competition to bioclimatic envelope models, the realism and accuracy of these models could be increased (Araújo & Luoto 2007).

### 1.4 Tropical elevational gradients as natural laboratories

Tropical forests form an ideal system in which to investigate effects of the biotic environment over species ranges. Compared with temperate species, tropical species are more sensitive to changes in temperature due to a lack of seasonal temperature variation (Janzen 1967, Ghalambor et al. 2006, McCain 2009). Species found in the tropics are therefore more likely to shift their ranges in response to climate change than those found in other biomes.

Elevational gradients in the tropics are more likely to exhibit changes in species ranges compared to topographically uniform areas. Much of the migration in the tropics will occur across altitude rather than across latitude as tropical forests feature a relatively strong elevation-temperature gradient compared to other latitudes and have a low rate of temperature change with latitude (Malhi et al. 2010). This means that cooler regions are much further away latitudinally than altitudinally in the tropics.

The neotropical forest spanning the Eastern flanks of the Andes, the region investigated in this study, is expected to be particularly sensitive among tropical regions to changes in climate. Palaeological records show a strong correlation between previous climate change and changes in forest composition (Bush et al. 2004, Urrego et al. 2010). Furthermore, the rate of regional temperature increase as a result of climate change in this region currently exceeds that of the global average (Vuille & Bradley 2000), range shifts are therefore expected to become apparent here before other tropical regions. It is hoped therefore, that studies conducted in this region will form a strong knowledge base for predicting range-shifts elsewhere.

Tropical forests are under-studied by investigations aiming to understand global ecological patterns (Malhi et al. 2010). This is despite tropical forests playing an important role in the global carbon cycle (Davidson et al. 2012) and contributing largely to global biodiversity trends (Gaston 2000). Tropical studies are often marred by the consequences of extreme weather, a hostile biotic environment, and the inaccessibility of remote locations. Thus, studies such as this one, which focus specifically on tropical will make an important contribution to a growing body of evidence on the functioning of tropical ecosystems. Specifically, this study focusses on a high elevation tropical ecosystem, which are understudied compared to other tropical ecosystems (Bubb et al. 2004).

## **1.5 This study, objectives and rationale**

This study investigates the acclimatory response of seedlings of evergreen neotropical tree species to variation in competition intensity across their elevational ranges. The competition variables measured are proxies for adult-seedling above- and below-ground competition and seedling-seedling competition. The study focusses on an elevational migration corridor in the Peruvian Andes along which tree species ranges are known to be shifting upslope (Feeley et al. 2011). Variation in seedling physiological and morphological traits in response to variation in competition intensity is used to evaluate whether these biotic interactions have the potential to affect future range-shift dynamics (RQ1). The strength of the competition-trait relationship is then compared to the general elevation-trait relationship to determine the relative importance of variation in competition intensity in influencing future range shifts (RQ2). A recommendation will be made as to whether competitive interactions should be included in future range-shift models in the tropics.

The plant traits measured in this study are both morphological and physiological. Analysis of chlorophyll fluorescence assesses the photosynthetic performance of individuals, with a reduced photosynthetic efficiency interpreted as evidence of plant stress (Ashraf & Harris 2013). Leaf chlorophyll content is also measured. Decreased leaf chlorophyll content is also interpreted as a sign of plant stress, being associated with senescence and nutrient deficiency (Gitelson et al. 2003). Decreased chlorophyll content (chlorosis) can be caused by acclimation to a more intense light regime, as a result of a deficiency in available soil nitrogen, or as a result of plant stress or senescence (Ashraf & Harris 2013). Variation in morphological plant traits: leaf thickness, leaf area, stem volume and the leaf:height ratio provides an insight into the ability of individuals to acclimate to different environmental conditions, thus showing whether a species is sensitive to changes in the environment.

## Research questions & null hypotheses

**RQ1:** Do competition variables explain variation in plant traits?

$H_{n1}$ : Competition variables explain no variation in plant traits.

$H_{n2}$ : No combination of competition variables and/or elevation predicts variation in plant traits better than elevation used in isolation.

**RQ2:** To what extent do competition variables and plant traits vary across elevation and among species?

$H_{n3}$ : Competition variables do not vary with elevation.

$H_{n4}$ : Within each species, plant trait variables do not vary with elevation.

$H_{n5}$ : The nature of the relationship between plant traits and elevation does not vary with species.

## 2. Methods

### 2.1 Study site

Measurements were conducted across 10 permanent 1 ha closed canopy forest plots in the Kosñipata Valley of Manú National Park, Peru (-13°N, -71°W, Figure 1, Table 1). The Kosñipata Valley has been identified as a potential migration corridor for lowland species to migrate to higher elevations in response to temperature increase (Feeley et al. 2011). Plots are situated between 400 and 3200 m.a.s.l. along this migration corridor (Table 1, Figure 2). The plots form part of a larger plot network established by the Andes Biodiversity and Ecosystem Research Group (ABERG) in 2003 (Malhi et al. 2010, Girardin, Espejob, Doughty, Huasco, Metcalfe, Durand-Baca, Marthews, Aragao, Farfan-Rios, García-Cabrera, Halladay, Fisher, Galiano-Cabrera, Huaraca-Quispe, Alzamora-Tayne, Eguiluz-Mora, Salinas-Revilla, Silman, Meir & Malhi 2013).

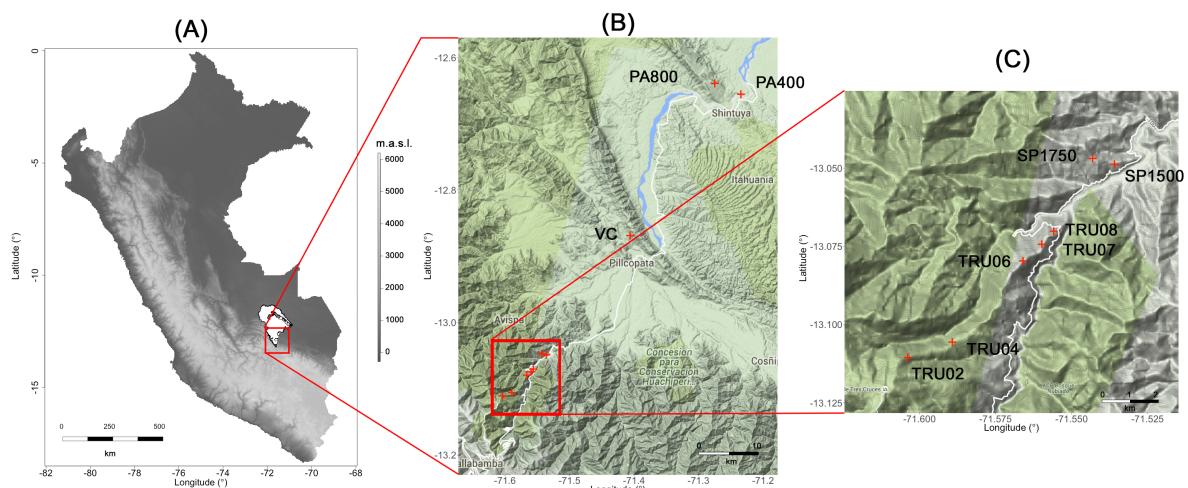


Figure 1: Maps showing the location of the study area and plot locations. **(A)** The site location within Peru with elevation shading, showing the proximity to Manú National Park (white area). **(B)** The location of the 1 ha plots within the Kosñipata Valley. **(C)** An enlargement of the Trocha Union and San Pedro plot groups. Red crosses indicate plot location, white lines in maps (B) and (C) indicate roads, text labels in (B) and (C) are plot codes, dark green areas in (B) and (C) denote the bounds of Manú National Park.

Table 1: Site characteristics for each 1 ha plot sampled in this study. ‘NA’ no data available. Adapted from Whitaker et al. (2014).

Site Code	Latitude (°)	Longitude (°)	Elevation (m.a.s.l.)	Annual Precipitation (mm year <sup>-1</sup> )	Mean Annual Air Temperature ± SD (°C)	Slope (°)	Total N (%)	Total C (%)	Soil pH
PA400	-12.655	-71.234	406	NA	NA	NA	NA	NA	NA
PA800	-12.639	-71.274	822	NA	NA	NA	15.6	3.4	NA
VC	-12.869	-71.406	861	3,087	20.7 ± 0.1	NA	16.0	1.5	3.9
SP1500	-13.049	-71.536	1,497	2,631	17.4 ± 1.5	22.7	10.5	1.0	4.1
SP1750	-13.047	-71.543	1,770	2,631	15.8 ± 1.3	40.1	26.0	1.9	4.3
TRU08	-13.070	-71.556	1,839	2,472	16.0 ± 1.3	41.8	31.0	2.0	4.3
TRU07	-13.074	-71.560	2,135	1,827	14.9 ± 1.1	18.0	37.0	2.1	4.0
TRU06	-13.080	-71.566	2,281	NA	NA	NA	NA	NA	NA
TRU04	-13.106	-71.589	2,733	2,318	11.1 ± 1.0	21.4	28.5	1.8	3.9
TRU02	-13.111	-71.604	3,213	NA	8.9 ± 1.0	11.8	44.5	2.6	3.8

The research area has a mean annual temperature range of ~12 °C, with an adiabatic lapse rate of 4.94 °C km<sup>-1</sup>, from 20.7 ± 0.02 °C (mean ± standard deviation) (VC, 861 m.a.s.l.) to 8.9 ± 1.0 °C (TRU02, 3213 m.a.s.l.) (Whitaker et al. 2014). Annual precipitation ranges from 1700 - 3087 mm year<sup>-1</sup>, with a hump-shaped distribution peaking at 1000 m.a.s.l., between SP1500 and VC. Despite low precipitation at higher elevations, sites are rarely moisture limited, due to limited evapotranspiration and frequent fog deposition within the cloud immersion zone, which extends from ~1500 to 3020 m.a.s.l. (Weg 2010).

Average soil temperature ranges from ~27 ± 0.3 °C (mean ± SD) in PA400 to ~12 ± 0.3 °C in TRU04 (Figure 10a). Soil moisture content ranged from 2-75%, showing no relationship with elevation (Figure 10b). Instead, micro-site effects reflecting geomorphological situation (proximity to run-off channels, rocky outcrops etc.) are likely to be the principal controls on soil moisture content (Moser et al. 2008, Girardin et al. 2010).

The elevational gradient encompasses several complete ecosystem turnovers, with lowland tropical rainforest (<800 m.a.s.l.), followed by pre-montane (800-1200 m.a.s.l.), lower montane (1200 - 2200 m.a.s.l.) and upper montane (2200 - 3400 m.a.s.l.) cloud forest (Girardin et al. 2010). Plots between 1500 and 3020 m.a.s.l. (SP1500, SP1750, TRU08, TRU04) are frequently immersed in cloud, having structural features of cloud forests (short stature trees, dense crowns, twisted branches). All plots were originally sited with the aim of reducing within plot heterogeneity in terms of forest structure, geological substrate and topography (Girardin et al. 2013a). Additionally, all montane plots (SP1750 - TRU02) were sited along a ridge-top; this reduces variation in non-elevationally dependent abiotic environmental variables within each site which are known to significantly impact montane forest dynamics, such as wind speed and aspect (Girardin et al. 2013b). Measurements were taken between July and August 2015, prior to the start of the autumn rainy season (Garreaud 2009).

## 2.2 Species

Nine tree species were chosen for comparison from a range of 1635 identified species found in the plots. Species were selected according to their contrasting ranges (Figure 2), differences in migratory pattern of their genus (Feeley et al. 2011), and because they are dominant species across their ranges (ABERG, unpublished data, Appendix VI). Despite having no quantitative range shift prediction information, *Iriartea deltoidea* and *Dictyocaryum lamarckianum* were included in order to observe potential differences

between monocot and dicot species, as both are monocots. Both *I. deltoidea* and *D. lamarkianum* are large-seeded palm species, as such, they are expected to be migrating upslope, similar to other large-seeded palms (Hillyer & Silman 2010). Seedlings of *Myrcia* spp. are difficult to reliably identify to species in the field and were thus sampled as a composite of three potential species: *Myrcia splendens*, *M. fallax*, and *M. rostrata*, referred to as *Myrcia* spp.. Species are referred to by two letter codes (AV, CR, etc.) hereafter (Table 2).

