

1 Changes in forest structure along an elevational gradient in the  
2 Peruvian Andes cause species-specific stress responses in tree  
3 seedlings

4 John L. Godlee

5 August 27, 2019

6 **Abstract**

- 7
- 8 We assessed the contribution of biotic competition factors to limiting elevational range  
9 shifts of tree species along an Amazon to Andes elevational gradient, focussing on tree  
10 seedlings as a key demographic bottleneck for future recruitment.
  - 11 Photosynthetic capacity measured using chlorophyll fluorescence estimated photosynthetic  
12 stress experienced by naturally occurring seedlings of seven tree species spanning the el-  
13 evational gradient. Physiognomic plant traits were also measured to assess the degree of  
14 local acclimatory response to elevationally dependent environmental factors.
  - 15 We used linear mixed effects models to compare the effect sizes of individual biotic compe-  
16 tition fixed effects against that of elevation. A matrix of multiple fixed effect mixed effects  
17 models were compared statistically to ascertain the best combination of predictors affecting  
18 seedling growth and stress metrics.
  - 19 •

20 **1 Introduction**

21 Rapid anthropogenic climate change is causing many species, across a wide range of taxa, to shift  
22 their distributions in space (Chen et al., 2011; Hughes, 2000; Parmesan, 2006). The primary forces  
23 driving this are an increase in temperature and changes in precipitation regime (Corlett and West-  
24 cott, 2013; McCain and Colwell, 2011). Chen et al. (2011) estimates that globally, across a range  
25 of taxonomic groups, species are experiencing mean latitudinal and altitudinal migration rates of  
26  $17.6 \pm 2.9$  km and  $12.2 \pm 1.8$  m per decade, respectively. Previous studies have suggested that the  
27 ability of species to respond to changes in mean annual temperature and precipitation regime will  
28 be important in determining species success over the coming century (Colwell et al., 2008; Chen  
29 et al., 2011; Feeley et al., 2012).

30 Species responses to climate change may occur either in the form of adaptation, *i.e.* changes  
31 in phenology, physiology and morphology, or through range shifts over space (Bellard et al., 2012).  
32 Range shifts have been observed in many studies across the world, particularly in temperate, sub-  
33 arctic and mountainous regions where temperature change is the most extreme (Lenoir and Sven-  
34 ning, 2015). The number of studies documenting adaptational responses are fewer, potentially  
35 indicating that climate change is occurring so rapidly as to prevent effective adaptational responses

(Mantyka et al., 2012). Range shift rates vary between species depending on their sensitivity to climate and their fecundity, which affects rate of recruitment into newly suitable areas (MacLean and Beissinger, 2017; Travis et al., 2013). This has the potential to create new species assemblages as species ranges begin to overlap more or less as they shift, with consequences for ecosystem functionality as novel forest assemblages are created. Predicting range shifts across space has become an active field of research, (see Bellard et al. 2012 and references therein), and is being used as a tool to inform conservation strategies to mitigate the effects of climate change on biodiversity and ecosystem functionality (Dawson et al., 2011).

The majority of species distribution models used to predict species range shifts as a conservation tool have used bioclimatic envelopes to constrain species' ranges (Pearson and Dawson, 2003; Sinclair et al., 2010). Bioclimatic envelopes are constructed by correlating current species range extent with observed environmental conditions within those boundaries, then projecting spatially explicit climate trends into the future under different climate change scenarios to predict how species range boundaries will adjust in response (e.g. Araújo et al. 2006; Berry et al. 2002; Peterson et al. 2002; Thuiller et al. 2005). These models have been criticised often for being overly simplistic, especially when applied at the local scale (McMahon et al., 2011), where other factors that have not been considered by the bioclimatic envelope model become important limiting factors for a species. Such factors include unmeasured environmental variables, physical factors such as topography, and biotic interactions with other species (Davis et al., 1998; Ettinger et al., 2011; Van der Putten et al., 2010).

When range shifts in a rapidly changing climate are driven by a single environmental variable like mean annual temperature, it is possible that a species will move into an area that is sub-optimal in other ways than those predicted by the model if range shifts outstrip acclimatory/adaptive potential. Range shifts into sub-optimal habitats may lead to reductions in local species abundance and/or richness (Colwell et al., 2008), changes in community composition (), ecosystem functioning (Bellard et al., 2012), and ecosystem service provision that are not predicted by bioclimatic envelope models (Dobson et al., 2006; Isbell et al., 2011). In order to accurately predict range shifts and their consequences for future ecosystem assembly, it is important that predictive range models be expanded to include variables which describe habitat as well as climate (Wisz et al., 2013).

For sessile taxa such as trees, range shifts occur as a result of differential recruitment and mortality over space, at the leading and trailing edges of their range (Corlett and Westcott, 2013). In communities of long-lived tree species however, the forest ecosystem may not shift in equilibrium with the climate as trees are resilient to gradual changes in climate, developing large root systems and below-ground water and nutrient reserves to buffer against stressful conditions; adult trees may persist where more sensitive seedlings perish (Bell et al., 2014; Lenoir et al., 2009). As seedlings recruit upslope into areas that are newly suitable in terms of temperature, they will encounter novel biotic environments. Forest trees, particularly those in moist tropical forests, often experience high levels of mortality during the seedling recruitment stage, creating a key demographic bottleneck that can impact a species' success, potentially limiting upslope migration (Coomes and Grubb, 2000). Seedling growth is affected by shade regimes created by adult tree canopy gaps. There is abundant evidence that shading from adult tree canopies reduces seedling growth rate and thus increases the probability of seedling mortality, with tropical forest tree seedlings frequently growing into canopy gaps (Valladares et al., 2016). Additionally however, seedlings of many tropical tree species are highly adapted to shade (Matsuraba et al., 2009), meaning that if a seedling germinates in an open space, especially at a higher elevation than normal, where UV-B intensity is higher, mortality by UV-B and heat damage to photosynthetic machinery is quite probable (Krause et al., 2001). Seedlings may also compete with adult trees for nutrients and rootspace, although there is some separation between seedling and adult tree rooting depths for most species (Lewis and Tanner, 2000), especially for the largest trees. This seedling mortality bottleneck provides a limiting factor to the success of tropical forest tree species experiencing range shifts. If seedlings germinate in areas that have a different overstorey shade regime, damage may occur leading to loss of photosynthetic

86 capacity, reducing growth rates and occasionally resulting in seedling mortality.

87 In montane cloud forests, elevational range shifts are occurring rapidly (Feeley et al., 2011).  
88 As mean annual temperatures rise, plant species are figuratively pushed up-slope, with higher  
89 recruitment at the upslope edge of their range and higher mortality / lower recruitment at the  
90 downslope edge of their range. Particularly in the tropics, as altitude increases, UV-B radiation  
91 intensity from insolation increases (?), with many species found at high altitudes having specific  
92 adaptations to avoid UV-B damage to photosynthetic machinery, such as vertically stacked palisade  
93 mesophyll cells and thick cuticles to reduce UV-B absorption, and generally smaller thicker leaves  
94 (?). Species found at low altitudes however, are less adapted to high UV-B environments, instead  
95 possessing adaptations to make the most of the diminished light levels found under thick tree canopy,  
96 particularly during the seedling growth stage. Montane forest physical structure also varies with  
97 elevation. Lowland forests often have lower tree density, with relatively few young trees in the light-  
98 deprived understorey, but a higher canopy cover due to adult trees being larger. Plant ground cover  
99 is generally greater at higher altitudes, with many epiphytic and ground-level herbaceous species  
100 (Martin et al., 2010). It therefore follows that as lowland species move upslope in response to  
101 increasing temperature, they may experience increased levels of damaging UV-B radiation as they  
102 recruit into areas of forest with thinner canopies, as well as other unknown stresses from variation in  
103 physical and biotic environment. This may lead to species' ranges narrowing from the bottom up,  
104 with increased mortality due to temperature at the bottom of the elevational range, but without  
105 increased recruitment at the top end of the elevational range due to increased mortality via UV-B  
106 exposure.

107 In this study, along a moist tropical forest elevational gradient in the Peruvian Andes, we inves-  
108 tigated the role of biotic effects from existing forest structure on the physiology and physiognomy  
109 of tree seedlings across their elevational ranges, in order to increase our knowledge of the dynam-  
110 ics of montane cloud forest tree species elevational range shifts. We tested three hypotheses: 1)  
111 Within a species, seedlings growing at higher elevations would experience higher levels of photosyn-  
112 thetic stress than those at lower elevations, 2) Species would differ in their degree of acclimation  
113 to variation in adult tree forest structure, and 3) A combination of biotic and abiotic explanatory  
114 variables would best explain variation in seedling physiognomic and physiological traits across their  
115 elevational range.

## 116 2 Materials and Methods

### 117 2.1 Study Site

118 Data collection was conducted across 10 permanent 1 ha forest plots in the Kosñipata Valley of  
119 Manú National Park, Peru (-13°N, -71°W, Figure 1, Table 1). The Kosñipata Valley has been  
120 identified as a migration corridor for lowland species to migrate to higher elevations in response  
121 to temperature increase (Feeley et al., 2011) and so is an appropriate location to study range shift  
122 drivers. Plots are situated between 400 and 3200 m.a.s.l. along this migration corridor (Table ??,  
123 Figure ??). The plots form part of a larger plot network established by the Andes Biodiversity  
124 and Ecosystem Research Group (ABERG) in 2003 (Malhi et al., 2010; Girardin et al., 2014), and  
125 are located within the “Tropical Andes” biodiversity hotspot identified in Myers et al. (2000). The  
126 plots used in this study contain 719 tree species, and the valley as a whole contains an estimated  
127 1167 tree species (ABERG unpublished data).