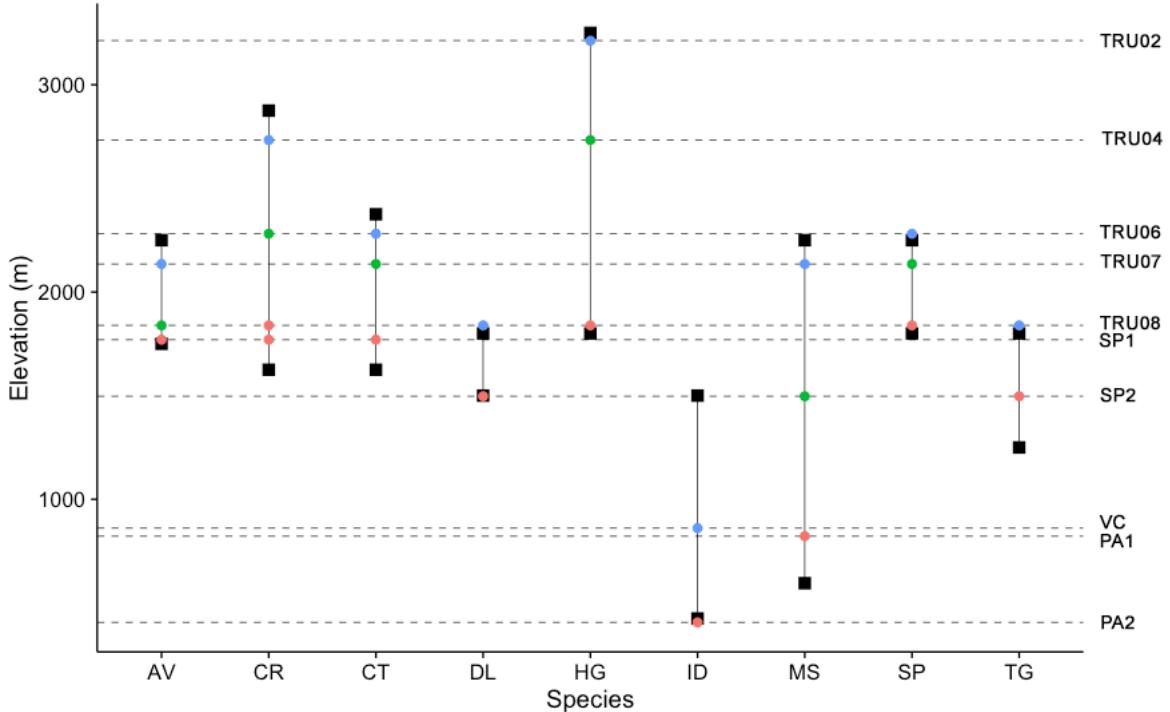


Figure 2: Elevational ranges of species sampled (■), elevations of the 10 plots sampled (grey dashed lines) with plot names on the right side, and sampling locations of each species indicating upper (●), central (●) and lower (●) elevation sample locations. Species show contrasting elevational ranges and contrasting range sizes. See Table 2 for species codes and Table 1 for plot characteristics.

### 2.3 Sampling strategy

Species were sampled in three plots, as close to the top, centre, and bottom of their elevational ranges as possible (Figure 2), to allow within species comparisons along each species range. *D. lamarkianum* was sampled at only the top and bottom of its range due to the relative location of plots along its range. *C. revoluta* was sampled in both TRU08 and SP1 due to a paucity of identifiable seedlings in SP1. *I. deltoidea* seedlings could not be located in SP2 despite its range extending above this elevation.

In each of the three plots per species, a maximum of 10 seedlings were opportunistically sampled. Seedlings were used as they were easy to locate and measure, not requiring the use of tree climbing equipment as with adult trees. Additionally, seedlings are believed to be a crucial developmental stage with high mortality, being particularly sensitive to environmental stressors and more likely to show clear signs of stress (Ettinger & HilleRisLambers 2013). Seedlings were defined as <1 m in height and bearing no woody parts.

Epiphytes and individuals connected by stolons or rhizomes to larger individuals were not sampled as these individuals may draw nutrients from their parent plant, invalidating correlations between observed plant traits and environmental variables. Seedlings with a minimum of two fully-expanded leaves and no visible signs of damage or herbivory were sampled to reduce sources of unknown bias in physiological measurements. To eliminate potential spatial pseudo-replication, only seedlings more than 5 m apart were

sampled. This ensured that competition were independent and did not overlap, and seedlings were unlikely to be competing with each other (Paine et al. 2008). Within a cluster of seedlings, the seedling to be measured was chosen at random by assigning each seedling a number and using a random number table, reducing human bias. Due to the spatial distribution of seedlings and the overall abundance of accessible seedlings, it was not possible to sample 10 seedlings per plot for some species (Table 2).

Table 2: The number of seedlings sampled at each sample plot for each species and the species codes used throughout the report.

Species Name	Bottom	Middle	Top
<i>Alzatea verticillata</i> Ruiz & Pav.	9	5	8
<i>Clethra revoluta</i> Ruiz & Pav.	7	9	9
<i>Clusia thurifera</i> Planch. & Triana	9	9	10
<i>Dictyocaryum lamarckianum</i> H.Wendl.	10	0	10
<i>Hedyosmum goudotianum</i> Solms	10	10	10
<i>Iriartea deltoidea</i> Ruiz & Pav.	10	0	10
<i>Myrcia</i> spp. DC.	10	8	10
<i>Schefflera patula</i> J.R.Forst. & G.Forst.	9	10	10
<i>Tapirira guianensis</i> Aubl.	10	0	10

## 2.4 Measurements

### Leaf physiology

For each seedling, the upper-most fully-expanded leaf without damage was selected for leaf physiological measurement. Chlorophyll-a fluorescence measurements were performed using a Walz mini-PAM II (Walz Effeltrich, Germany). On a randomly selected area of the adaxial leaf surface, avoiding prominent leaf veins,  $F_v/F_m$  chlorophyll fluorescence was measured (Genty et al. 1989) (Equation 1). Measurements were conducted after a minimum of 30 minutes in complete darkness to ensure dark adaptation (Campbell et al. 2007).

$$F_v/F_m = (F_m - F_o)/F_m \quad (1)$$

Where  $F_m$  is the maximal fluorescence in the dark and  $F_o$  is the minimal fluorescence in the dark (Maxwell & Johnson 2000). Dark-adapted  $F_v/F_m$  measures the photosynthetic efficiency of the leaf by relaxing the reaction centres prior to the fluorescence measurement.  $F_v/F_m$  is preferable to other chlorophyll fluorescence measures as it removes the ‘noise’ created by environmental conditions at the time of measurement, instead providing a measure of the underlying photosynthetic efficiency. A reduction in  $F_v/F_m$  is indicative of plant stress. Here, individuals with  $F_v/F_m$  values  $<0.7$  are said to be experiencing stress (Maxwell & Johnson 2000).

Leaf relative chlorophyll content (SPAD) was measured three times at random locations on the adaxial leaf surface, avoiding prominent veins to ensure an accurate measurement, using a multi-spectral SPAD-meter (Minolta SPAD-502Plus, Spectrum Technologies, Plainfield, Illinois, USA).

### Whole-plant and leaf morphology

After physiological measurements the same leaf was removed from the seedling and hydrated for a minimum of 48 hours in order to reverse any leaf curling or contraction in thickness due to desiccation. With the petiole removed, each leaf was photographed and projected leaf area calculated using ImageJ software (version 1.50g7, NIH, Bethesda, Maryland, USA). Leaf area was log transformed for analysis as

results spanned multiple orders of magnitude. Mean leaf thickness was calculated using a digital micrometer (0-25 mm, Precision Technologies International, Tamworth, Staffordshire, UK) on three random points on the leaf, avoiding prominent leaf veins.

To quantify whole-seedling morphological characteristics I measured stem height, stem width below the lowest set of leaves using the digital micrometer, and counted the number of fully expanded leaves (excluding cotyledons). Stem volume ( $V$ ) was calculated from stem radius ( $r$ ) and height ( $h$ ), assuming a cylinder of constant diameter:

$$V = \pi r^2 h \quad (2)$$

To account for differences in seedling growth stage and to reduce the number of collinear variables in statistical analysis, stem height and number of leaves was expressed as the number of leaves per unit stem height (leaves cm<sup>-1</sup>).

### **Competitive interaction intensity**

To assess seedling-seedling competition intensity, the number of herbaceous plants within a 1 m radius was measured. A 1 m radius acts as a maximum distance over which seedlings are expected to compete with other individuals for nutrients, and water. To assess the below-ground competition effect of adult trees on seedlings, an adapted version of the Iterative Hegyi Index was implemented (Hegyi 1974, Lee et al. 2004, Seifert et al. 2014). The adapted ‘Iterative Seedling Index’ (ISI) uses measures of adult tree DBH (Diameter at Breast Height, ~1.3 m from ground level) and distances of competitor trees to calculate a value for each seedling, higher values indicate greater estimated competition strength between the surrounding adult trees and the seedling:

$$ISI_i = \log\left(\sum_{j=1}^n \left(\frac{1}{DIST_{ij}} D_j\right)\right) \quad (3)$$

where  $D_j$  is the DBH of a competitor tree and  $DIST_{ij}$  is the euclidean distance between seedling  $i$  and competitor tree  $j$ . ISI was log transformed for analysis, as results spanned multiple orders of magnitude. The ‘iterative’ aspect refers to the selection of competitor trees. The radius around the seedling is divided into 12 30°sectors, only the nearest tree >10 cm DBH within each sector is measured (Figure 3). The size of the competition radius ( $C_R$ ) is defined as:

$$C_R = 2 \times \sqrt{\frac{10,000}{N}} \quad (4)$$

where  $N$  is the number of trees >10 cm DBH per ha (stand density). Stand density data was taken from ABERG census data within each plot (ABERG unpublished data) and used to estimate  $C_R$  for VC, for which no stand density data exists (Figure 4).  $C_R$  was rounded to the nearest metre for ease of measurement (Table 3). An iterative selection method for competitive trees assumes that if the path between two trees is blocked, the intensity of competition between them will be greatly reduced (Gadow & Hui 1999).

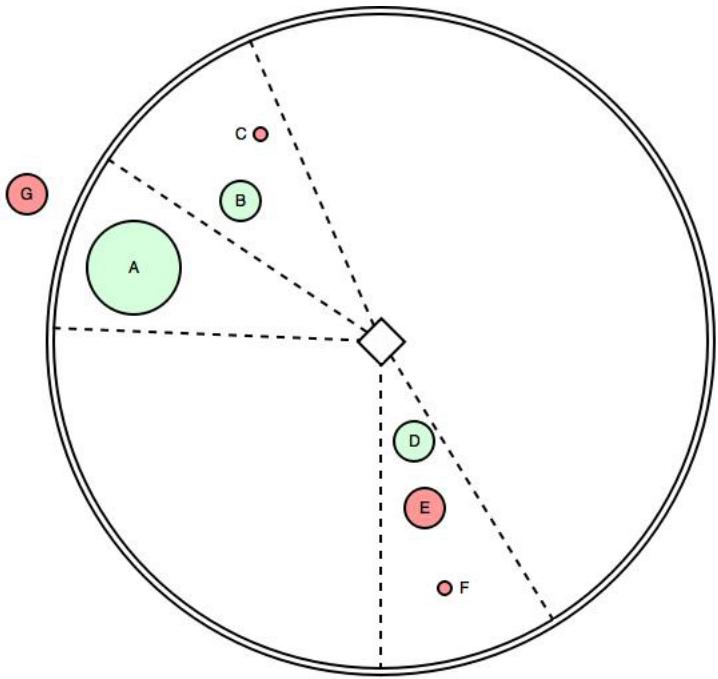


Figure 3: Schematic diagram showing the iterative selection of active competitor trees for the Iterative Seedling Index (ISI) (Equation 3). Trees marked in green (A, B, D) are active competitors, trees marked in red (C, E, F, G) are non-active competitors, coloured circles radius is equivalent to tree DBH. The double circle is the competition radius, defined by  $C_R$  (Table 3, Equation 4). The diamond ( $\diamond$ ) is the seedling of interest. Dashed lines represent 30° zones within which to choose one active competitor. D is the active competitor of its zone as it is the nearest competitor of a suitable DBH ( $>10$  cm). F is not an active competitor as it is  $<10$  cm DBH. G is not an active competitor as it is outside the competition radius. Adapted from Lee et al. (2004).

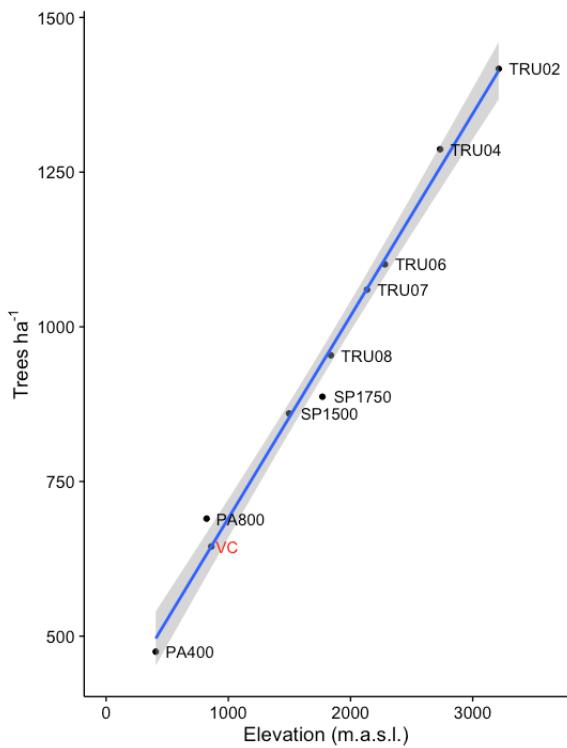


Figure 4: Linear regression of number of trees per hectare per for each plot, used to estimate number of trees per hectare for **VC**.  $\text{adjR}^2 = 0.896$ ,  $F_{(1, 7)} = 579.5$ ,  $p < 0.001$ . Shaded areas are 95% confidence intervals.

Table 3: The competition radii calculated for each plot, rounded to the nearest metre.

Site Code	Trees $\text{ha}^{-1}$	$C_R$ (m)
PA400	475	9
PA800	690	8
VC	645	8
SP1500	860	7
SP1750	887	7
TRU08	954	6
TRU07	1060	6
TRU06	1101	6
TRU04	1287	6
TRU02	1417	5

In order to measure above-ground adult-seedling competition above each seedling, hemispherical photographs were taken of the canopy, avoiding lens flare and cloudless conditions (Frazer et al. 2001), in order to calculate the Leaf Area Index (LAI) above each seedling, which quantifies adult tree shading effects. Specifically LAI (4-ring) was reported, calculated as the effective LAI integrated over the Sun zenith angle 0 to 60°(Sternberg et al. 1994). LAI is expressed as the projected leaf area per unit ground area ( $\text{m}^2 \text{ m}^{-2}$ ).

## **Abiotic environmental variables**

In order to quantify abiotic environmental variables, which have been demonstrated to covary with elevation in other studies, soil temperature and soil moisture were each measured at three approximately equally spaced points close to the base of each seedling. Leaf litter and other obstructions were removed to uncover bare soil. Soil moisture was measured using an ML3 - ThetaProbe Soil Moisture Sensor (Delta-T, Cambridge, UK). Soil temperature was measured using an unlicensed temperature probe (accuracy =  $\pm 0.01$  K).

## **2.5 Statistical analyses**

All statistical analyses were conducted using R, version 3.2.4 (R Core Team 2016). Full R code is supplied in Appendix VII.

### **Relationship between competitive interactions and plant traits ( $H_{n1}$ , $H_{n2}$ )**

All fixed effects and response variables were standardised using for this analysis in order to make effect sizes more readily comparable (Grueber et al. 2011, Gelman & Su 2014). Standardisation rescales each variable so values fall between 0 and 1. To test the presence and strength of the relationship between each competition variable and each plant trait ( $H_{n1}$ ), linear mixed models (LMMs) were conducted using all combinations of singular competition variables (fixed effects) and plant traits (response variable). Site was incorporated as a random intercept term to account for site level variation in competition variables and non-independence of measurements at the site level. Species was also included as a random effect in order to account for baseline differences in plant traits among species as a result of differing ecology. Species was included as either a random intercept or random slope term depending on which produced a model of better quality, assessed using Akaike Information Criterion (AIC) (Akaike 1998).

Prior to multiple fixed effect LMM analysis, the standardized fixed effects (competition variables) were checked for collinearity using Variance Inflation Factors (VIF) (Table 4). All VIFs were below the critical threshold of 1.5, indicating no detrimental collinearity (Zuur et al. 2009).

To assess whether a combination of competition variables and elevation predicted changes in plant traits appreciably better than just elevation ( $H_{n2}$ ), the quality of LMMs using different combinations of fixed effects was compared using AIC, Akaike weights ( $W_i$ ) and the variance explained by the fixed effects ( $R^2_M$ ) and the whole model ( $R^2_C$ ) using pseudo-r-squared estimations. Akaike weights measure the likelihood that the given model is better than the next best model in the group of models being compared. Multiple fixed effect models maintained the random effects structure that best fitted each fixed effect when used on its own in the previous models.

### **Variation in competitive interactions and plant traits across elevation and between species ( $H_{n3}$ , $H_{n4}$ , $H_{n5}$ )**

Fixed effects and response variables were not standardised for these analyses as effect sizes were not being compared. LMMs were conducted in order to determine the relationship between competition variables and elevation. Each site was allowed to vary by intercept to account for site level differences in environment and accounting for non-independence of measurements at the site level ( $H_{n3}$ ). Herbaceous plant abundance count data fitted using generalised LMMs assuming Poisson and negative binomial distributions to determine the best distribution assumption for this data (Appendix I). The best fitting model was identified using AIC and  $R^2_C$ .

LMMs tested the variation in each plant trait with elevation ( $H_{n4}$ ), allowing the slope of each species to vary across elevation in order to observe differences in species response to elevation ( $H_{n5}$ ). Site was added as a random intercept to account for site level differences in environment and to account for site-level clustering of measurements.

Table 4: The variance inflation factors (VIF) of the four fixed effects used in mixed models to explain changes in plant traits.

Fixed Effect	VIF
Elevation	1.104
LAI	1.074
ISI	1.060
Herbaceous Plant abundance	1.033

### 3. Results

#### 3.1 Effect of competition on plant traits

##### Determination of random effects structure

In order to inform the error structure of subsequent models, error structures were compared using AIC. Single fixed effect LMMs in which the slopes of each species were allowed to vary by either intercept or slope and intercept were compared to show whether species differ appreciably in their trait response to the various competition variables and elevation (fixed effects) (Figure 5, Appendix III). Physiological leaf trait models were not of a better quality when species were given their own slopes. All morphological traits had at least one model where a random slope structure for species produced a model of better quality. Leaf area was better using a random slope for all except herbaceous plant abundance. The optimal random effect structure identified here is maintained throughout the subsequent models, with species being allowed to vary in their slopes for those environmental variables where a random slope model was of better quality. Where  $\Delta\text{AIC}_{\text{rsri}}$  values where  $-2 < \Delta\text{AIC}_{\text{rsri}} < 2$  a random intercept structure is maintained, in order to maximise parsimoniousness.

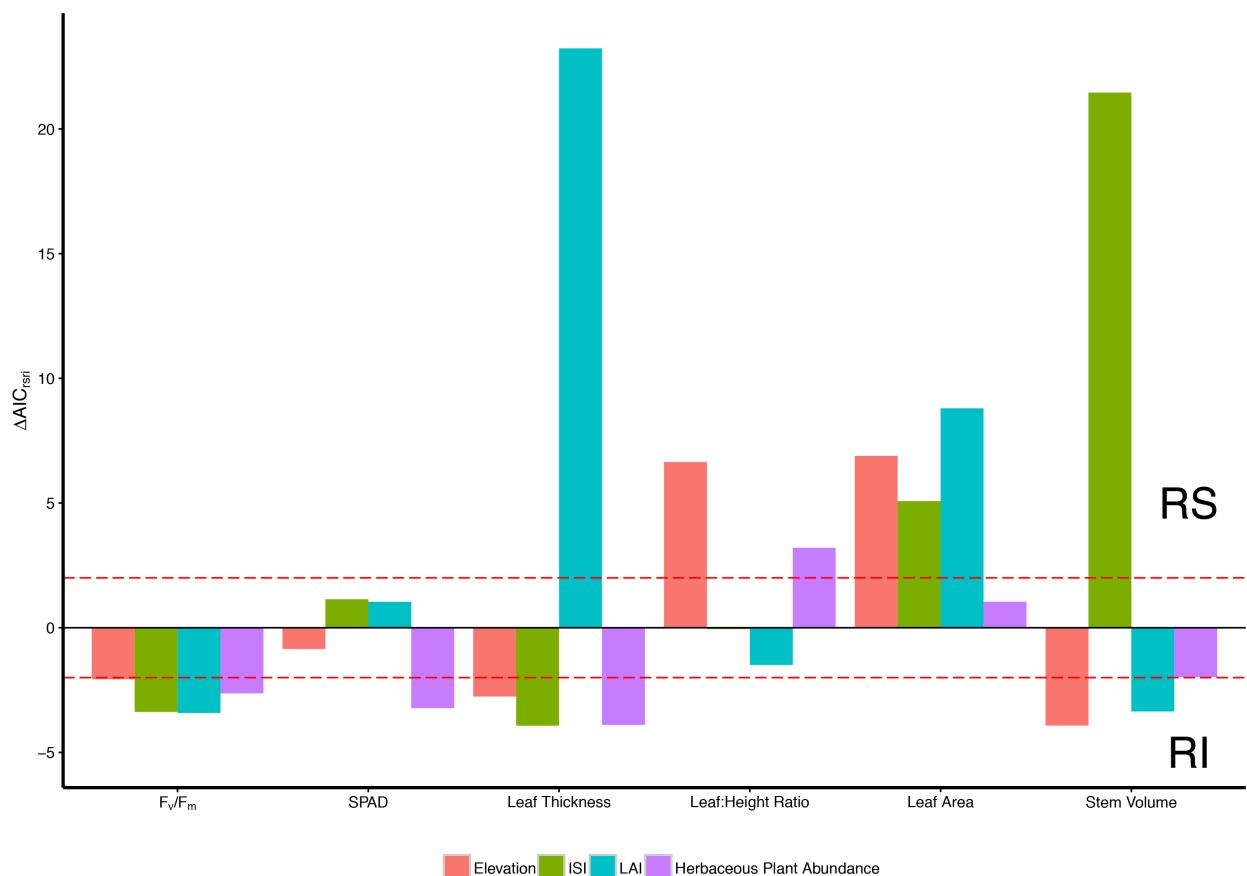


Figure 5:  $\Delta\text{AIC}_{\text{rsri}}$  ( $\text{AIC}_{\text{random intercept}} - \text{AIC}_{\text{random slope}}$ ) compares the model quality of single fixed effect models predicting each of the six plant traits using either a random slope or a random intercept for the random effect of species. A positive  $\Delta\text{AIC}_{\text{rsri}}$  indicates that the random slope model is of better quality (RS), while a negative  $\Delta\text{AIC}_{\text{rsri}}$  indicates that the random intercept model is of better quality (RI). Models are shaded according to the fixed effect used.  $\Delta\text{AIC}$  values  $-2 > \Delta\text{AIC} < 2$  (within the red dashed lines) indicate that neither the random intercept or random slope model was appreciably better.

### The comparative influence of individual competition variables ( $H_{n1}$ )

The best quality single fixed effect models (using either independent intercepts or slopes for each species) were compared using  $\Delta AIC_r$  against a random effects model, the variance explained by the whole model ( $R_C^2$ ) and the fixed effects ( $R_M^2$ ), and slope coefficients (Figure 6, Figure 7) to compare their relative effect on plant traits.

LMMs were better than random effects models in 15/24 cases ( $\Delta AIC_r > 2$ ) (Figure 6a). Competition variables account for only a small percentage of the variance in each plant trait, with the highest  $R_M^2$  being ISI predicting stem volume ( $R_M^2 = 4.3\%$ ). All models including species as a random slope term were an improvement over a random effects model (Figure 6b). Elevation has a greater influence over plant traits than any competition variable in all cases (Figure 6b).

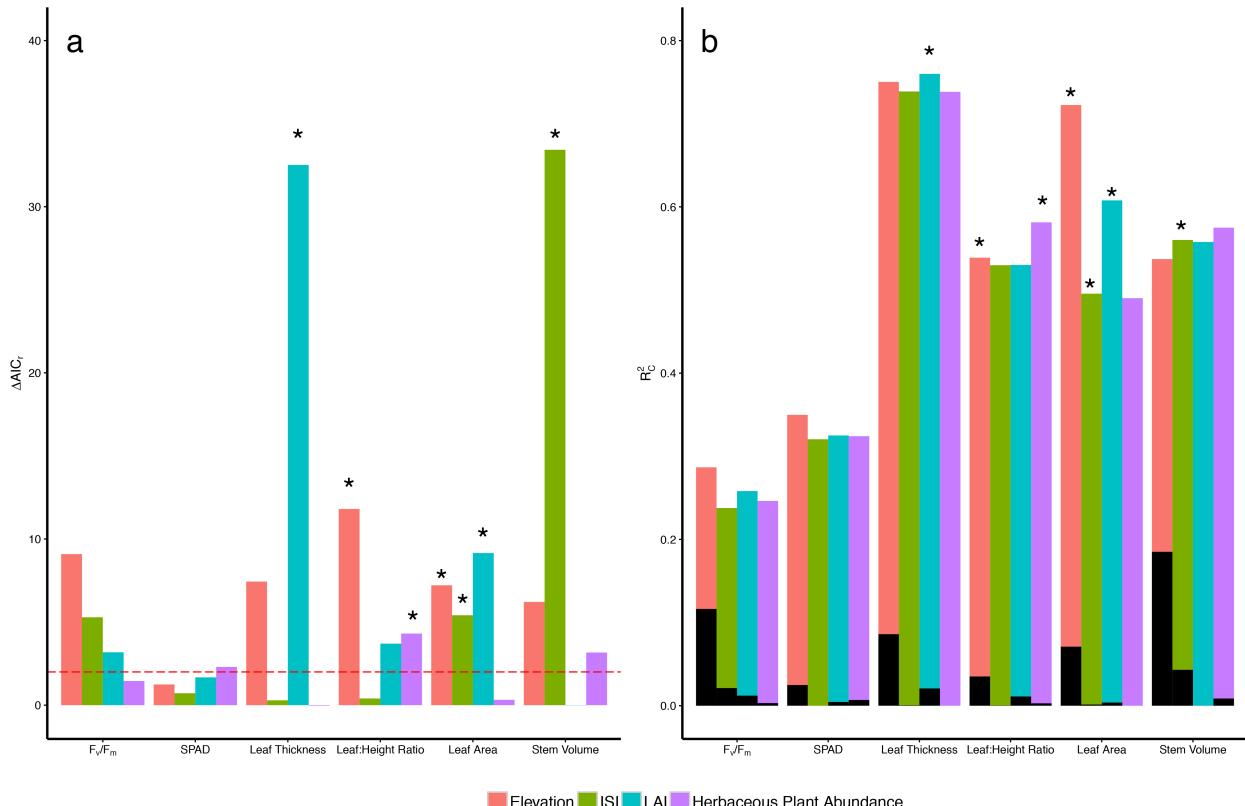


Figure 6:  $\Delta AIC_r$  values (a) and  $R_C^2/R_M^2$  values (b) for the best fitting (random slope or random intercept) single fixed effect models, grouped by plant trait.  $\Delta AIC_r$  values are generated by comparing the best fit model with a random effects model. The red dashed line at  $\Delta AIC_r = 2$ , indicates that models below this threshold are not clearly better than a random effects model. Black bars indicate  $R_M^2$  values, the variance explained by the fixed effect in each model. Models marked with asterisks allowed the slopes of each species to vary, as opposed to only allowing the intercept to vary.