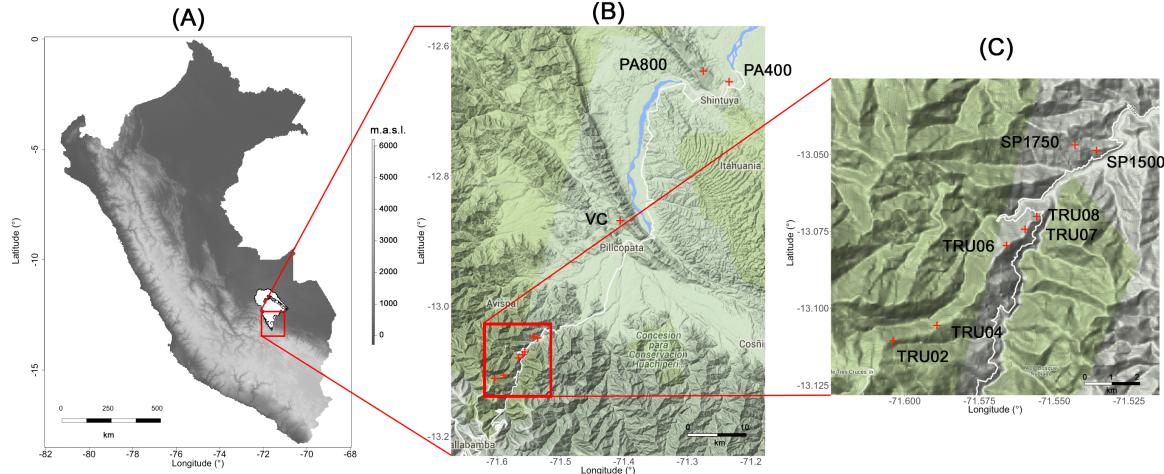


Figure 1: Maps showing the location of the study area and plot locations. (A) The site location within Peru with elevation shading, showing the proximity to Manú National Park (white area). (B) The location of the 1 ha plots within the Kosñipata Valley. (C) An enlargement of the Trocha Union and San 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_Code	Elevation	Annual_Precip	Annual_Air_Temp	Slope_deg	Total_C	Total_N	Soil_pH
PA400	406						
PA800	822						
VC	861	3087	20.700		16	1.450	3.850
SP1500	1497	2631	17.400	22.700	10.500	1	4.050
SP1750	1770	2631	15.800	40.100	26	1.850	4.250
TRU08	1839	2472	16	41.800	31	2	4.300
TRU07	2135	1827		18	37	2.100	4
TRU06	2281		14.900				
TRU04	2733	2318	11.100	21.400	28.500	1.750	3.900
TRU02	3213		8.900	11.800	44.500	2.600	3.750

## 128 2.2 Study species

129 We chose seven tree species for comparison from a total of 719 identified species within the 10 study  
 130 plots. Species were selected according to their contrasting ranges (Figure ??), differences in genus  
 131 migratory pattern (Feeley et al., 2011), and because each species is dominant across its range in the  
 132 Kosñipata Valley (ABERG, unpublished data, [Appendix VI](#)). Seedlings of *Myrcia* spp. are difficult  
 133 to reliably identify to species in the field due to similar morphology and were thus sampled as a  
 134 composite of three potential species: *Myrcia splendens*, *M. fallax*, and *M. rostrata*, the only *Myrcia*  
 135 species known to be present in our plots from ABERG censuses. They are referred to as *Myrcia*  
 136 spp. from here onwards.

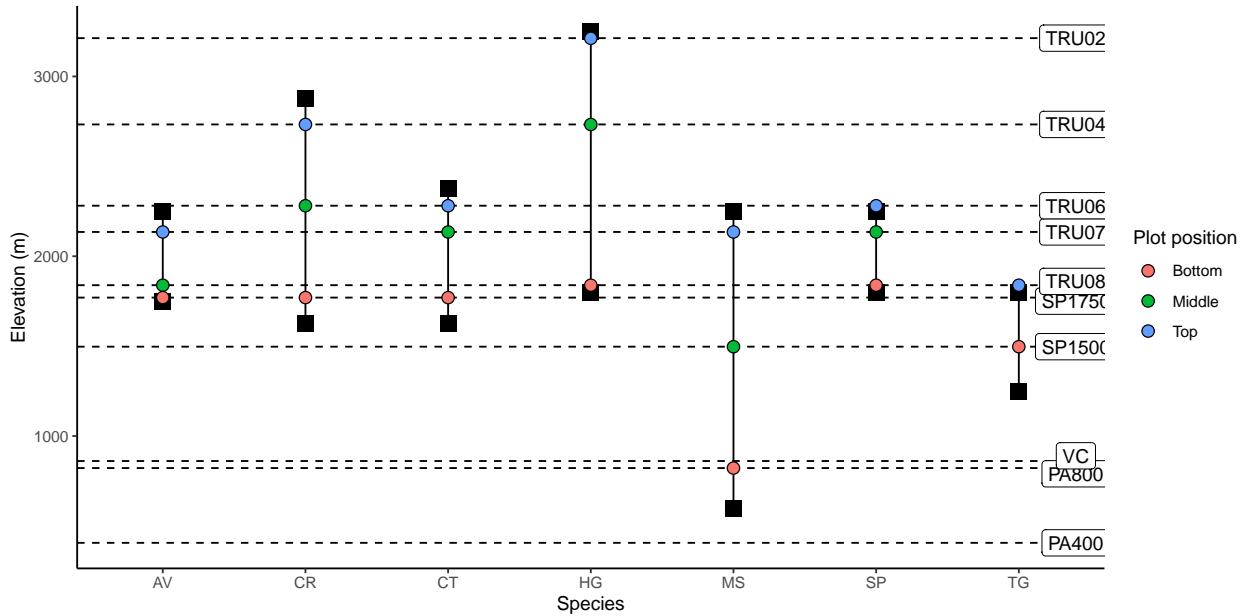


Figure 2: Elevation of study plots for each species (coloured points) with the upper and lower range extents for each species (black squares). Plot elevations are marked as dashed lines.

Table 2

Species code	Species	Bottom	Middle	Top
AV	<i>Alzatea verticillata</i>	SP1750=7	TRU08=5	TRU07=6
CR	<i>Clethra revoluta</i>	SP1750=7	NA	TRU04=8
CT	<i>Clusia thurifera</i>	SP1750=9	TRU07=9	NA
HG	<i>Hedyosmum goudotianum</i>	TRU08=10	TRU04=10	TRU02=11
MS	<i>Myrcia</i> spp.	PA800=10	SP1500=8	TRU07=10
SP	<i>Schefflera patula</i>	TRU08=9	TRU07=12	NA
TG	<i>Tapirira guianensis</i>	SP1500=10	NA	TRU08=10

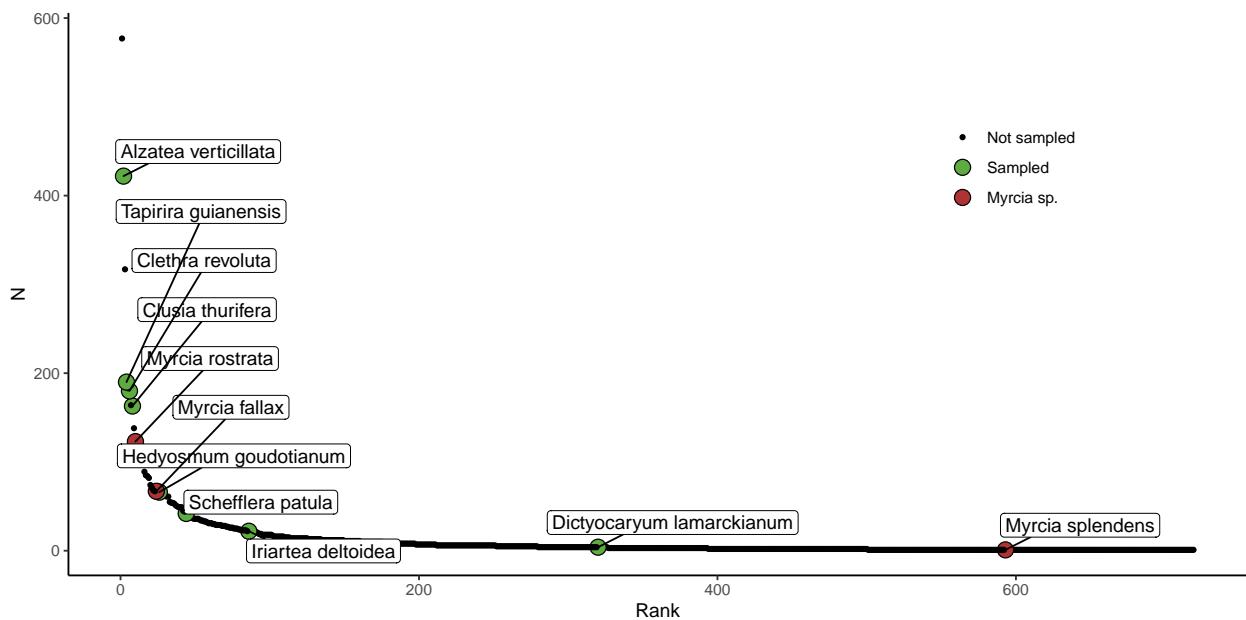


Figure 3: Rank abundance curve of all individuals >10 cm DBH of all species found in the plots measured in this study. Census data from 2014 (ABERG, unpublished data). Species sampled as part of this study are highlighted in red. *Myrcia* species which form the composite *Myrcia* spp. are highlighted in green.

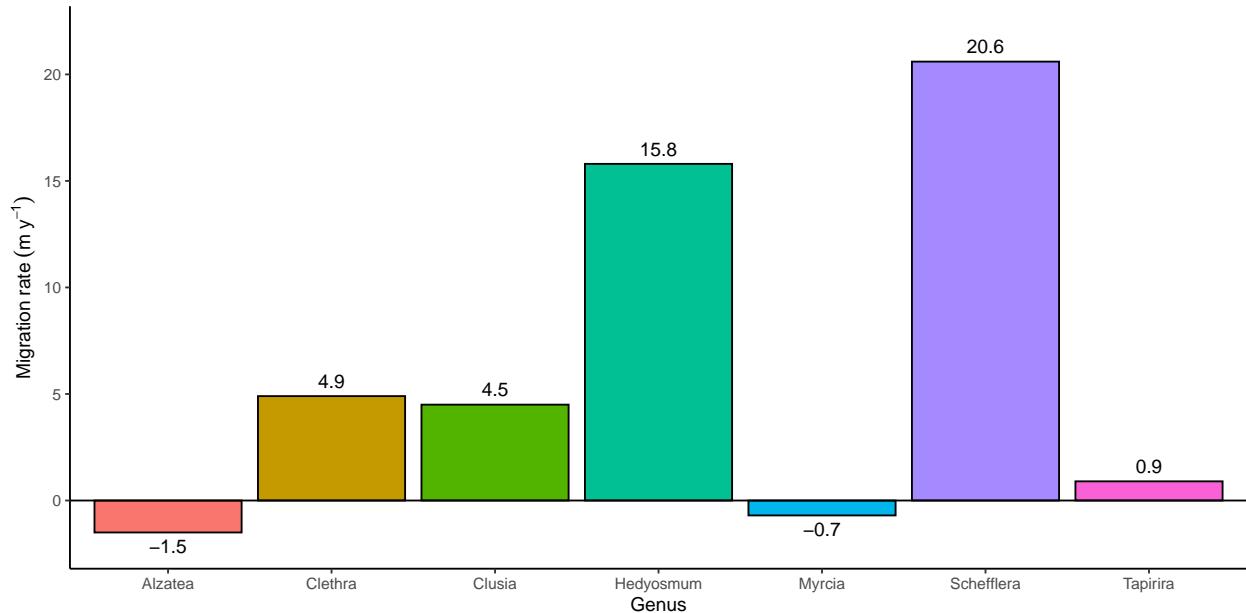


Figure 4: Estimated elevational migration rates within the Kosñipata valley for selected genera of which species are studied here. Migration rates are estimated using shifts in the centre of gravity of tree basal area as measured in the ABERG 1 Ha plot network.