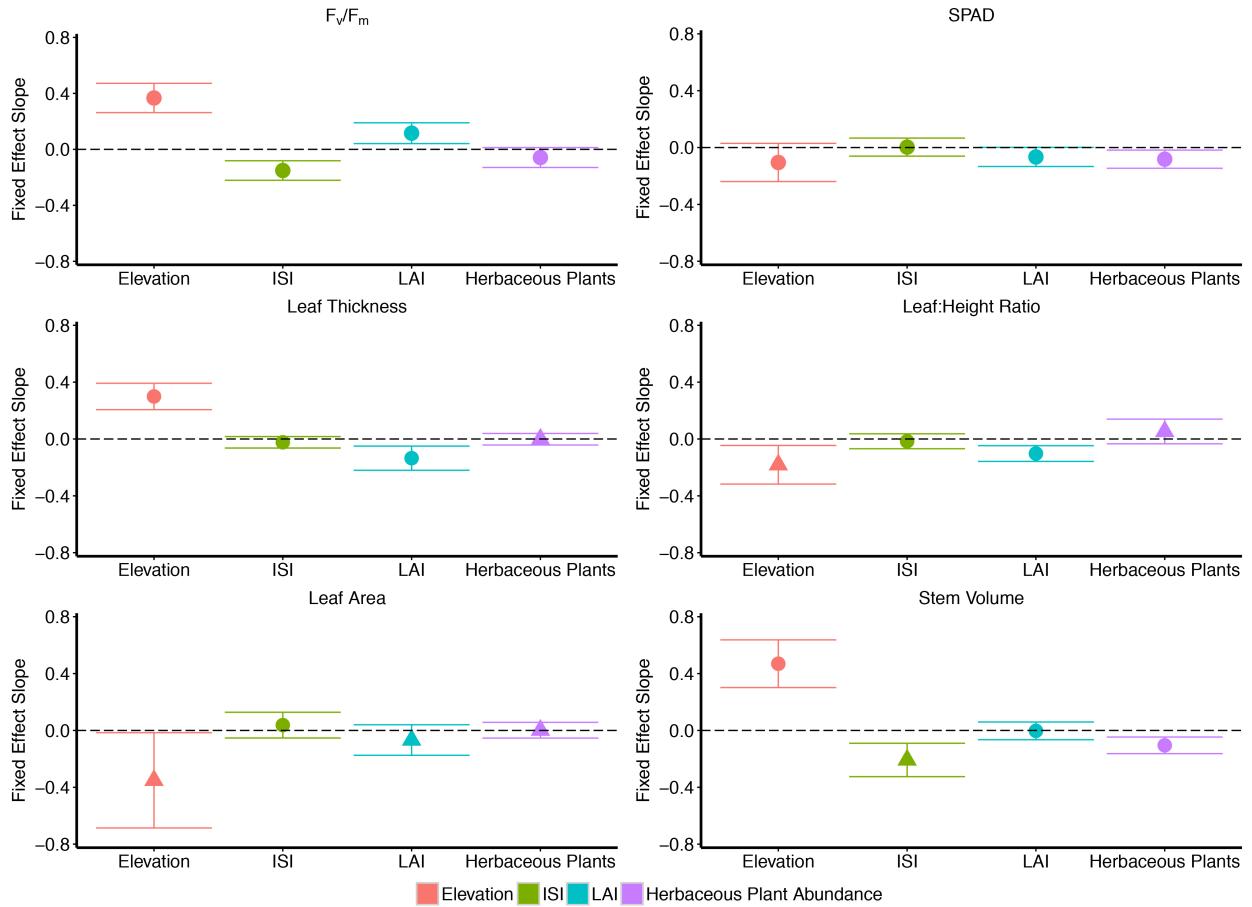


Figure 7: Fixed effect slopes (points) and standard errors (error bars) for each single fixed effect model. Each panel represents all the models for one plant trait. Model slopes for models where species' slopes were allowed to vary by slope are triangles while those models only allowing species intercept variation are circles. Fixed effects and response variables were standardised to allow easier comparison of effect sizes. Points and error bars are shaded according to the fixed effect used in the model.

### Comparison of multiple fixed effect models ( $H_{n2}$ )

Table 5 shows the fixed effects and model fit measures from the best fitting multiple fixed effect models used to predict plant traits. For plant traits where one or more of the single fixed effect models was better when using a random slope (Figure 5), the species slopes were allowed to vary for those fixed effects (Table 5 - [✓]) in some model iterations.

All of the best models except the one predicting SPAD included elevation as a fixed effect alongside competition variables. All of the best models were better than a model using only elevation (Appendix IV). The best models for leaf:height ratio, leaf area and stem volume used random slopes for all the fixed effects identified as varying among species in the single predictor models. The fixed effects in the multiple fixed effect models still accounted for a small percentage of the variation in plant traits, ranging from 0.4% (SPAD), to 17.3% (stem volume).

When multiple fixed effects were used in a model, the standard errors surrounding the slopes of those fixed effects were reduced (Figure 8, Appendix II). The effect of herbaceous plant abundance became larger in the multiple fixed effects model compared to the single fixed effect model. The best LMM for SPAD was no better than a random effects model ( $\Delta AIC_r = -1.0$ ) and was 14.2% likely to be better than the next best model, which included only elevation ( $W_i = 0.142$ ).

Table 5: The form of the best fitting multi-fixed effect model for each plant trait, showing the fixed effects used and various measures of model quality. [✓] indicates that a random slope term was included for this fixed effect.

Plant Trait	Elevation	ISI	LAI	Herbaceous plants	$\Delta AIC_r$	$W_i$	$R_C^2$	$R_M^2$
$F_v/F_m$	✓	✓	✓	✗	8.8	0.421	0.320	0.140
SPAD	✗	✗	✓	✗	-1.0	0.142	0.325	0.004
Leaf Thickness	✓	✓	✓	✗	12.4	0.365	0.761	0.120
Leaf:Height Ratio	[✓]	✓	✓	[✓]	10.7	0.620	0.578	0.064
Leaf Area	[✓]	✓	[✓]	[✓]	5.8	0.296	0.801	0.071
Stem Volume	✓	[✓]	✓	✓	32.3	0.610	0.575	0.173

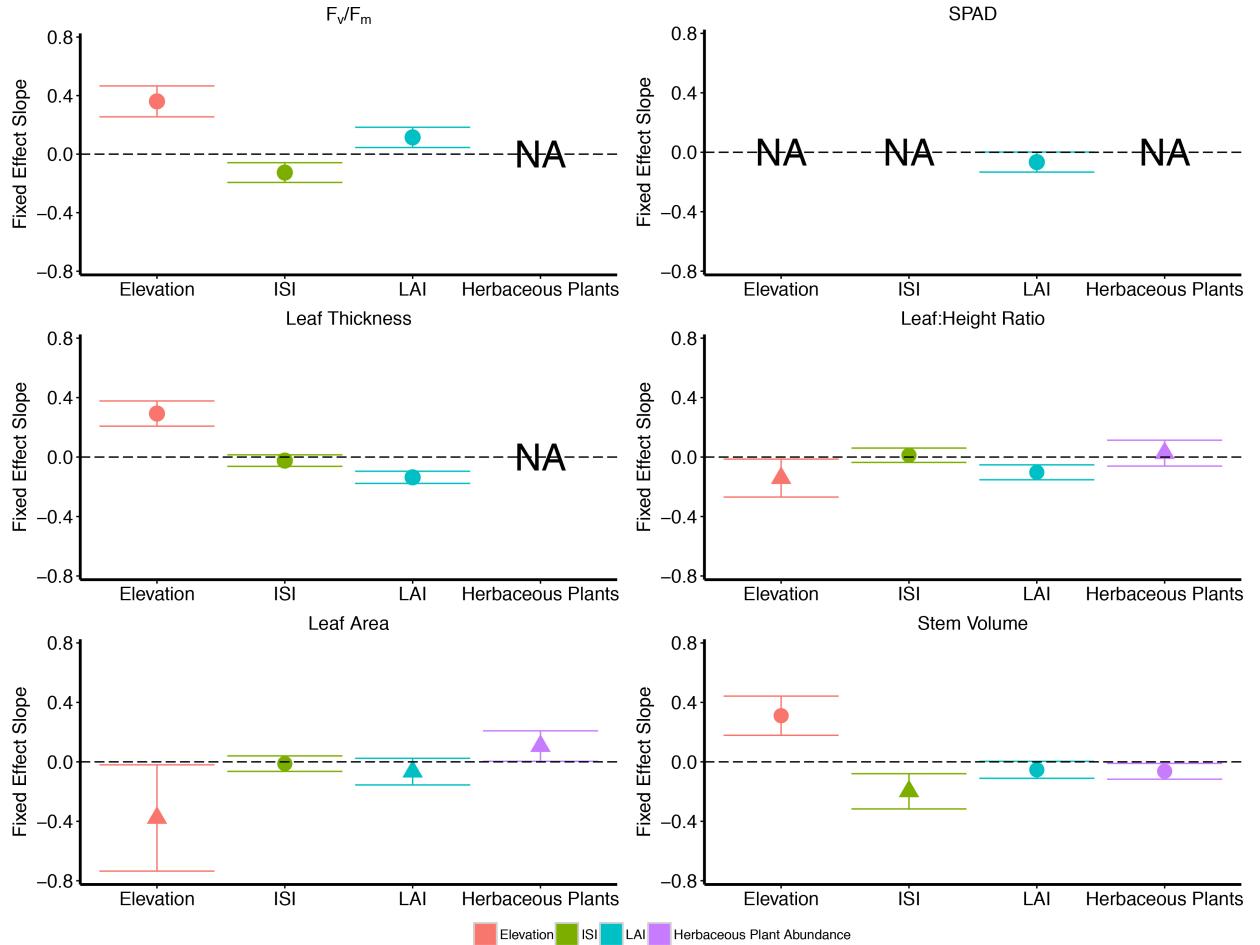


Figure 8: Fixed effect slopes (points) and standard errors (error bars) for the best multiple predictor models for each plant trait. Predictor variables were all standardised to allow easier comparison of effect sizes. Each panel shows the fixed effect slopes for each fixed effect used in the best model for a given plant trait. Points and error bars are shaded according to the fixed effect used in the model. “NA” indicates that the given fixed effect was not included in the best model.