### 137 2.3 Sampling and Measurement

138 Species were sampled in three plots representing the top, middle and bottom elevational extents of  
 139 their ranges (Figure 2). Within each plot, a maximum of 10 seedlings were sampled. To minimise  
 140 the chance of pseudo-replication of sampled seedlings, seedlings closer than 10 m to another sampled

141 seedling were excluded from the analysis, as it could not be guaranteed that the stems were not  
142 connected by a stolon or rhizome. It also ensured that competition measurements were truly  
143 independent. Within a cluster of seedlings within 5 m of each other, each seedling was assigned a  
144 number and a random number generator was used to choose a single seedling for measurement.

145 Proxies for photosynthetic efficiency were measured on the highest fully-expanded leaf of each  
146 seedling. Leaf photosynthetic efficiency can be used as an indicator of physiological stress levels.  
147 Plants with a lower photosynthetic efficiency are more stressed than those with a higher efficiency.  
148 Chlorophyll- $\alpha$  fluorescence was measured using a Walz Mini-PAM II (Walz Effeltrich, Germany),  
149 on a randomly selected area of adaxial leaf surface, avoiding prominent leaf veins. Chlorophyll- $\alpha$   
150 measurements were used to calculate  $F_v/F_m$  according to ?:

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

151 Where  $F_m$  is the maximal fluorescence in the dark and  $F_o$  is the minimal fluorescence in the  
152 dark (Maxwell and Johnson, 2000). Fluorescence measurements were taken after exposing the  
153 seedling to 30 minutes of total darkness, to ensure complete dark adaptation (Campbell et al.,  
154 2007). Dark-adapted  $F_v/F_m$  measures the photosynthetic capacity of the leaf by relaxing the  
155 reaction centres prior to the fluorescence measurement.  $F_v/F_m$  is preferable to other chlorophyll  
156 fluorescence measures as it removes the noise created by environmental conditions at the time of  
157 measurement, instead providing a measure of the underlying photosynthetic capacity. A reduction  
158 in  $F_v/F_m$  is indicative of plant stress. Here, individuals with  $F_v/F_m$  values <0.7 are considered to  
159 be experiencing stress (Maxwell and Johnson, 2000).

160 In addition to  $F_v/F_m$ , leaf chlorophyll content was measured using a multi-spectral SPAD-meter  
161 (Minolta SPAD-502Plus, Spectrum Technologies, Plainfield, Illinois, USA). To account for variation  
162 in chlorophyll content across the leaf (Serrano, 2008), SPAD measurements were taken at three  
163 random points on the leaf. The leaf midvein, other prominent veins, and areas of obvious leaf  
164 necrosis were avoided in these measurements. The mean of the SPAD values was used to calculate  
165 an estimate leaf chlorophyll content using the conversion factor outlined in Coste et al. (2010) for  
166 neotropical broadleaf tree species:

$$Chl_{\alpha} = 117.1 \times \frac{SPAD}{148.84 - SPAD} \quad (2)$$

## 167 2.4 Leaf and whole-plant morphological measurements

## 168 2.5 Competition measurements

169 To assess adult-seedling competition interactions we used two metrics, Leaf Area Index of canopy  
170 foliage, and a metric approximating the degree of crowding from surrounding adult trees. Leaf  
171 Area Index (LAI) was calculated from hemispherical photographs of the forest canopy above each  
172 seedling. Photographs were captured under uniformly overcast cloud conditions to avoid lens flare  
173 and to aid in delineation of foliage from sky during processing (?). Images were taken with a  
174 Coolpix 4500 compact camera, with a Nikon FC-E8 hemispherical fisheye converter lens. Images  
175 were constrained to a 60° circular azimuthal field of view in order to restrict LAI calculations to  
176 the part of the sky where the majority of photosynthetically active radiation penetrates the canopy  
177 (??). Images were then converted to 8-bit grayscale and binarized manually in ImageJ Version 1.51

178 (Schneider et al., 2012) to separate sky from plant material. Binarized images were then analyzed  
 179 using Hemiphot (ter Steege, 2018) in R to estimate LAI as the projected leaf area per unit ground  
 180 area ( $\text{m}^2 \text{ m}^{-2}$ ).

181 To approximate crowding from adult trees, we used an adapted version of the Iterative Hegyi  
 182 Index (Hegyi, 1974; Lee et al., 2004; Seifert et al., 2014). Our adapted ‘Iterative Seedling Index’  
 183 (*ISI*) uses adult tree trunk diameter at ~1.3 m from ground level (Diameter at Breast Height,  
 184 DBH) and the distance of trees from the seedling to calculate an index for each seedling. Higher  
 185 *ISI* values may result from combinations of greater adult tree DBH and adult trees being closer to  
 186 the seedling, higher values indicate greater competition pressure from surrounding adult trees:

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

187 where  $D_j$  is the DBH of a competitor tree and  $DIST_{ij}$  is the euclidean distance between seedling  
 188  $i$  and competitor tree  $j$ . *ISI* was log transformed for analysis, as results spanned multiple orders of  
 189 magnitude. The ‘iterative’ aspect refers to the selection of competitor trees. An iterative selection  
 190 method for competitive trees assumes that if the path between two trees is blocked by some obstacle,  
 191 e.g. another tree, the intensity of competition between them will be greatly reduced (?). The radius  
 192 around the seedling is divided into 12 30° sectors, where only the nearest tree >10 cm DBH within  
 193 each sector is measured (Figure ??). The size of the competition radius ( $C_R$ ) is defined as:

$$C_R = 2 \times \sqrt{\frac{10000}{N}} \quad (4)$$

194 where  $N$  is the number of trees >10 cm DBH per ha (stand density). Stand density data  
 195 was taken from ABERG census data within each plot (ABERG unpublished data) and used to  
 196 interpolate the value of  $C_R$  for plot VC, for which no stand density data exists. We fitted a linear  
 197 regression between the elevation and trees  $\text{ha}^{-1}$  of each plot, and interpolated the trees  $\text{ha}^{-1}$  of plot  
 198 VC using the regression fit (Figure 6).  $C_R$  was rounded to the nearest metre for ease of measurement  
 199 (Table ??).

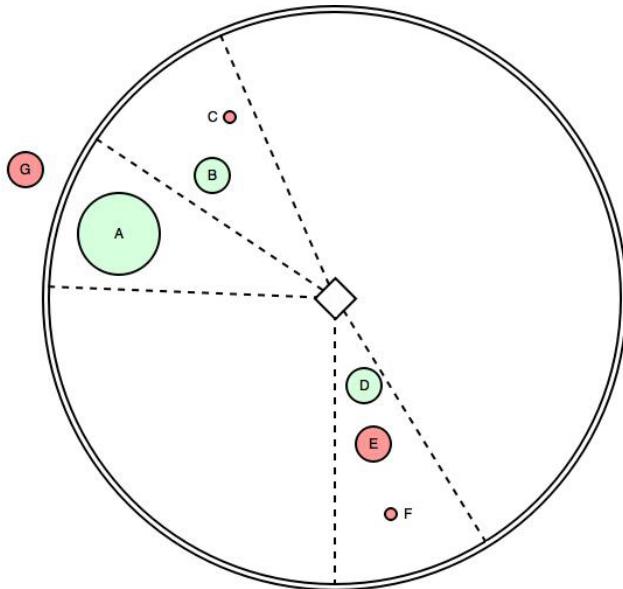


Figure 5: Schematic diagram showing the iterative selection of active competitor trees for the Iterative Seedling Index (ISI) (Equation 3). Trees marked in green (A, B, D) are active competitors for the tree of interest (black diamond). Trees marked in red (C, E, F, G) are non-active competitors, coloured circle radius represents tree DBH. The double circle defines the Competition Radius ( $C_R$ ) (Table ??, Equation 4). 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).

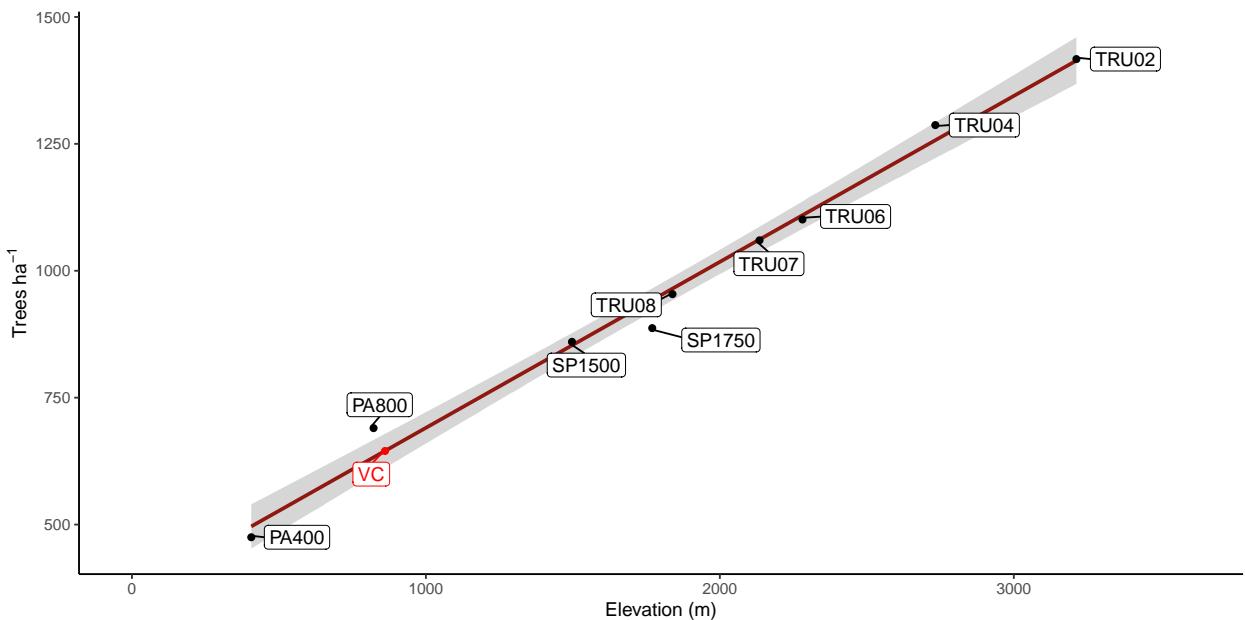


Figure 6: Linear regression with 95% confidence interval of number of trees per hectare for each site, used to estimate number of trees per hectare for site VC.  $R^2 = 0.896$ ,  $F_{(1,7)} = 579.5$ ,  $p < 0.001$ .

200 **2.6 Statistical Analysis**

201 A matrix of single predictor linear mixed effects models were compared to test for the presence and  
202 strength of the causal relationship between each of the two competition variables and each of the  
203 six plant traits. The fixed effect of elevation was also included in order to compare the effects of  
204 competition to that of elevation. All fixed effects were standardised to allow easy comparison of  
205 effect sizes, according to (?Gruber et al., 2011; ?). Model comparison was performed on models fitted  
206 using Maximum Likelihood (ML) estimates (Bolker et al., 2008). Model quality was compared using  
207 Akaike Information Criteria (*AIC*) (Akaike, 1992), Akaike weights ( $W_i$ ), and fixed effect marginal  
208 pseudo- $R^2$  values ( $R_M^2$ ).

209 In order to inform the error structure of single fixed effect mixed effects models, error structures  
210 of were compared using *AIC* values on pairs of single fixed effect linear mixed effects models, where  
211 the slopes of each species were allowed to vary by either intercept or by slope and intercept, to  
212 show whether species differ appreciably in their trait response to the various competition variables  
213 and elevation (fixed effects) (Figure ??, Appendix III). Where  $\Delta AIC_{rsri}$  scores between pairs of  
214 models were  $-2 < \Delta AIC_{rsri} > 2$  a random intercept structure was maintained in the single fixed effect  
215 models, in order to maximise parsimoniousness. Models reported in the results use the optimal  
216 error structure.

217 The best quality single fixed effect models (using either independent intercepts or slopes for each  
218 species) were compared using  $\Delta AIC_r$  against a random effects model, the variance explained by the  
219 whole model ( $R_C^2$ ) and the fixed effects ( $R_M^2$ ) using the *MuMIn* package (Bartoń, 2019), and slope  
220 coefficients (Figure ??, Figure ??) to compare their relative effect on plant traits.

$$Y_{ij} = \beta_0 + \beta_1 X_{ij} + u_{0j} + u_{1j} X_{ij} + \epsilon_{ij} \quad (5)$$

221 where  $Y_{ij}$  is the response variable of species  $i$  at site  $j$ ,  $X_{ij}$  is the fixed effect value of species  $i$   
222 in site  $j$ .

223 The random intercept grouping effect of site was used to account for pseudo-replication in site  
224 characteristics for seedlings sampled along the elevation gradient.

225 To better understand the potential multiplicative effects of competition variables we also com-  
226 pared linear mixed effects models with combinations of fixed effects, using *AIC*,  $W_i$  and  $R_M^2$ , to  
227 find the model which best explained variation in each plant trait.

228 To understand variation between species in their physiological and morphological response to  
229 competition effects, slopes for each species were calculated and compared in the best fitting linear  
230 model, re-estimated using Reduced Maximum Likelihood (REML).

231 All statistical analyses were conducted using R, version 3.2.4 (R Core Team, 2019). Linear mixed  
232 effects models were conducted using the *lme4* package (Bates et al., 2015).

### 233 3 Results

#### 234 3.1 Variation in plant traits across elevation

235 All species except *Myrcia* spp. (MS) showed a general positive trend in photosynthetic efficiency  
 236 ( $DF_v/F_m$ ) across their respective elevational ranges. Linear models of photosynthetic efficiency  
 237 over elevation showed that none of the species level regressions dipped below the critical threshold  
 238 of 0.7, which indicates plant stress. Of the 151 measured seedlings, 12 had a  $DF_v/F_m$  below 0.7. Of  
 239 those stressed seedlings, 4 were *Alzatea verticillata* (AV), 2 were *Clethra revoluta* (CR) and 1 each  
 240 from *Clusia thurifera* (CT) and *Myrcia* spp.. Chlorophyll- $\alpha$  generally decreased with elevation, with  
 241 negative trends in *A. verticillata* (AV), *C. thurifera* (CT), *Myrcia* spp. (MS), *Schefflera patula* (SP)  
 242 and *Tapirira guianensis* (TG). *C. revoluta* (CR) and *Hedyosmum goudotianum* (HG) had positive  
 243 trends.

244 The relationship between physiognomic plant traits and elevation varied between species. Leaf:height  
 245 ratio generally decreased over elevation, except for *A. verticillata* (AV) which showed a negative U-  
 246 shaped relationship and *H. goudotianum* (HG) which showed a positive hump-shaped relationship.  
 247 Leaf area generally increased with elevation, though *C. thurifera* (CT), *S. patula* (SP), and *Myrcia*  
 248 spp. (MS) showed negative relationships. Leaf thickness was generally unaffected by elevation, ex-  
 249 cept in *C. thurifera* (CT), which had a negative relationship. Stem volume was similarly unaffected  
 250 by elevation, except in *S. patula*, where it decreased with elevation and in *H. goudotianum* (HG)  
 251 where it increased, driven by very large seedlings at the top end of the elevation gradient.

252 Species with restricted elevational ranges were more likely to have steeper relationships of both  
 253 physiological and physiognomic plant traits across elevation, e.g. *A. verticillata* (AV), *C. thurifera*  
 254 (CT), *S. patula* (SP) and *T. guianensis* (TG). These species also inhabit the cloud zone of the  
 255 forest.

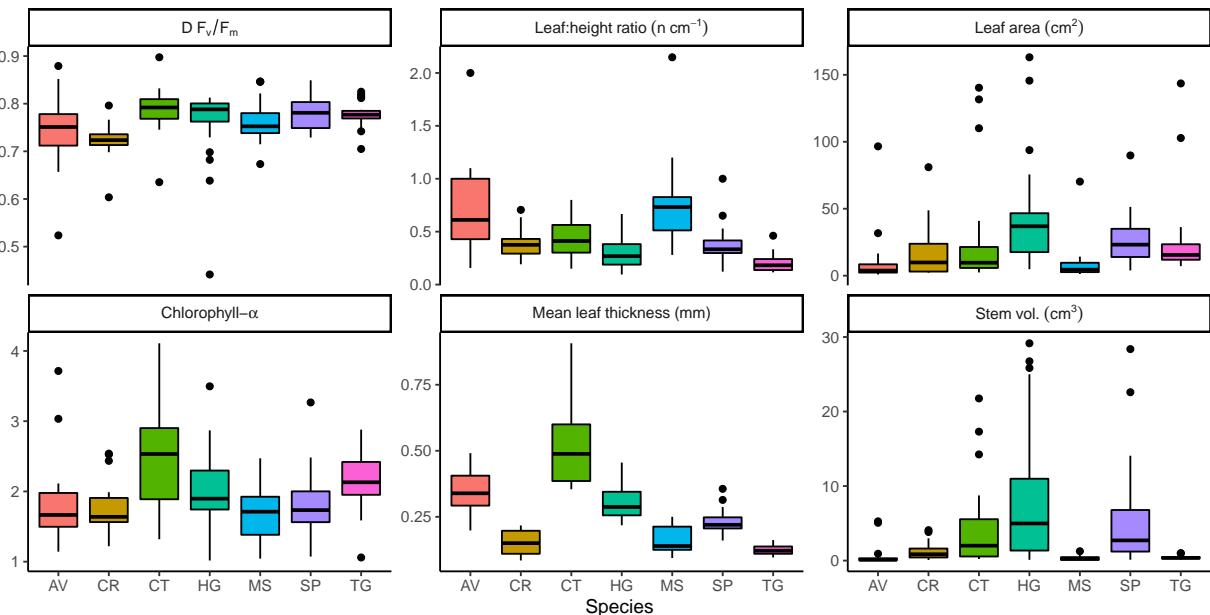


Figure 7: Box plots showing the variation in plant trait values within each species.