### 3.2 Variation in competition variables across elevation ( $H_{n3}$ )

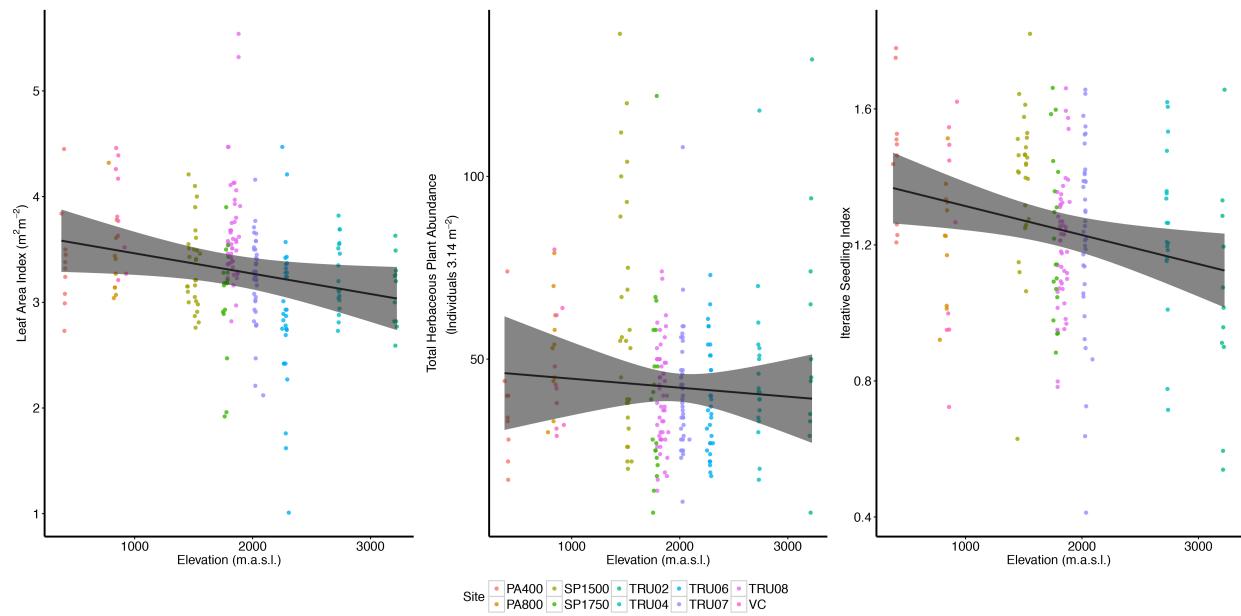


Figure 9: Linear mixed model regressions showing how each of the three competition variables vary with elevation. The black line and shaded ribbon show the regression fit and 95% confidence intervals, respectively. Points are shaded according to site, which was added as a random intercept term.

LMMs were conducted for each of the three competition variables (Figure 9, Table 6), giving each site a random intercept. The AIC of each model was compared to a random effects model to assess the explanatory power of elevation. Only ISI varied clearly with elevation, (slope =  $-8.44 \times 10^{-5}$ , SE =  $3.661 \times 10^{-5}$ ,  $\Delta AIC_r = 8.0$ ), though elevation explained 4.8% of the variation in ISI. Total herbaceous plant abundance did not vary with elevation, with a random effects model being better than the mixed model ( $\Delta AIC_r = -4.3$ ). LAI decreased with elevation (slope =  $-1.92 \times 10^{-4}$ , SE =  $9.121 \times 10^{-5}$ ,  $\Delta AIC_r = 1.8$ ), but this variation may have been due to site level differences ( $\Delta AIC_r < 2$ ). Elevation explained 5.1% of the variance in LAI. None of the competition variables showed a clear trend with elevation, with large within site variation in all sites (Figure 9).

Table 6: Model output for three mixed models explaining how competition variables vary with elevation.

	<i>Response variable:</i>		
	Leaf Area Index (m <sup>2</sup> m <sup>-2</sup> )	Total Herbaceous Plant Abundance (3.14 m <sup>-2</sup> )	Iterative Seedling Index
Elevation	−0.0002 (0.0001)	−0.00005 (0.0001)	−0.0001 (0.00003)
Constant	3.656 (0.178)	3.835 (0.276)	1.400 (0.063)
Observations	225	227	193
ΔAIC <sub>r</sub>	1.8	−4.3	8.0
R <sub>C</sub> <sup>2</sup>	0.189	NA	0.087
R <sub>M</sub> <sup>2</sup>	0.051	NA	0.048
Model Type	LMM	GLMM	LMM
Family	Gaussian	Negative Binomial	Gaussian

### 3.3 Variation in abiotic environmental variables across elevation

LMMs including site as a random intercept term were conducted to ascertain soil temperature and moisture varied across elevation. Soil temperature decreased with elevation (slope = 4 × 10<sup>−3</sup>, SE = 4 × 10<sup>−4</sup>, R<sub>C</sub><sup>2</sup> = 0.953, ΔAIC<sub>r</sub> = 11.6) (Figure 10a). Soil temperature was poorly predicted at extreme high and low elevations. Soil moisture did not vary appreciably with elevation, with a random effects model explaining the variation more parsimoniously (slope = 3 × 10<sup>−3</sup>, SE = 3 × 10<sup>−3</sup>, R<sub>C</sub><sup>2</sup> = 0.414, ΔAIC<sub>r</sub> = −1203.985). The fixed effect of elevation accounted for 2.2% of the variance in soil moisture.

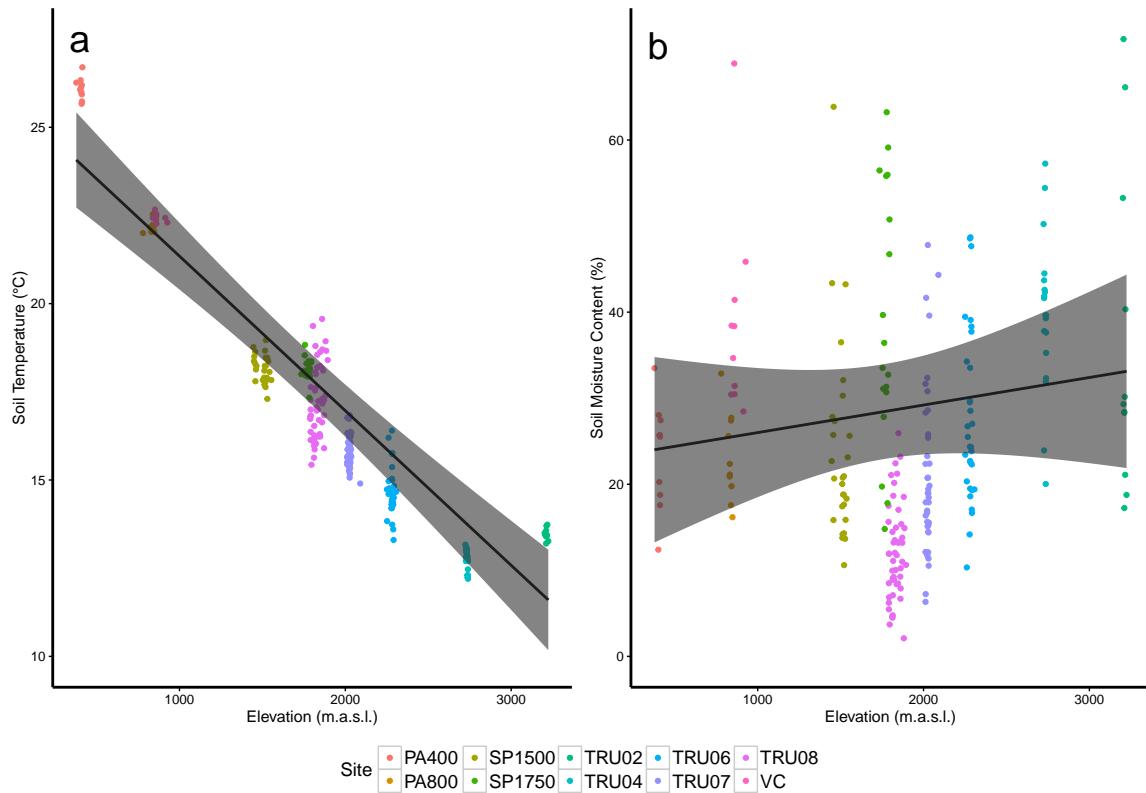


Figure 10: Linear mixed models showing the variation in soil temperature **(a)** and soil moisture **(b)** across elevation. Points are shaded according to site. The thick black line and shaded ribbon show the regression fit and 95% confidence intervals, respectively. Soil temperature shows a clear decrease with elevation, while soil moisture features high variability within sites.

### 3.4 Variation in plant traits across elevation ( $H_{n4}$ , $H_{n5}$ )

LMMs allowing each species to vary in slope allowed variation among species to be identified from the model output. Across species, only leaf thickness was better explained by a model including elevation than a model including only the random effects of site and species (Table 7). All other plant traits had no clear relationship with elevation ( $\Delta AIC_r < 2$ ).

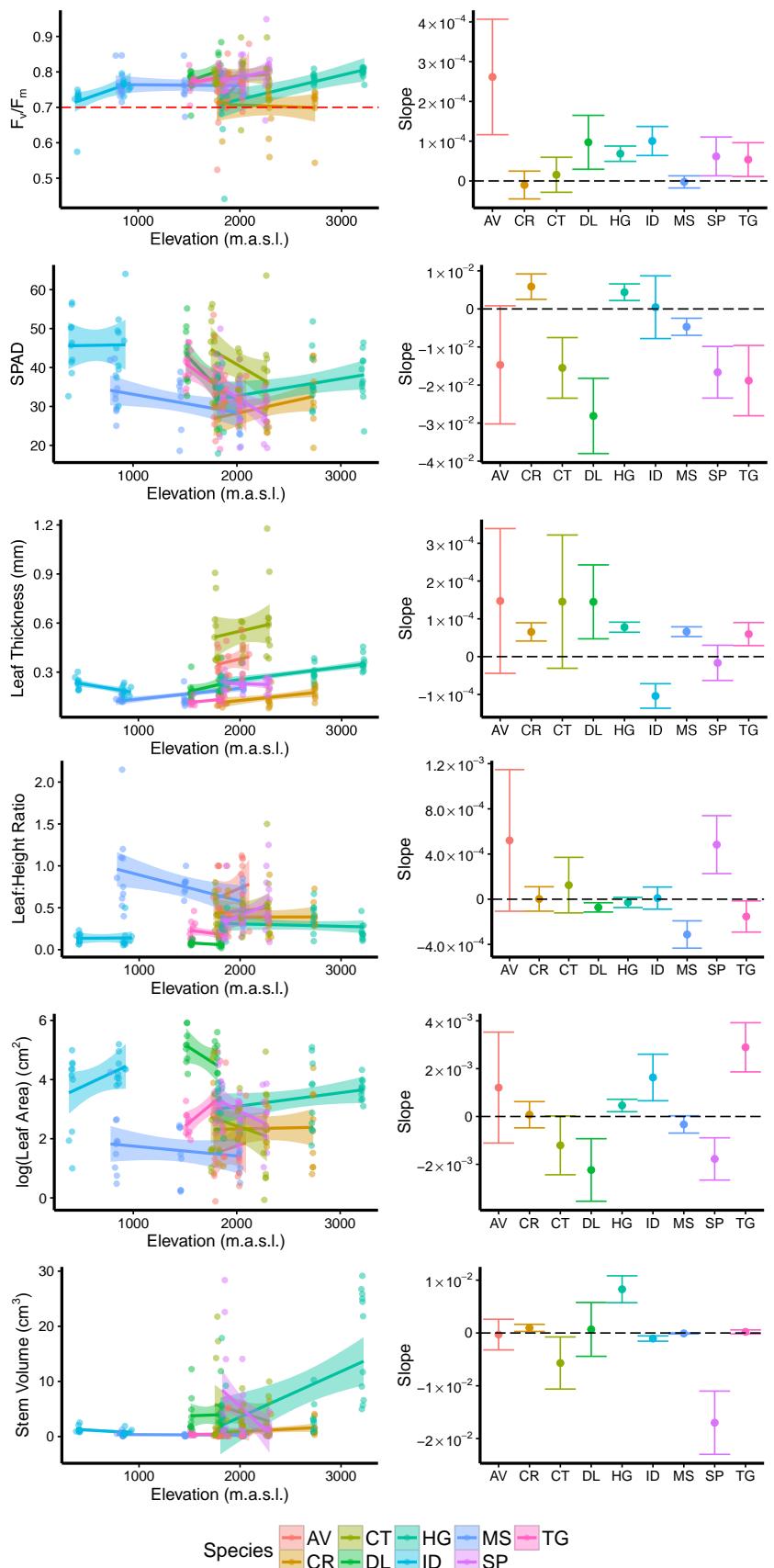


Figure 11: Scatterplots with linear regressions show the slopes for each species (lines) with 95% confidence interval (ribbon) with individual seedling measurements (points). Interval plots show the variation in slopes among species for each plant trait (points) with standard errors (error bars).

Table 7: Model output for six mixed models explaining how plant traits vary with elevation.