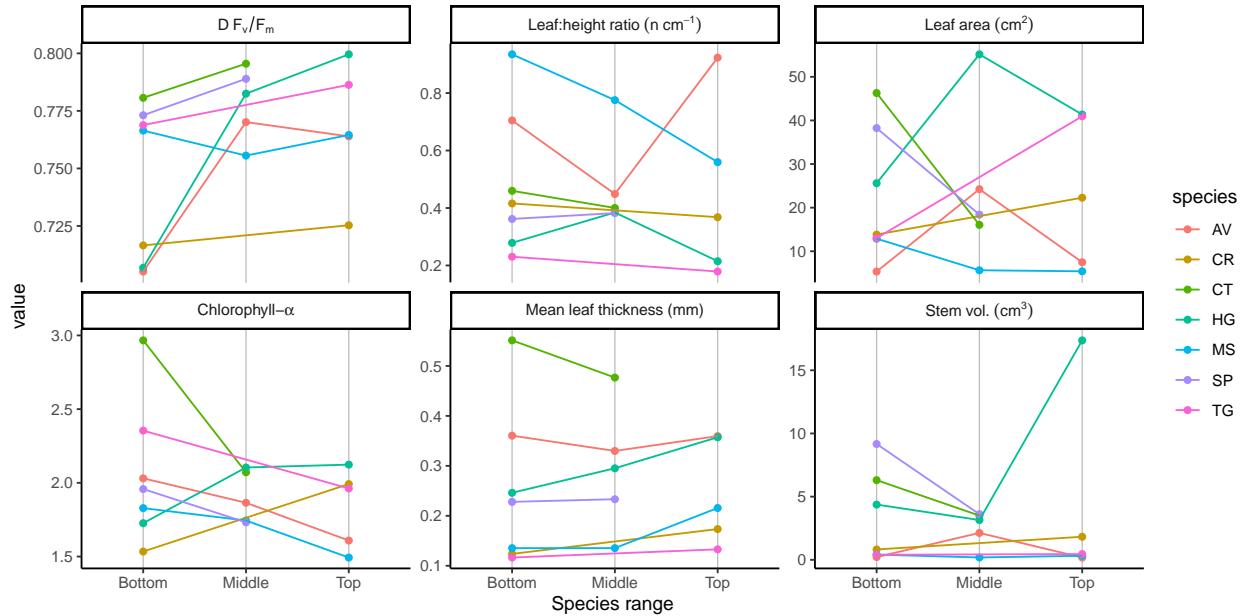


Figure 8: Interaction plots showing the variation in plant trait values within each species.

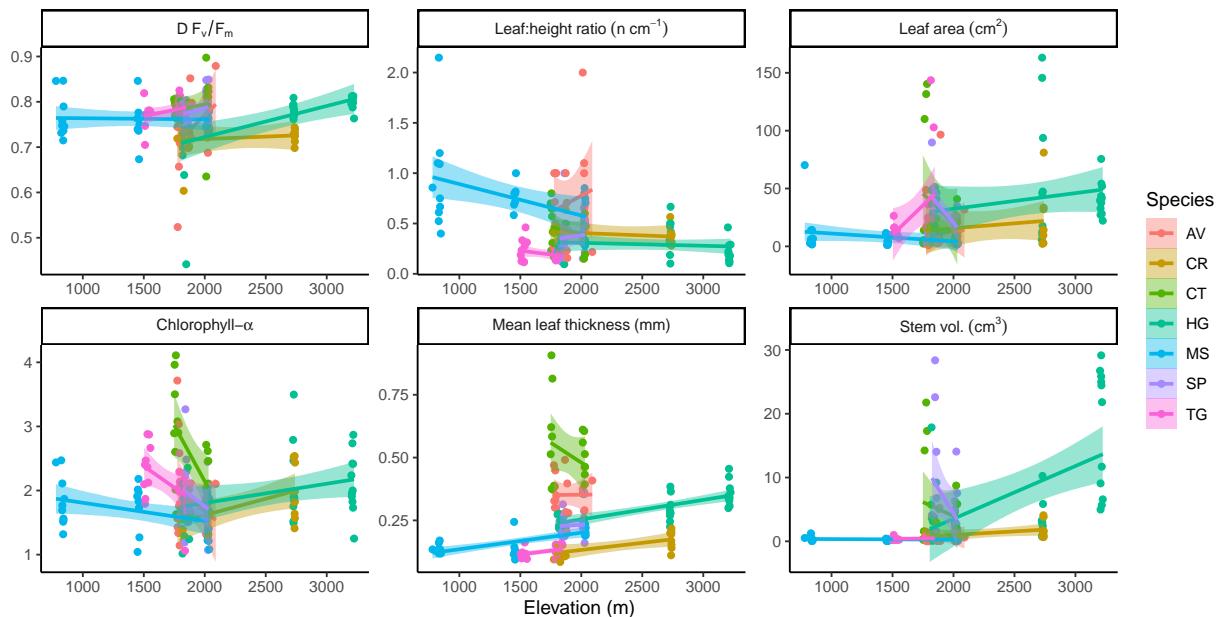


Figure 9: Scatter plots with linear model fits for each species, showing the variation in plant stress variables and plant traits across elevation.

### 256 3.2 Directional effects of adult competition on plant traits

257 Random slope terms per species for single fixed effects models between plant traits and environmental  
 258 variables produced models of better quality than random intercept terms per species in 8/18  
 259 cases. All models with  $DF_v/F_m$  as the response variable were of better quality when the random  
 260 slope term was included (Figure ??). Only  $DF_v/F_m \sim \text{Elev.}$ , Leaf:Height ratio  $\sim \text{Elev.}$ , Stem vol.  $\sim \text{ISI}$ ,  
 261 Leaf thickness  $\sim \text{Elev.}$  and Leaf thickness  $\sim \text{LAI}$  produced models better than equivalent random ef-  
 262 fects models. Even so, these models explained very little of the variation in plant traits, with the  
 263 highest  $R^2_m$  being for the model of Stem vol.  $\sim \text{Elev.}$  ( $R^2_m = 0.19$ ). In the single predictor mixed effects

264 models, models with elevation as the fixed effect consistently outperformed other single predictor  
 265 mixed effects models

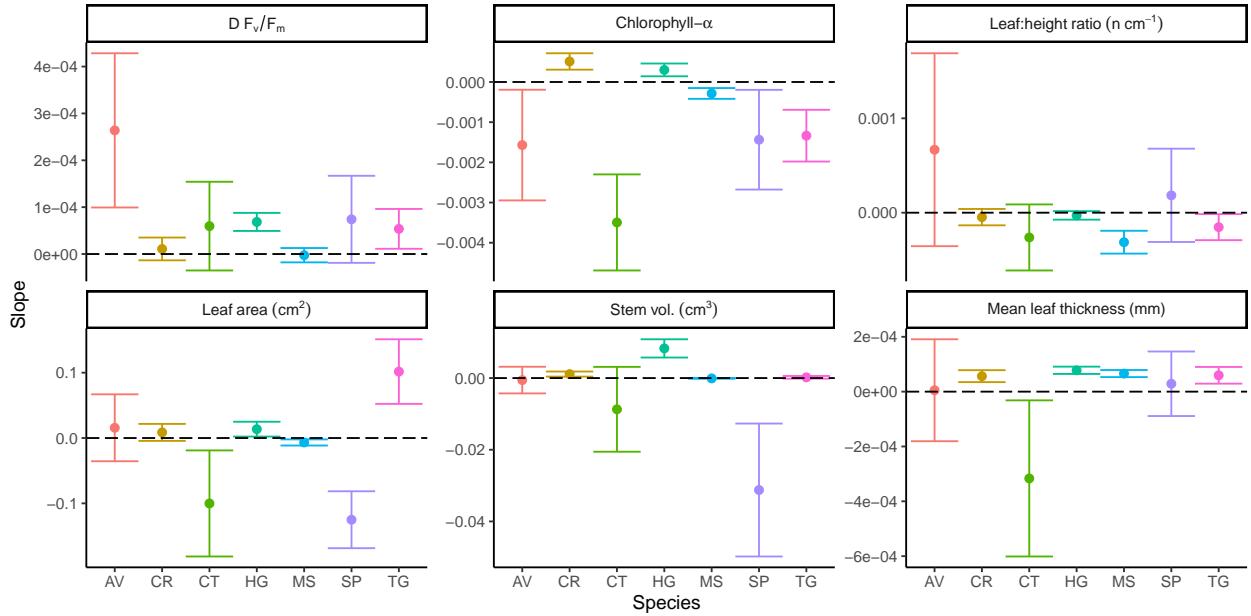


Figure 10: Interval plots showing the effect sizes (slopes) of each fixed effect in single fixed effect linear mixed effects models of plant traits against forest structure variables and elevation, for comparison.