	Response variable:					
	F <sub>v</sub> /F <sub>m</sub>	SPAD	Leaf	Leaf:height	log(leaf area)	Stem
			thickness (mm)	ratio (leaves cm <sup>-1</sup> )		volume (cm <sup>3</sup> )
Elevation	0.000 03 (0.000 01)	-0.002 (0.003 )	0.0001 (0.000 02)	-0.0001 (0.000 1)	0.0001 (0.000 2)	0.004 (0.002 )
Constant	0.714 (0.024 )	41.473 (5.965 )	0.132 (0.053 )	0.487 (0.131 )	2.827 (0.358 )	-4.020 (3.970 )
Observations	225	223	223	227	220	227
ΔAIC <sub>r</sub>	1.61	-8.67	6.03	-10.97	-6.35	0.42
R <sup>2</sup> <sub>M</sub>	0.075	0.022	0.068	0.011	0.001	0.156
R <sup>2</sup> <sub>C</sub>	0.379	0.530	0.746	0.476	0.553	0.611

F<sub>v</sub>/F<sub>m</sub> increased with elevation (Figure 11). All species had a positive relationship with elevation except *Myrcia* spp., and *C. revoluta* which did not vary over elevation. Although the overall effect of elevation of F<sub>v</sub>/F<sub>m</sub> was positive, there was a high standard error in this estimate, indicating a low likelihood that there is any consistent variation in F<sub>v</sub>/F<sub>m</sub> across elevation. *A. verticillata* had the steepest positive trend which bore a large standard error. Elevation explained 7.5% of the variation in F<sub>v</sub>/F<sub>m</sub>, while the random effects of species and site accounted for 30.4%. *C. revoluta* had the greatest number of individuals with F<sub>v</sub>/F<sub>m</sub> values below the arbitrary 0.7 threshold indicating plant stress (Maxwell & Johnson 2000), though the number of individuals falling below this threshold did change not markedly across elevation.

SPAD had greatly differing slopes among species, *A. verticillata*, *C. thurifera*, *D. lamarckianum*, *Myrcia* spp., *S. patula* and *T. guianensis* had negative slopes, *I. deltoidea* had a slope near 0, *H. goudotianum* and *C. revoluta*, had positive slopes (Figure 11). Elevation accounted for only 2.2% of the variation in SPAD, while the random effects of site and species account for 50.8% (Table 7).

Leaf thickness increased with elevation. *I. deltoidea* had a negative slope, *S. patula* did not vary, all other species had similar positive slopes. *A. verticillata* and *C. thurifera* had the greatest variance in leaf thickness, with a leaf thickness ranges of 0.8 mm and 0.4 mm respectively.

Leaf:height ratio appeared to decrease with elevation, but this estimate has a large standard error, indicating that there may be no real relationship. Species varied in slope direction, *Myrcia* spp., *D. lamarckianum* and *T. guianensis* decreased, *S. patula*, *A. verticillata* and *C. thurifera* increased, all other species showed no clear change with elevation.

Variation in leaf area across elevation was best explained when log transformed, a non-log transformed model failed to converge. Leaf area appeared to decrease over elevation but species varied in the direction of their slopes. *A. verticillata*, *I. deltoidea*, *H. goudotianum*, and *T. guianensis* increased with elevation, while *S. patula*, *D. lamarckianum*, and *C. thurifera* decreased with elevation. *Myrcia* spp. and *C. revoluta* varied little. Elevation explained 0.1% of the variation in leaf area.

Stem volume appeared to increase with elevation, but this relationship is largely dominated by the influence of *H. goudotianum*, which features some particularly high stem volumes in its upper plot. *I. deltoidea*, *Myrcia* spp., *A. verticillata*, *T. guianensis* and *C. revoluta* show little variation in their stem volume, while *H. goudotianum*, *S. patula*, *C. thurifera* and *D. lamarckianum* show great variation, with a

long tail of high values in most plots. *H. goudotianum* is the only species which increases over elevation, *S. patula* and *C. thurifera* decrease, while all other species show little variation across elevation.

## 4. Discussion

This study aimed to (a) determine whether plant traits were affected by competition variables, (b) assess how the effects of competition compared to that of elevation, and (c) assess the degree to which plant trait-elevation relationships vary among species. It was found that competition variables never influence a given plant trait more than elevation. Adult-seedling competition effects (LAI and ISI) affect plant traits more than seedling-seedling competition (herbaceous plant abundance). LAI and ISI have contrasting effects on plant traits.

### 4.1 Effect of competition and elevation on plant traits

Single fixed effect models demonstrated that the three competition variables influence some plant traits ( $\Delta AIC_r > 2$ , Figure 6a). The effect size of individual competition variables however, did not exceed that of elevation for any plant traits (Figure 6b, Figure 7). The three competition variables, which represent different types of competition, vary in their effects on seedling traits.

#### Leaf physiology

Together, SPAD and  $F_v/F_m$  are useful measures of a plant's health and the integrity of its photosynthetic apparatus (Clark et al. 2000). SPAD is used as a proxy for leaf chlorophyll content (Richardson et al. 2002), while  $F_v/F_m$  measures the efficiency with which a leaf can utilise light for photosynthesis (Maxwell & Johnson 2000). This study found contrasting effects of elevation on SPAD and  $F_v/F_m$ . As elevation increased, photosynthetic efficiency increased but chlorophyll content decreased slightly (Figure 7). There is however, large variation in SPAD within sites and elevation explains little of the variance in SPAD (Figure 11), meaning this relationship may be erroneous. Competition variables explained comparatively little variation in  $F_v/F_m$  or SPAD compared to morphological leaf traits (Figure 11b).

#### Photosynthetic efficiency

Single fixed effect models showed that an increase in canopy density (LAI) caused an increase in photosynthetic efficiency ( $F_v/F_m$ ) (Figure 7). Specifically, an increase in photosynthetic efficiency under denser canopy may be the result of a more temporally constant microclimate (Amissah et al. 2015). A denser canopy regulates diurnal temperature oscillations by more effectively trapping warm air between the canopy and the forest floor, reducing temperature stress on the plant (Larcher 2003). Increased shading under denser canopy also reduces the potential for seedling desiccation and cavitation, which can cause damage to seedling leaves. As Sun-flecks move across the forest floor they result in rapid leaf temperature increase (Rozendaal et al. 2006, Poorter et al. 2010). Additionally, a reduction in direct sunlight reduces the potential for UV-B damage to photosynthetic apparatus (Dobrikova et al. 2013). Diurnal temperature oscillations are generally of greater range at higher elevations (Seidel et al. 2005) as is the UV-B insolation fraction (Piazenna 1996), suggesting that the beneficial effects of increased canopy density on photosynthetic efficiency may become greater at higher elevations. In this region however, persistent cloud cover at higher elevations throughout the day may result in no increase in incident UV-B, the majority being absorbed by cloud condensation nuclei before it reaches the leaf (Flint et al. 2003).

Canopy density decreases with elevation (Figure 9), though this trend may be the result of wide within site variance ( $\Delta AIC_r < 2$ ). This trend concurs with more conclusive results from other studies which show a clear decrease in canopy density with elevation (Kitayama & Aiba 2002, Moser et al. 2008). The more variable relationship seen in this study may be the result of bias in the sampling strategy. LAI was not measured systematically across each site, instead being measured above each sampled seedling. It is expected that seedlings will grow successfully only under canopy where the average light intensity falls between a minimum needed for growth and a maximum that ensures temperature and UV-B stress does

not cause the seedling to perish. In this study therefore, extreme canopy densities were probably not sampled. The presence of bias in our sampling strategy is supported by comparing the range of LAI measurements in other studies. For example, Asner et al. (2003), in a review of 61 tropical evergreen forests, found that LAI ranged from 1.5 to 8. (after outlier exclusion), whereas our LAI estimate ranged from only 1.0 to 5.5, implying that a representative LAI sample was not achieved within each plot.

It is expected that a decrease in canopy density with elevation will lead to more individuals showing signs of stress at higher elevations, due to the factors discussed above. An increase in plant stress limits overall fitness as energy is allocated more to acclimation processes than to fecundity (Reu et al. 2011). This may hinder further upward migration, especially in species with limited dispersal distance such as *I. deltoidea* which relies on seed dispersal by large mammals (predominantly primates) (Russo 2005, Kuprewicz 2013) over short distances. In this instance however, there is no clear decrease in  $F_v/F_m$  with elevation within any species ( $\Delta AIC_r = 1.61$ ), with 8/9 species show an increase in  $F_v/F_m$  with elevation (Figure 11). This suggests that the effect of canopy density in decreasing photosynthetic efficiency across elevation is masked by other environmental variables.

In contrast to the effects of LAI, ISI caused a decrease in photosynthetic efficiency. This suggests that the mechanisms by which LAI may affect photosynthetic efficiency (shading, temperature regulation) differ from those of ISI (nutrient competition, water competition, predation mutualisms) (Lewis & Tanner 2000). Other studies have shown a nutrient competition effect between adult trees and nearby seedlings. Palik et al. (1997) demonstrated that adult trees of greater basal area (equivalent to DBH) cause a larger reduction in soil available nitrogen which subsequently decreased the growth of pine seedlings. Similarly, Barberis & Tanner (2005) showed that trenching around neotropical tree seedlings in order to decrease root competition increased the growth and leaf nutrient content of the seedlings. In this set of plots, soil moisture is rarely a limiting factor, and insect predators are much rarer in cloud forests than lowland forests (Rodriguez-Castaeda et al. 2010). This suggests that any negative effect of increased ISI on photosynthetic efficiency would be the result of nutrient competition by adult trees.

ISI decreases with elevation (Figure 9) and a decrease in ISI causes an increase in photosynthetic efficiency. The increase in  $F_v/F_m$  with elevation may therefore be partly the result of decreased adult-seedling nutrient competition at higher elevations. The large effect of elevation however, implies that other unmeasured environmental variables influence this trend more than simply a decrease in ISI.

Herbaceous plant density had little effect on  $F_v/F_m$ . In the single predictor models, the slope was the smallest of all the environmental variables and explained the least variance (Figure 6, Figure 7). In the multi-predictor models the best fitting model did not include herbaceous plant density (Table 5). Other studies have shown that size-asymmetric competition with adults has a much greater role in structuring forest ecosystems than seedling-seedling competition, especially in tropical forests where seedlings are relatively scarce compared to adult trees (Moles & Westoby 2004, Powers et al. 2004). Paine et al. (2008) estimated the area around tree seedlings in neotropical forests within which seedlings affect the availability of resources both above- and below-ground to other seedlings, finding that most zones did not overlap at all. This implies that seedling-seedling competition in neotropical forests is insignificant.

Maxwell & Johnson (2000) suggest that generally, optimum  $F_v/F_m$  is ~0.83, and that if  $F_v/F_m$  falls below ~0.8, it is indicative of some kind of plant stress. It is important to note however, that this optimum is likely to vary markedly among species and has been criticised as yet another arbitrary threshold for a dynamic phenomenon (Ghouil et al. 2003). As a conservative estimate, here plants are defined as experiencing physiological stress when  $F_v/F_m < 0.7$ . Figure 11 shows that only a few individuals fall below this threshold, suggesting that few individuals along the elevational gradient are experiencing stress. Only *C. revoluta* features reduced photosynthetic capacity with elevation. *C. revoluta* also has the most individuals below the 0.7 threshold. This could be evidence that *C. revoluta* individuals experience greater stress at increasing elevations, but the relationship shown here is not strong enough to be conclusive, with large

variation within each plot that *C. revoluta* seedlings were sampled. Alternatively other species which feature an increase in photosynthetic efficiency may be experiencing stress at lower elevations, giving support for the hypothesis given by Campbell et al. (2007), in which species ranges contract from the bottom up. Temperature increase is the most likely source of this increased stress at the lower limits of species ranges, though stress induced by antagonistic interactions from previously lower elevation species that have shifted upslope faster is also possible. Herbivores for example are expected to move upslope faster than tree species due to their mobility and shorter life-cycles (Chen et al. 2011).

### **SPAD**

SPAD value was not clearly influenced by any of the measured competition variables, or elevation (Figure 7). SPAD varied largely both within and among species, with large standard errors surrounding the estimates of each species (Figure 11, Table 7). The best fitting multiple fixed effect LMM for SPAD did not include elevation (Figure 5), though this model was only 14.2% more likely to be the best model than the next best model and the fixed effect of LAI accounted for only 0.4% of the variance in SPAD (Figure 5).

The lack of meaningful variation in SPAD contrasts other studies that have shown increases in chlorophyll content in response to shading (Brand 1997, Rijkers et al. 2000, Rozendaal et al. 2006, Dai et al. 2009, Zervoudakis et al. 2012) and soil nitrogen content (Cechin & De Fátima Fumis 2004). In this study however, SPAD did not vary with LAI (shading), ISI (soil nutrient availability) or herbaceous plant abundance.

The species with the smallest ranges show the steepest decrease in SPAD with elevation (Figure 11). From this one could suggest that specialists are more sensitive to increases in elevation in terms of their photosynthetic apparatus. Species with small ranges are interpreted as being more specialist in their environmental requirements (Thuiller et al. 2005).

### **Summary**

Most species demonstrated an increase in  $F_v/F_m$  with elevation, while SPAD showed little meaningful variation in response to elevation. Adult-seedling competition variables had contrasting effects on  $F_v/F_m$  while seedling-seedling competition had no effect. A decrease in ISI with elevation may have contributed to the observed increase in  $F_v/F_m$  with elevation though it is possible that this trend is actually a result of increased stress at lower elevations in response to temperature stress or herbivory stress.  $H_{n1}$  is therefore accepted for SPAD and rejected for  $F_v/F_m$ . The best multiple fixed effect model for  $F_v/F_m$  included all competition variables,  $H_{n2}$  is therefore rejected for  $F_v/F_m$ . SPAD is predicted equally poorly by elevation and competition variables.