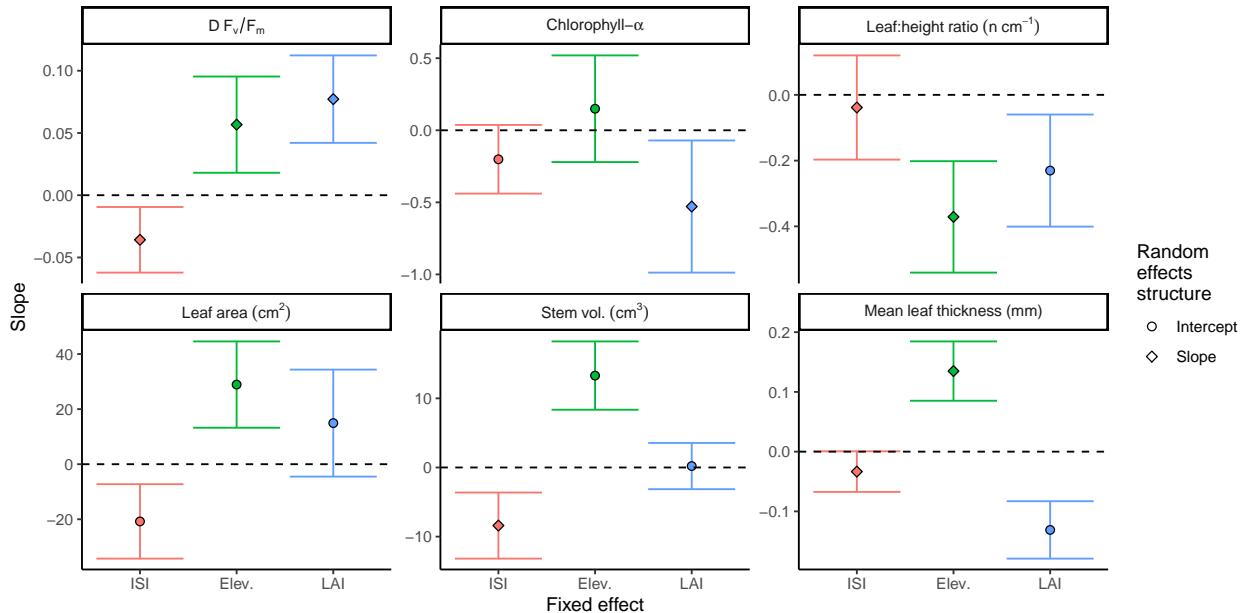


Figure 11

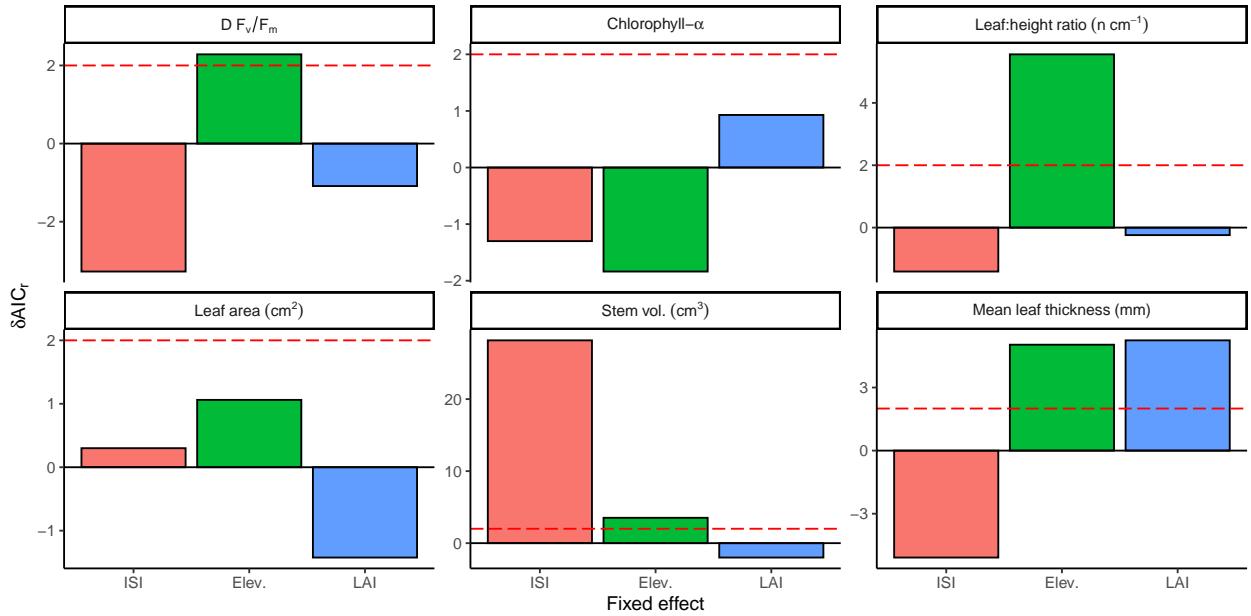


Figure 12: The difference in AIC values between each single fixed effect model and a corresponding random effects model using no fixed effects. A  $\Delta\text{AIC}_r > 2$  means the model is of appreciably higher quality than the random effects model. The horizontal dashed red line indicates this threshold.

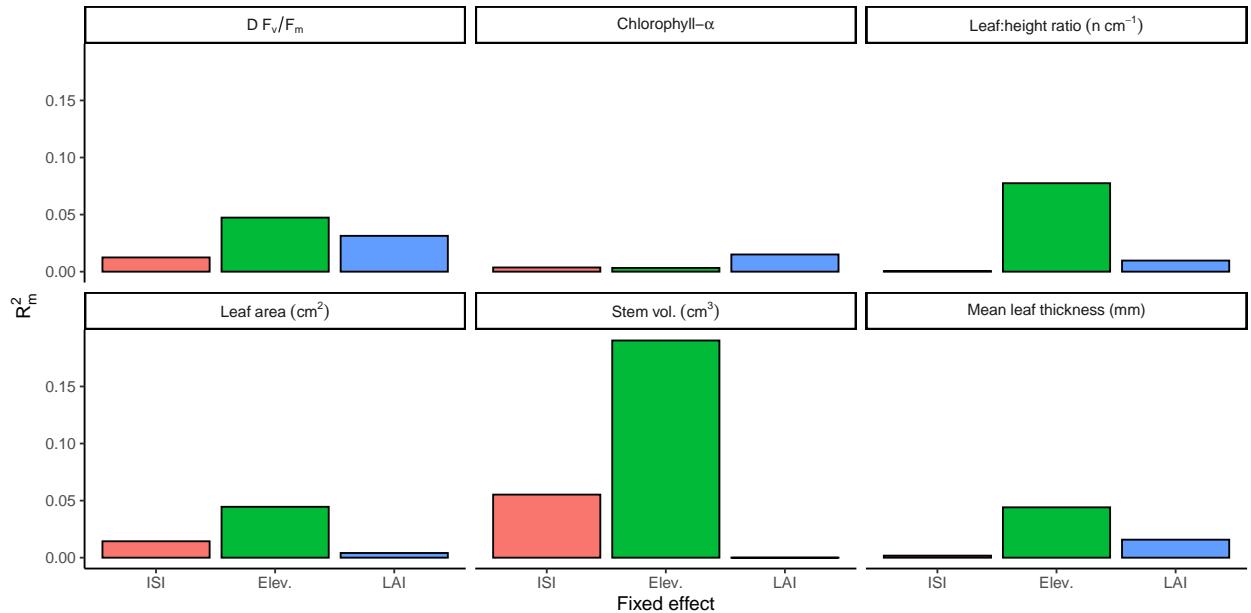


Figure 13: The variance explained by each single fixed effect model. The pale bars indicate the variance explained by the whole model while the bold bars indicate the variance explained just by the fixed effect in the model.

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

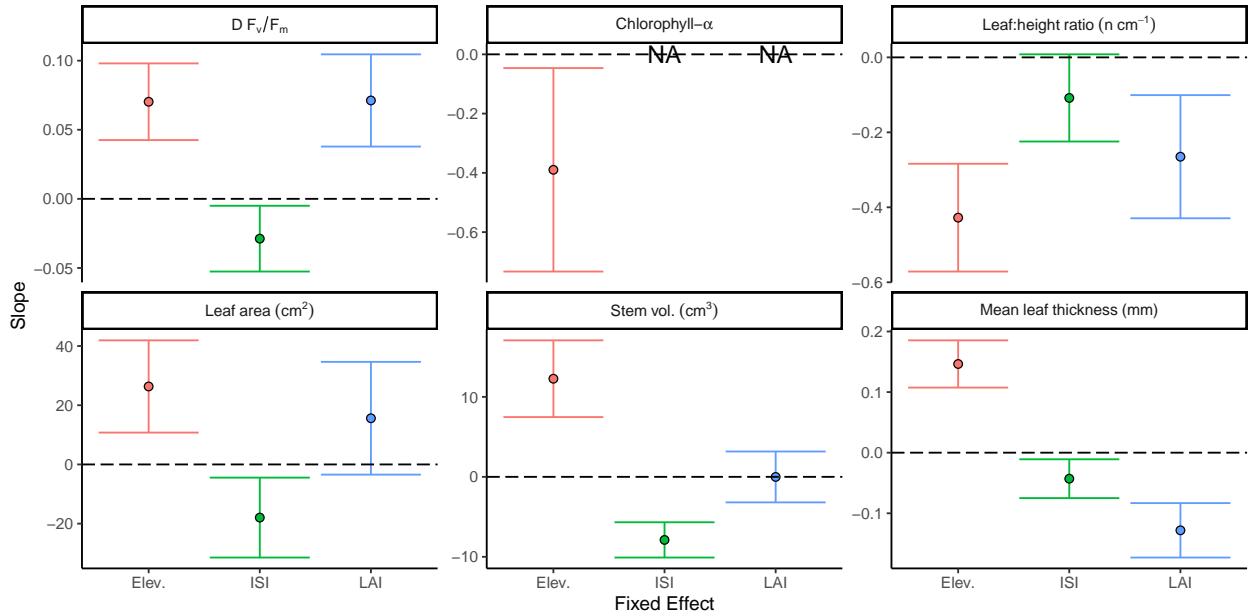


Figure 14

270 All of the best multiple predictor mixed effects models included elevation as a fixed effect. All  
 271 of the best models, except the model predicting leaf Chlorophyll- $\alpha$ , included adult competition  
 272 predictor variables alongside that of elevation (Figure 14). The variance explained by these best  
 273 multiple predictor mixed effects models remained small however, [MORE ON THIS](#)

## 274 Discussion

275 This study aimed to (a) determine whether tree seedling physiological and physiognomic plant traits  
 276 were affected by competition from adult trees, (b) assess how the effects of competition compared to  
 277 that of elevation, and (c) assess the degree to which plant trait-elevation relationships vary among  
 278 species. It was found that adult competition variables never influence a given plant trait more than  
 279 elevation, but that combinations of elevation and competition variables better predict variation in  
 280 plant traits than elevation alone. Adult-seedling competition effects (LAI and ISI) have contrasting  
 281 effects on plant traits.

## 282 4 Effect of competition and elevation on plant traits

283 Single fixed effect models demonstrated that the three competition variables influence some plant  
 284 traits ( $\Delta\text{AIC}_r \geq 2$ , Figure ??a). The effect size of individual competition variables however, did  
 285 not exceed that of elevation for any plant traits (Figure ??b, Figure ??). The three competition  
 286 variables, which represent different types of competition, vary in their effects on seedling traits.

## 287 Leaf physiology

288 Together, SPAD and  $F_v/F_m$  are useful measures of a plant's health and the integrity of its photo-  
 289 tonsynthetic apparatus (?). SPAD is used as a proxy for leaf chlorophyll content (?), while  $F_v/F_m$

measures the efficiency with which a leaf can utilise light for photosynthesis (Maxwell and 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 ??). There is however, large variation in SPAD within sites and elevation explains little of the variance in SPAD (Figure ??), 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 ??b).

## 297 Photosynthetic efficiency

298 Single fixed effect models showed that an increase in canopy density (LAI) caused an increase in  
299 photosynthetic efficiency ( $F_v/F_m$ ) (Figure ??). Specifically, an increase in photosynthetic efficiency  
300 under denser canopy may be the result of a more temporally constant microclimate (?). A denser  
301 canopy regulates diurnal temperature oscillations by more effectively trapping warm air between  
302 the canopy and the forest floor, reducing temperature stress on the plant (?). Increased shading  
303 under denser canopy also reduces the potential for seedling desiccation and cavitation, which can  
304 cause damage to seedling leaves. As Sun-flecks move across the forest floor they result in rapid leaf  
305 temperature increase (??). Additionally, a reduction in direct sunlight reduces the potential for  
306 UV-B damage to photosynthetic apparatus (?). Diurnal temperature oscillations are generally of  
307 greater range at higher elevations (?) as is the UV-B insolation fraction (?), suggesting that the  
308 beneficial effects of increased canopy density on photosynthetic efficiency may become greater at  
309 higher elevations. In this region however, persistent cloud cover at higher elevations throughout the  
310 day may result in no increase in incident UV-B, the majority being absorbed by cloud condensation  
311 nuclei before it reaches the leaf (?).

312 Canopy density decreases with elevation (Figure ??), though this trend may be the result of  
313 wide within site variance ( $\Delta AIC_r \geq 2$ ). This trend concurs with more conclusive results from other  
314 studies which show a clear decrease in canopy density with elevation (??). The more variable  
315 relationship seen in this study may be the result of bias in the sampling strategy. LAI was not  
316 measured systematically across each site, instead being measured above each sampled seedling. It  
317 is expected that seedlings will grow successfully only under canopy where the average light intensity  
318 falls between a minimum needed for growth and a maximum that ensures temperature and UV-B  
319 stress does not cause the seedling to perish. In this study therefore, extreme canopy densities were  
320 probably not sampled. The presence of bias in our sampling strategy is supported by comparing the  
321 range of LAI measurements in other studies. For example, ?, in a review of 61 tropical evergreen  
322 forests, found that LAI ranged from 1.5 to 8. (after outlier exclusion), whereas our LAI estimate  
323 ranged from only 1.0 to 5.5, implying that a representative LAI sample was not achieved within  
324 each plot.

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

334 In contrast to the effects of LAI, ISI caused a decrease in photosynthetic efficiency. This suggests  
335 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 and Tanner, 2000). Other studies have shown a nutrient competition effect between adult trees and nearby seedlings. ? 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, ? 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 (?). 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 ??) 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 ??, Figure ??). In the multi-predictor models the best fitting model did not include herbaceous plant density (Table ??). 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 (??). ? 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 and 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 (?). As a conservative estimate, here plants are defined as experiencing physiological stress when  $F_v/F_m < 0.7$ . Figure ?? 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).

## 376 Chlorophyll- $\alpha$

SPAD value was not clearly influenced by any of the measured competition variables, or elevation (Figure ??). SPAD varied largely both within and among species, with large standard errors surrounding the estimates of each species (Figure ??, Table ??). The best fitting multiple fixed effect LMM for SPAD did not include elevation (Figure ??), 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

382 for only 0.4% of the variance in SPAD (Figure ??).

383 The lack of meaningful variation in SPAD contrasts other studies that have shown increases in  
384 chlorophyll content in response to shading (?????) and soil nitrogen content (?). In this study  
385 however, SPAD did not vary with LAI (shading), ISI (soil nutrient availability) or herbaceous plant  
386 abundance.

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

## 391 Summary

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

## 400 Leaf and plant morphology

401 Leaf thickness increased with elevation. Other studies have also found positive correlations between  
402 leaf thickness and elevation, identifying climatic drivers such as mean daily insolation and diurnal  
403 temperature variation (?), which lead to reduced leaf pay-back times and a need to grow leaves that  
404 can survive the more variable environmental conditions found at higher elevations (?). Increased  
405 UV-B results in an increase in cuticle thickness, to reduce the concentration of UV-B absorbed by  
406 photosystem II (PSII) where it can cause damage and thus photoinhibition (??). In this study  
407 however, it is unclear whether the insolation UV-B fraction does increase with elevation as it was  
408 not measured. Additionally, it is expected that frequent cloud immersion in the high elevation  
409 sites would reduce UV-B absorption and thus the need for thick cuticles. Leaf thickness decreased  
410 under increased canopy density (Figure ??), adding support to the conclusion that increased direct  
411 sunlight is the cause of the decrease in leaf thickness with elevation.

412 Leaf area variation was explained poorly by both competition variables. Previous studies have  
413 shown a clear decrease in leaf area with elevation, citing decreases in canopy density and an increase  
414 in nutrient competition with elevation as drivers of this variation (?). Plants with access to higher  
415 resource levels generally invest in leaves which can achieve a higher photosynthetic rate per energy  
416 input in leaf construction, at the expense of leaf longevity (?). In the plots studied here however,  
417 available nitrogen does not decrease with elevation, though elevational variation in other nutrients  
418 is not known.

419 Leaf:height ratio decreased with elevation (Figure ??) meaning that plants became less leafy  
420 per unit stem height as elevation increased. However this relationship explained very little of the  
421 variance in leaf:height ratio (Table ??). Competition variables had little effect on leaf:height ratio  
422 (Figure ??). Few studies have focussed specifically on measures of leaf:height ratio or number of

423 leaves as an adaptive/acclimatory trait though we may interpret that a reduction in “leafiness” is  
424 an extension of the trend seen in reduced leaf area with elevation. Seedlings may be more likely to  
425 produce fewer leaves in order to allocate more biomass to structural support in those leaves that  
426 are grown (?).

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

### 437 **Summary**

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

## 448 **5 Variation in plant traits with elevation**

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

## 457 **Variation among species**

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

463 *deltoides* show no difference to dicot species in terms of their plant trait-elevation relationship.  
464 *A. verticillata* has a comparatively large variance for all trait-elevation relationships except stem  
465 volume. This implies that *A. verticillata* is either more sensitive to changes in climate, or that it  
466 has a larger acclimatory range than other species; both may be true. *A. verticillata* has a very small  
467 elevational range (Figure ??) but is also one of the most common tree species found along this set of  
468 plots (Appendix VI). This supports the theory that common species have a wider acclimatory range  
469 and that species with small ranges are sensitive to environmental variation. In contrast, *Myrcia*  
470 spp. has little variation in plant traits compared to other species but has the largest elevational  
471 range, the *Myrcia* spp. species sampled are among the rarer species sampled.

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

## 486 Summary

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

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

## 501 6 Predictions for future species migration

502 This study confirms that adult-seedling competition intensity decreases with elevation ( $H_{n3}$ ), and  
503 that this decrease causes some proportion of the effect of elevation on plant traits, though this  
504 proportion is likely to be small as LMMs show that elevation still has the greatest influence over  
505 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.

## 7 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 over the course of a season (?). 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 (?).

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 (??). Rare species are more likely to occupy specialist niches, which are narrower on a local geographical scale than those of generalist species (?). The evolutionary histories of specialists means 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. ?, and ? 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.

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

558 The study did not use experimental treatments. It could be argued therefore that measured  
559 seedlings would have been unlikely to show stress at all, as seedlings would not have grown to the  
560 minimum size needed for measurement otherwise.

## 561 8 Further research

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

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

## 572 Conclusion

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

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

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

589 There was marked variation between species in their plant trait response to elevation. This

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

595 Forest structure based competition affects physiological stress independently of elevation

## 596 References

- 597 Akaike, H. (1992), 'Information theory and an extension of the maximum likelihood principle',  
598 *Breakthroughs in Statistics* pp. 610–624.
- 599 Araújo, M. B., Thuiller, W. and Pearson, R. G. (2006), 'Climate warming and the decline of  
600 amphibians and reptiles in europe', *Journal of Biogeography* **33**, 1712–1728.
- 601 Bartoń, K. (2019), *MuMIn: Multi-Model Inference*. R package version 1.43.6.
- 602 Bates, D., Mächler, M., Bolker, B. M. and Walker, S. C. (2015), 'Fitting linear mixed-effects models  
603 using lme4', *Journal of Statistical Software* **67**(1), 1–48.
- 604 Bell, D. M., Bradford, J. B. and Lauenroth, W. K. (2014), 'Early indicators of change: diversgent  
605 climate envelopes between tree life stages imply range shifts in the western united states', *Global  
606 Ecology and Biogeography* **23**, 168–180.
- 607 Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. and Courchamp, F. (2012), 'Impacts of  
608 climate change on the future of biodiversity', *Ecology Letters* **15**, 365–377.
- 609 Berry, P. M., Dawson, T. P., Harrison, P. A. and Pearson, R. G. (2002), 'Modelling potential impacts  
610 of climate change on the bioclimatic envelope of species in britain and ireland', *Global Ecology &  
611 Biogeography* **11**, 453–462.
- 612 Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H.  
613 and White, J. S. (2008), 'Generalized linear mixed models: a practical guide for ecology and  
614 evolution', *Trends in Ecology and Evolution* **24**(3), 127–135.
- 615 Campbell, C., Atkinson, L., Zaragoza-Castells, J., Lundmark, M., Atkin, O. and Hurry, V. (2007),  
616 'Acclimation of photosynthesis and respiration is asynchronous in response to changes in temper-  
617 ature regardless of plant functional group', *New Phytologist* **176**, 375–389.
- 618 Chen, I., Hill, J. K., Ohlemüller, R., Roy, D. B. and Thomas, C. D. (2011), 'Rapid range of species  
619 associated with high levels of climate warming', *Science* **333**, 1024–1026.
- 620 Colwell, R. K., Brehm, G., Cardelús, C. L., Gilman, A. C. and Longino, J. T. (2008), 'Global  
621 warming, elevational range shifts and lowland biotic attrition in the wet tropics', *Science* **322**, 258–  
622 261.
- 623 Coomes, D. A. and Grubb, P. J. (2000), 'Impacts of root competition in forests and woodlands: a  
624 theoretical framework and review of experiments', *Ecological Monographs* **70**(2), 171–207.
- 625 Corlett, R. T. and Westcott, D. A. (2013), 'Will plant movemenets keep up with climate change?',  
626 *Trends in Ecology & Evolution* **28**(8), 482–488.
- 627 Coste, S., Baraloto, C., Leroy, C., Marcon, É., Renaud, A., Richardson, A. D., Roggy, J., Schimann,  
628 H., Uddling, J. and Hérault, B. (2010), 'Assessing foliar chlorophyll contents with the spad-502  
629 chlorophyll meter: a calibration test with thirteen tree species of tropical rainforest in french  
630 guiana', *Annals of Forest Science* **67**(6), 607–607.