### **Leaf and plant morphology**

Leaf thickness increased with elevation. Other studies have also found positive correlations between leaf thickness and elevation, identifying climatic drivers such as mean daily insolation and diurnal temperature variation (Niinemets 2001), which lead to reduced leaf pay-back times and a need to grow leaves that can survive the more variable environmental conditions found at higher elevations (Milla & Reich 2011).

Increased UV-B results in an increase in cuticle thickness, to reduce the concentration of UV-B absorbed by photosystem II (PSII) where it can cause damage and thus photoinhibition (Vass et al. 1997, Szilard et al. 2007). In this study however, it is unclear whether the insolation UV-B fraction does increase with elevation as it was not measured. Additionally, it is expected that frequent cloud immersion in the high elevation sites would reduce UV-B absorption and thus the need for thick cuticles. Leaf thickness decreased under increased canopy density (Figure 7), adding support to the conclusion that increased direct sunlight is the cause of the decrease in leaf thickness with elevation.

Leaf area variation was explained poorly by both competition variables. Previous studies have shown a clear decrease in leaf area with elevation, citing decreases in canopy density and an increase in nutrient competition with elevation as drivers of this variation (Pan et al. 2013). Plants with access to higher

resource levels generally invest in leaves which can achieve a higher photosynthetic rate per energy input in leaf construction, at the expense of leaf longevity (Mediavilla & Escudero 2009). In the plots studied here however, available nitrogen does not decrease with elevation, though elevational variation in other nutrients is not known.

Leaf:height ratio decreased with elevation (Figure 7) meaning that plants became less leafy per unit stem height as elevation increased. However this relationship explained very little of the variance in leaf:height ratio (Table 7). Competition variables had little effect on leaf:height ratio (Figure 7). Few studies have focussed specifically on measures of leaf:height ratio or number of leaves as an adaptive/acclimatory trait though we may interpret that a reduction in “leafiness” is an extension of the trend seen in reduced leaf area with elevation. Seedlings may be more likely to produce fewer leaves in order to allocate more biomass to structural support in those leaves that are grown (Onoda & Anten 2011).

Stem volume decreased with ISI (Figure 7). This may have contributed to the increase in stem volume with elevation, as ISI decreases with elevation (Figure 9). Other studies have found that stem volume increases with average wind speed in order to provide greater stem support (Onoda & Anten 2011), and that stems become more elongated as diurnal temperature range increases (Myster & Moe 1995). Wind speed is expected to increase with elevation as is diurnal temperature range, providing further support for the trend seen here. An increase in stem volume with elevation suggests that tree seedlings are allocating less biomass to other parts such as the leaves, meaning that plant growth may be slower at higher elevations. This is supported by the negative relationship between leaf area and elevation, and the negative relationship between leaf:height ratio and elevation, which suggests that seedlings produce fewer, smaller leaves as elevation increases.

### **Summary**

Stem volume was the only morphological plant trait that showed clear variation with a competition variable (ISI), therefore  $H_{n1}$  is accepted for all other morphological plant traits. All morphological plant traits were best explained by a multiple fixed effect model including elevation and a combination of competition variables, therefore  $H_{n2}$  is accepted for all morphological plant traits. Morphological plant traits varied across elevation in a manner similar to that identified by previous studies, responding to elevation dependent abiotic environmental variables such as temperature and nutrient availability. The strength of the relationships seen here is not as great as that demonstrated by other studies, possibly because of the comparatively low sample size per species in this study compared to larger reviews and the presence of confounding environmental variables that were not accounted for in statistical analysis.

## **4.2 Variation in plant traits with elevation**

Within each species, plant traits vary across elevation, with slope standard errors overlapping zero in only a few instances (Figure 11).  $H_{n4}$  can therefore be rejected, and it can be concluded that the individuals sampled in this study are acclimating their morphology in response to elevationally dependent environmental variables. The difference in magnitude and direction of the relationships shows that species are responding differently to changes in elevation. Supporting the observations and predictions of other studies that species are likely to migrate at different rates to climate change. Those species showing increased morphological change with elevation are expected to be more sensitive to changes in climate and are thus more likely to show greater migration rates.

### **Variation among species**

Species varied largely in the direction, magnitude and variance of their plant trait response to elevation (Figure 11), therefore  $H_{n5}$  is rejected. Variation among species in slope implies that species differ in their sensitivity to changing environmental conditions across elevation. *D. lamarckianum* and *I. deltoidea*, the two monocot species, show no similarity in their plant trait response to elevation, often having different slope directions for a given plant trait. Together, *D. lamarckianum* and *I. deltoidea* show no difference to

dicot species in terms of their plant trait-elevation relationship. *A. verticillata* has a comparatively large variance for all trait-elevation relationships except stem volume. This implies that *A. verticillata* is either more sensitive to changes in climate, or that it has a larger acclimatory range than other species; both may be true. *A. verticillata* has a very small elevational range (Figure 2) but is also one of the most common tree species found along this set of plots (Appendix VI). This supports the theory that common species have a wider acclimatory range and that species with small ranges are sensitive to environmental variation. In contrast, *Myrcia* spp. has little variation in plant traits compared to other species but has the largest elevational range, the *Myrcia* spp. species sampled are among the rarer species sampled.

Leaf thickness had a similar positive relationship with elevation in 7/9 species, whereas *I. deltoidea* and *S. patula* featuring reduced leaf thicknesses with elevation (Figure 11). *C. thurifera* had exceptionally high variance compared to other species, this is due to dense and prominent leaf vein structure in this species (Appendix V). For many *C. thurifera* individuals, the diameter of the micrometer used to measure leaf thickness was too wide to be placed between the prominent leaf veins, leading to an over-estimation of leaf thickness for these individuals. Regardless, *C. thurifera* showed a similar increase in leaf thickness with elevation. *I. deltoidea* had the steepest decrease in leaf thickness over elevation (Figure 11). This trend may be a peculiarity of the species or a result of environmental conditions at the upper sample plot for this species (VC). It is impossible to confirm whether site level variation at VC had a peculiar effect on *I. deltoidea* leaf thickness as *I. deltoidea* was the only species sampled at this site. Potentially, the greater leaf thickness at PA400 compared to VC is due to an adaptation to increased herbivory pressure at PA400. There is no evidence for this increase in herbivory in lowland plots other than a general trend that herbivory pressure decreases with elevation in tropical forests (Rodriguez-Castaeda et al. 2010).

## Summary

Tree seedlings are responding to changes in elevationally dependent environmental variables by altering their morphology. Additionally, the strength of the plant trait response varies between species, suggesting that some species are more sensitive to environmental change than others.

The lack of a clear relationship between plant traits and competition intensity, suggests that tree seedlings are not affected by the biotic environment at the extremes of their ranges more than they are by other environmental variation. Species will therefore continue to migrate upslope, largely unimpeded by changes in biotic environment. It is possible that species will encounter biotic environmental thresholds beyond which adaptation and acclimation are no longer able to prevent stress and increased mortality. In order to answer these questions experimental transplantation is recommended, in order to place individuals outside of their current range. Even then, experimental transplants do not account for potentially rapid micro-evolution that may occur as species migrate into novel environments. Sufficiently rapid micro-evolution could result in species being able to migrate upslope almost indefinitely, as they adapt and become more able to acclimate to changing climates.

## 4.3 Predictions for future species migration

This study confirms that adult-seedling competition intensity decreases with elevation ( $H_{n3}$ ), and that this decrease causes some proportion of the effect of elevation on plant traits, though this proportion is likely to be small as LMMs show that elevation still has the greatest influence over plant traits, despite including competition variables alongside elevation in multiple fixed effect models. As such, species may continue to move upslope as temperature increases, without being negatively affected physiologically at the upper limits of their ranges by adapting their morphology to the changing environment. The results from this study however, cannot be used to determine what will happen if a species reaches its adaptational limits as its range shifts. Given that few species experienced physiological stress, it is suggested that none of the species sampled have reached this limit yet. The exception being *C. revoluta*, which shows some evidence of increased physiological stress with elevation and relatively flat relationships between elevation

and plant traits, though this trend cannot be confirmed without more study.

Most species featured a decrease in photosynthetic efficiency at the bottom of their elevational ranges. This implies that these species may experience progressively greater plant stress at the bottom of their ranges as temperature increases, and the bottom of their range will continue to shift upslope as a result. This study cannot infer whether the contraction of species' lower range limits will be faster or slower than the expansion of the upper range limit, though other studies have suggested that lower range limits will shift upslope faster than upper limits (Campbell et al. 2007), owing to climate change proceeding faster than micro-evolutionary processes to adapt to higher elevations. This will lead to an overall reduction in range size for many species.

#### **4.4 Limitations of this study**

This study sampled seedling physiology over a narrow time period. While  $F_v/F_m$  and SPAD are unlikely to vary on a daily basis, they may do so over the course of a season (Porcar-Castell 2008). Seedlings are likely to alter their leaf physiology and morphology in response to a temporally heterogeneous environment throughout the course of their life. As canopy gaps open and close the light and precipitation regime will change. The measured physiological responses of individuals therefore may not be representative of its physiology over a lifetime. Furthermore, this study only measured seedlings, ignoring other life stages. This means the results of this study cannot be used to directly infer the effects of biotic interactions on plant traits across entire populations. It is likely however, that established adult trees will be less sensitive to competition from other adult trees and completely insensitive to competition from seedlings (Paine et al. 2008).

Nine tree species were selected for this study. Although these species are common in the areas we sampled (Appendix VI), there are many other species which may react more or less to the biotic environment. There is evidence that rare species are more affected by environmental factors (Lyons et al. 2005, Mouillot et al. 2013). Rare species are more likely to occupy specialist niches, which are narrower on a local geographical scale than those of generalist species (Boulangeat et al. 2012). The evolutionary histories of specialists mean they are less likely to be able to acclimate to novel environments. Compared to the common species studied here, rare species will not have such a large direct effect on globally significant ecosystem services such as carbon sequestration, albedo, and drainage. This does not mean that rare species do not have the potential to heavily influence ecosystem services indirectly. Lyons & Schwartz (2001), and Lyons et al. (2005) found that less common species play vital supporting roles in maintaining ecosystem functions such as enhancing invasion resistance and making limiting resources available to other species .

There is large potential for falsely inferring causation from the results of this study. Along elevational gradients many environmental factors both abiotic and biotic co vary. For example, this study concluded that an increase in ISI caused a decrease in photosynthetic efficiency. However, it was found that ISI covaries with elevation, along with many other potential unmeasured environmental variables, therefore photosynthetic efficiency may have merely inversely correlated with ISI rather than ISI causing the variation in photosynthetic efficiency, despite well-documented supporting evidence.

This study is deliberately wide in its scope, using competition intensity proxies in order to infer the influences of many ecosystem processes such as nutrient competition, shading, etc.. By not explicitly testing the effects of these mechanistic processes, which are complex in their effects, we cannot determine the relative contribution of each process implicit in each competition proxy. It is recommended therefore that experiments under constant environmental conditions explicitly test the effect of variation in ecosystem processes which are implied to change as a result of variation in the competition proxies measured here, such as nutrient availability and shading.

The study did not use experimental treatments. It could be argued therefore that measured seedlings

would have been unlikely to show stress at all, as seedlings would not have grown to the minimum size needed for measurement otherwise.

#### **4.5 Further research**

On the basis of this study, which shows that adult-seedling competition intensity varies across elevation and that this variation forms part of the observed plant trait response to elevation, it is recommended that future studies aim to identify competition intensity thresholds beyond which individuals cannot acclimate to the environmental conditions. The location of thresholds should be confirmed using experimental transplantation of seedlings to different elevations to observe variation in plant traits.

In order to determine whether changes in competition intensity also affect adult trees, and thus recruitment, similar studies should be performed on adult trees. This would help to improve the accuracy of species range-shift models by adding the potential variation found within populations and allowing demographically explicit models.

### **5. Conclusions**

This study has provided an estimation of the relative effects of seedling-seedling and adult-seedling competition on neotropical tree seedling plant traits, thereby evaluating the potential for competition effects to limit vertical range shifts in response to anthropogenically induced temperature increase. This study found that the intensity of adult-seedling competition affected photosynthetic efficiency, stem volume and leaf thickness. Investigation of the variation in these competition proxies over elevation showed that competition effects form part of a complement of environmental variables that covary across elevation, resulting in an overall variation in plant traits with elevation.

Multiple fixed effect models were of better quality when including competition variables alongside elevation as predictors of plant traits. In light of this, it is suggested that adult-seedling competition proxies or more direct measures of adult-seedling competition are included in future species distribution models alongside climatic variables in order to more accurately and precisely predict species migrations.

This study cannot make direct predictions of how species will react to environmental conditions outside of those measured here. Instead it is suggested that future studies focus on experimental transplantation of seedlings to elevations outside of their current ranges in order to build more realistic predictions of future range shift potential.