- 631 Davis, M. A., Wrage, K. J. and Reich, P. B. (1998), 'Competition between tree seedlings and  
632 herbaceous vegetation: support for a theory of resource supply and demand', *Journal of Ecology*  
633 **86**, 652–661.
- 634 Dawson, T. P., Jackson, S. T., House, J. I., Prentice, I. C. and Mace, G. M. (2011), 'Beyond  
635 predictions: biodiversity conservation in a changing climate', *Science* **332**, 53–58.
- 636 Dobson, A., Lodge, D., Alder, J., Cumming, G. S., Keymer, J., McGlade, J., Mooney, H., Rusak,  
637 J. A., Sala, O., Wolters, V., Wall, D., Winfree, R. and Xenopoulos, M. A. (2006), 'Habitat loss,  
638 trophic collapse, and the decline of ecosystem services', *Ecology* **87**(8), 1915–1924.
- 639 Ettinger, A. K., Ford, K. R. and HilleRisLambers, J. (2011), 'Climate determines upper, but not  
640 lowe, altitudinal range limits of pacific northwest conifers', *Ecology* **92**(6), 1323–1331.
- 641 Feeley, K. J., Malhi, Y., Zelazowski, P. and Silman, M. R. (2012), 'The relative importance of defor-  
642 estation, precipitation change, and temperature sensitivity in determining the future distributions  
643 and diversity of amazonian plant species', *Global Change Biology* **18**, 2636–2647.
- 644 Feeley, K. J., Silman, M. R., Bush, M. B., Farfan, W., Cabrera, K. G., Malhi, Y., Meir, P., Revilla,  
645 N. S., Quisiyupanqui, M. N. R. and Saatchi, S. (2011), 'Upslope migration of andean trees',  
646 *Journal of Biogeography* **38**, 783–791.
- 647 Girardin, C. A. J., Espejob, J. E. S., Doughty, C. E., Huasco, W. H., Metcalfe, D. B., Durand-Baca,  
648 L., Marthews, T. R., Aragao, L. E. O. C., Farfan-Rios, W., García-Cabrera, K., Halladay, K.,  
649 Fisher, J. B., Galiano-Cabrera, D. F., Huaraca-Quispe, L. P., Alzamora-Taype, I., Eguiluz-Mora,  
650 L., Salinas-Revilla, N., Silman, M. R., Meir, P. and Malhi, Y. (2014), 'Productivity and carbon  
651 allocation in a tropical montane cloud forest in the peruvian andes', *Plant Ecology & Diversity*  
652 **7**(1-2), 107–123.
- 653 Gruber, C. E., Nakagawa, S., Laws, R. J. and Jamieson, I. G. (2011), 'Multimodel inference in  
654 ecology and evolution: challenges and solutions', *Journal of Evolutionary Biology* **24**, 699–711.
- 655 Hegyi, F. (1974), A simulation model for managing jack-pine stands, in 'Royal College of Forestry,  
656 editor', Royal College of Forestry, Stockholm, Sweden, pp. 74–90.
- 657 Hughes, L. (2000), 'Biological consequences of global warming: is the signal already apparent?',  
658 *Trends in Ecology and Evolution* **15**(2), 56–61.
- 659 Isbell, F., Calcagno, V., Hector, A., Connolly, J., Harpole, W. S., Reich, P. B., Scherer-Lorenzen, M.,  
660 Schmid, B., Tilman, D., van Ruijven, J., Weigelt, A., Wilsey, B. J., Zavaleta, E. S. and Loreau,  
661 M. (2011), 'Hugh plant diversity is needed to maintain ecosystem services', *Nature* **477**, 199–203.
- 662 Krause, G. H., Koroleva, O. Y., Dalling, J. W. and Winter, K. (2001), 'Acclimation of tropical tree  
663 seedlings to excessive light in simulated tree-fall gaps', *Plant, Cell and Environment* **24**, 1245–  
664 1352.
- 665 Lee, W., von Gadow, K., Chung, D., Lee, J. and Shin, M. (2004), 'Dbh growth model for *Pinus*  
666 *densiflora* and *Quercus variabilis* mixed forests in central korea', *Ecological Modelling* **176**, 187–  
667 200.
- 668 Lenoir, J., Gégout, J., Pierrat, J., Bontemps, J. and Dhôte, J. (2009), 'Differences between tree  
669 species seedling and adult altitudinal distribution in mountain forests during the recent warm  
670 period (1986-2006)', *Ecography* **32**, 765–777.
- 671 Lenoir, J. and Svensson, J. C. (2015), 'Climate-related range shifts - a global multidimensional  
672 synthesis and new research directions', *Ecography* **38**, 15–28.
- 673 Lewis, S. L. and Tanner, E. V. J. (2000), 'Effects of above- and belowground competition on growth  
674 and survival of rain forest tree seedlings', *Ecology* **81**(9), 2525–2538.

- 675 MacLean, S. A. and Beissinger, S. R. (2017), ‘Species’ traits as predictors of range shifts under  
676 contemporary climate change: a review and meta-analysis’, *Global Change Biology* **23**, 4094–  
677 4105.
- 678 Malhi, Y., Silman, M., Salinas, N., Bush, M., Meir, P. and Saatchi, S. (2010), ‘Introduction: ele-  
679 vation gradients in the tropics: laboratories for ecosystem ecology and global change research’,  
680 *Global Change Biology* **16**, 3171–3175.
- 681 Mantyka, C. S., Martin, T. G. and Rhodes, J. R. (2012), ‘Interactions between climate and habi-  
682 tatt loss effects on biodiversity: a systematic review and meta-analysis’, *Global Change Biology*  
683 **18**, 1239–1252.
- 684 Martin, P. H., Fahey, T. J. and Sherman, R. E. (2010), ‘Vegetation zonation in a neotropical  
685 montane forest: environment, disturbance and ecotones’, *Biotropica* **43**(5), 533–543.
- 686 Matsuraba, S., Krause, G. H., Aranda, J., Virgo, J., Beisel, K. G., Jahns, P. and Winter, K. (2009),  
687 ‘Sun-shade patterns of leaf carotenoid composition in 86 species of neotropical forest plants’,  
688 *Functional Plant Biology* **36**, 20–36.
- 689 Maxwell, K. and Johnson, G. N. (2000), ‘Chlorophyll fluorescence - a practical guide’, *Journal of*  
690 *Experimental Botany* **51**(345), 659–668.
- 691 McCain, C. M. and Colwell, R. K. (2011), ‘Assessing the threat to montane biodiversity from discon-  
692 cordant shifts in temperature and precipitation in a changing climate’, *Ecology Letters* **14**, 1236–1245.
- 693 McMahon, S. M., Harrison, S. P., Armbruster, W. C., Bartlein, P. J., Beale, C. M., Edwards,  
694 M. E., Kattge, J., Midgley, G., Morin, X. and Prentice, I. C. (2011), ‘Improving assessment and  
695 modelling of climate change impacts on global terrestrial biodiversity’, *Trends in Ecology and*  
696 *Evolution* **26**(5), 249–259.
- 697 Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B. and Kent, J. (2000),  
698 ‘Biodiversity hotspots for conservation priorities’, *Nature* **403**, 853–858.
- 699 Parmesan, C. (2006), ‘Ecological and evolutionary responses to recent climate change’, *Annual*  
700 *Review of Ecology, Evolution and Systematics* **37**, 637–669.
- 701 Pearson, R. G. and Dawson, T. P. (2003), ‘Predicting the impacts of climate change on the dis-  
702 tribution of species: are bioclimate envelope models useful?’, *Global Ecology & Biogeography*  
703 **12**, 361–371.
- 704 Peterson, A. T., Ball, L. G. and Cohoon, K. P. (2002), ‘Predicting distributions of mexican birds  
705 using ecological niche modelling methods’, *Ibis* **144**, E27–E32.
- 706 R Core Team (2019), *R: A Language and Environment for Statistical Computing*, R Foundation for  
707 Statistical Computing, Vienna, Austria.
- 708 Schneider, C. A., Rasband, W. S. and Eliceiri, K. W. (2012), ‘Nih image to imagej: 25 years of  
709 image analysis’, *Nat Methods* **9**(7), 671–675.
- 710 Seifert, T., Seifert, S., Seydack, A., Durrheim, G. and von Gadow, K. (2014), ‘Competition effects  
711 in an afrotropical forest’, *Forest Ecosystems* **1**(13), 1–15.
- 712 Serrano, L. (2008), ‘Effects of leaf structure on reflectance estimates of chlorophyll content’, *Inter-  
713 national Journal of Remote Sensing* **29**, 17–18.
- 714 Sinclair, S. J., White, M. D. and Newell, G. R. (2010), ‘How useful are species distribution models  
715 for managing biodiversity under future climates?’, *Ecology and Society* **15**(1), 1–13.

- 716 ter Steege, H. (2018), *Hemiphot.R: Free R scripts to analyse hemispherical photographs for canopy*  
717 *openness, leaf area index and photosynthetic active radiation under forest canopies*, Leiden, The  
718 Netherlands. Unpublished report.
- 719 Thuiller, W., Richardson, D. M., Pyšek, P., Midgley, G. F., Hughes, G. O. and Rouget, M. (2005),  
720 'Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale',  
721 *Global Change Biology* **11**, 2234–2250.
- 722 Travis, J. M. J., Delgado, M., Bocedi, G., Baguette, M., Bartoń, K., Bonte, D., Boulangeat, I.,  
723 Hodgson, J. A., Kubisch, A., Penteriani, V., Saastamoinen, M., Stevens, V. M. and Bullock,  
724 J. M. (2013), 'Dispersal and species' responses to climate change', *Oikos* **122**, 1532–1540.
- 725 Valladares, F., Laanisto, L., Niinemets, Ü. and Zavala, M. A. (2016), 'Shedding light on shade:  
726 ecological perspectives of understorey plant life', *Plant Ecology & Diversity* **9**(3), 237–251.
- 727 Van der Putten, W. H., Macel, M. and Visser, M. E. (2010), 'Predicting species distribution and  
728 abundance responses to climate change: why it is essential to include biotic interactions across  
729 trophic levels', *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**, 2025–  
730 2034.
- 731 Wisz, M. S., Pottier, J., Kissling, W. D., Pellissier, L., Lenoir, J., Damgaard, C. F., Dormann,  
732 C. F., Forchhammer, M. C., Grytnes, J., Guisan, A., Heikkinen, R. K., Hoye, T. T., Kähn,  
733 I., Luoto, M., Maiorano, L., Nilsson, M., Normand, S., Öckinger, Schmidt, N. M., Termansen,  
734 M., Timmermann, A., Wardle, D. A., Aastrup, P. and Svenning, J. (2013), 'The role of biotic  
735 interactions in shaping distributions and realised assemblages of species: implications for species  
736 distribution modelling', *Biological Reviews* **88**, 15–30.