There was marked variation between species in their plant trait response to elevation. This provides supporting evidence for conclusions of other studies which either predict or demonstrate that species differ in their sensitivity to variation in environment and will therefore be likely to vary in their rate of upslope migration. The presence of species specific range shift trends supports the conclusion that biotic environmental effects should be included in range-shift models, as they are only likely to become stronger over time as species ranges overlap.

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## 7. Appendices

Appendix I: Model comparison of generalised linear mixed models assuming different error distributions, of the relationship between elevation and herbaceous plant abundance. A negative binomial distribution has a higher  $\Delta\text{AIC}_r$  and was thus chosen as the best model.

Model Type:		
	GLMM Poisson	GLMM Negative Binomial
Elevation	−0.001 (0.001)	−0.000 05 (0.000 1)
Constant	4.898 (1.173)	3.835 (0.276)
Observations	227	227
$\Delta\text{AIC}_r$	−287.2	−4.3

Appendix II: Full mixed effects model output for the best multiple fixed effects model explaining each plant trait. 'NA' indicates that a fixed effect was not used in the best model.

	Response variable:					
	$F_v/F_m$	SPAD	Leaf Thickness (mm)	Leaf:height ratio (leaves cm <sup>−1</sup> )	log(Leaf area) (mm <sub>2</sub> )	Stem Volume (cm <sup>3</sup> )
<b>Fixed Effects</b>						
LAI	0.115 (0.069)	−0.066 (0.067)	−0.136 (0.041)	−0.103 (0.050)	−0.066 (0.090)	−0.054 (0.057)
Herbaceous Plant Abundance	NA (NA)	NA (NA)	NA (NA)	0.026 (0.087)	0.106 (0.103)	−0.064 (0.053)
ISI	−0.126 (0.068)	NA (NA)	−0.024 (0.039)	0.012 (0.048)	−0.012 (0.052)	−0.198 (0.119)
Elevation	0.361 (0.106)	NA (NA)	0.293 (0.085)	−0.141 (0.128)	−0.377 (0.358)	0.310 (0.132)
Constant	−0.003 (0.083)	0.076 (0.101)	0.018 (0.137)	0.016 (0.105)	−0.028 (0.118)	0.038 (0.098)
Observations	191	191	191	191	189	191
$\Delta\text{AIC}_r$	8.8	−1.0	12.4	10.7	5.8	32.3
$R^2_C$	0.320	0.325	0.761	0.578	0.802	0.575
$R^2_M$	0.140	0.004	0.120	0.030	0.071	0.173

Appendix III: Comparison of models allowing species to vary either by intercept or slope ( $\Delta\text{AIC}_r$  and the comparison of the best of these two models to a random effects model ( $\Delta\text{AIC}_r$ , Slope,  $R_C^2$ ). Elev. = Elevation, LAI = Leaf Area Index, HPA = Herbaceous Plant Abundance, ISI = Iterative Seedling Index. RS/RI indicates whether a random intercept (RI) or random slope (RS) model was of better quality according to AIC.

	Fixed Effect	$\Delta\text{AIC}_{\text{rsri}}$	RS/RI	$\Delta\text{AIC}_r$	Slope	$R_C^2$
$F_v/F_m$	Elev.	-11.8	RI	-13.4	0.000 03	0.287
	LAI	-3.4	RI	-7.5	0.01	0.258
	HPA	-2.6	RI	-5.7	-0.0001	0.246
	ISI	-3.3	RI	-9.6	-0.03	0.238
SPAD	Elev.	-8.8	RI	-43.8	-0.001	0.305
	LAI	1.0	RS	-45.3	-1.40	0.355
	HPA	-3.2	RI	-44.8	-0.031	0.324
	ISI	1.1	RS	-44.4	1.4	0.338
Leaf Thickness (mm)	Elev.	-10.0	RI	-207.5	0.0001	0.750
	LAI	23.2	RS	-232.5	-0.04	0.760
	HPA	-3.9	RI	-200.0	-0.000 01	0.738
	ISI	-3.9	RI	-200.3	-0.01	0.739
Leaf:height ratio (leaves cm <sup>-1</sup> )	Elev.	-9.5	RI	-72.3	-0.001	0.416
	LAI	-2.3	RI	-72.7	0.7	0.402
	HPA	-3.8	RI	-74.4	-0.03	0.419
	ISI	-1.0	RS	-71.8	1.3	0.418
log(Leaf area) (mm <sup>2</sup> )	Elev.	-0.3	RI	-86.6	0.001	0.491
	LAI	8.8	RS	-95.4	-8.5	0.608
	HPA	1.0	RS	-87.6	0.1	0.554
	ISI	5.1	RS	-91.7	9.0	0.496
Stem volume (cm <sup>3</sup> )	Elev.	-4.5	RI	-74.3	4.3	0.537
	LAI	-3.4	RI	-68.1	-35.8	0.558
	HPA	-2.0	RI	-71.3	-27.9	0.575
	ISI	21.5	RS	-101.5	-4866.6	0.560

Appendix IV: Full model comparison of multiple fixed effect models for each plant trait (a - f), ranked by AIC.  $\Delta\text{AIC}_r$  is the  $\Delta\text{AIC}$  between a random effects model and that model. Models highlighted in **bold** were chosen as the best model on the basis of  $\Delta\text{AIC}_r$ ,  $R_C^2$  and  $W_i$  and reported in the main text. Elev. = Elevation, ISI = Iterative Seedling Index, LAI = Leaf Area Index, HPA = Herbaceous Plant Abundance, Sp = Random effect of Species, Site = Random effect of site. Model fixed effects bracketed by [...] were allowed to vary by slope between species.

### a: $F_v/F_m$

Model code	AIC	$\Delta\text{AIC}_r$	$W_i$	$R_C^2$	$R_M^2$
<b>Elev. + ISI + LAI + Sp + Site</b>	264.4	-8.8	0.421	0.320	0.140
Elev. + ISI + LAI + HPA + Sp + Site	266.1	-7.1	0.178	0.322	0.141
Elev. + ISI + LAI + Sp + Site	266.4	-6.7	0.152	0.313	0.135
Elev. + Sp + Site	266.9	-6.3	0.122	0.287	0.116
Elev. + LAI + HPA + Sp + Site	267.6	-5.6	0.085	0.303	0.128
ISI + Sp + Site	270.7	-2.5	0.018	0.238	0.021
ISI + LAI + HPA + Sp + Site	271.9	-1.3	0.010	0.261	0.034
LAI + Sp + Site	272.8	-0.4	0.006	0.258	0.012
Sp + Site	273.2	0.0	0.005	0.242	<0.001
HPA + Sp + Site	274.5	1.3	0.003	0.246	0.003

### b: SPAD

Model code	AIC	$\Delta\text{AIC}_r$	$W_i$	$R_C^2$	$R_M^2$
Sp + Site	235.0	0.0	0.240	0.321	<0.001
HPA + Sp + Site	235.4	0.4	0.195	0.324	0.007
<b>LAI + Sp + Site</b>	236.0	1.0	0.143	0.325	0.004
Elev. + Sp + Site	236.5	1.5	0.115	0.305	0.011
ISI + Sp + Site	237.0	2.0	0.089	0.320	<0.001
LAI + HPA + Sp + Site	237.3	2.3	0.075	0.310	0.025
ISI + LAI + HPA + Sp + Site	238.0	3.0	0.054	0.330	0.013
Elev. + ISI + HPA + Sp + Site	238.8	3.8	0.036	0.310	0.020
Elev. + ISI + LAI + HPA + Sp + Site	239.3	4.3	0.028	0.311	0.024
Elev. + ISI + LAI + Sp + Site	239.5	4.5	0.026	0.305	0.014

### c: Leaf Thickness

Model code	AIC	$\Delta\text{AIC}_r$	$W_i$	$R_C^2$	$R_M^2$
Elev. + LAI + HPA + Sp + Site	65.7	-12.5	0.386	0.758	0.123
<b>Elev. + ISI + LAI + Sp + Site</b>	65.9	-12.4	0.365	0.761	0.120
Elev. + ISI + LAI + HPA + Sp + Site	67.3	-11.0	0.176	0.759	0.122
LAI + Sp + Site	70.947	-7.3	0.029	0.741	0.017
Elev. + ISI + LAI + [HPA] + Sp + Site	71.2	-7.0	0.025	0.760	0.120
Elev. + Sp + Site	72.8	-5.5	0.011	0.750	0.086
LAI + HPA + Sp + Site	74.2	-4.1	0.006	0.739	0.019
Elev. + ISI + HPA + Sp + Site	76.5	-1.7	0.002	0.751	0.086
Sp + Site	78.3	0.0	0.001	0.739	<0.001
ISI + Sp + Site	79.9	1.7	<0.001	0.739	0.001
[HPA] + Sp + Site	84.16	5.9	<0.001	0.740	<0.001

**d:** Leaf:Height Ratio

Model code	AIC	$\Delta AIC_r$	$W_i$	$R^2_C$	$R^2_M$
<b>[Elev.] + ISI + LAI + [HPA] + Sp + Site</b>	158.5	-10.7	0.620	0.578	0.030
[Elev.] + Sp + Site	159.8	-9.5	0.334	0.539	0.035
Elev. + LAI + HPA + Sp + Site	166.3	-3.0	0.013	0.578	0.064
Elev. + ISI + LAI + Sp + Site	166.3	-3.0	0.013	0.578	0.064
LAI + Sp + Site	167.9	-1.4	0.006	0.530	0.011
Elev. + ISI + LAI + HPA + Sp + Site	168.0	-1.3	0.005	0.577	0.065
Sp + Site	169.3	0.0	0.003	0.530	<0.001
Elev. + ISI + HPA + Sp + Site	169.4	0.1	0.003	0.530	0.063
<b>[HPA] + Sp + Site</b>	170.5	1.2	0.002	0.527	0.002
ISI + Sp + Site	171.2	1.9	0.001	0.530	<0.001
LAI + HPA + Sp + Site	171.4	2.2	0.001	0.529	0.012

**e:** Leaf Area

Model code	AIC	$\Delta AIC_r$	$W_i$	$R^2_C$	$R^2_M$
[LAI] + Sp + Site	181.9	-6.8	0.485	0.608	0.004
<b>[Elev.] + ISI + [LAI] + [HPA] + Sp + Site</b>	182.9	-5.8	0.296	0.802	0.071
[Elev.] + Sp + Site	183.9	-4.9	0.184	0.722	0.071
Sp + Site	188.8	0.0	0.016	0.490	<0.001
[HPA] + Sp + Site	189.7	1.0	0.010	0.554	0.002
ISI + Sp + Site	190.7	2.0	0.006	0.491	<0.001
Elev. + ISI + LAI + Sp + Site	194.7	5.9	0.001	0.493	<0.001
LAI + HPA + Sp + Site	194.7	5.9	0.001	0.492	<0.001
Elev. + LAI + HPA + Sp + Site	194.7	6.0	0.001	0.492	<0.001
Elev. + ISI + HPA + Sp + Site	194.7	6.0	0.001	0.492	<0.001
Elev. + ISI + LAI + HPA + Sp + Site	196.7	7.9	<0.001	0.493	<0.001

**f:** Stem Volume

Model code	AIC	$\Delta AIC_r$	$W_i$	$R^2_C$	$R^2_M$
<b>Elev. + [ISI] + LAI + HPA + Sp + Site</b>	177.8	-32.3	0.610	0.575	0.173
[ISI] + Sp + Site	178.7	-31.4	0.389	0.560	0.043
Elev. + ISI + HPA + Sp + Site	194.6	-15.6	<0.001	0.595	0.229
Elev. + ISI + LAI + HPA + Sp + Site	196.4	-13.7	<0.001	0.597	0.230
Elev. + ISI + LAI + Sp + Site	198.5	-11.6	<0.001	0.578	0.219
LAI + HPA + Sp + Site	199.8	-10.3	<0.001	0.593	0.044
Elev. + Sp + Site	205.9	-4.2	<0.001	0.537	0.185
Elev. + LAI + HPA + Sp + Site	206.9	-3.3	<0.001	0.554	0.194
HPA + Sp + Site	209.0	-1.2	<0.001	0.575	0.009
Sp + Site	210.1	0.0	<0.001	0.558	<0.001
LAI + Sp + Site	212.1	2.0	<0.001	0.558	<0.001

Appendix V: Photographs of seedlings representative of the average growth form of the nine species sampled.

Figure 12: *Alzatea verticillata*

Figure 13: *Clethra revoluta*

Figure 14: *Clusia thurifera*

Figure 15: *Dictyocaryum lamarckianum*

Figure 16: *Hedyosmum goudotianum*

Figure 17: *Iriartea deltoidea*

Figure 18: *Myrcia* spp.

Figure 19: *Schefflera patula*

Figure 20: *Tapirira guianensis*

Appendix VI: Rank abundance curve of all individuals >10 cm DBH of all species found in the plots measured in this study. Census data from 2014 (ABERG, unpublished data). Species sampled as part of this study are highlighted in red (●). *Myrcia* species which form the composite *Myrcia* spp. are highlighted in green (●).

