

1 Changes in forest structure along an Amazon-Andes elevational  
2 gradient cause species-specific acclimatory responses in tree  
3 seedlings

4 John L. Godlee

5 September 1, 2019

6 **Abstract**

- 7
- 8 We assessed the contribution of forest canopy layer structural properties to limiting elevational range shifts of tree species along an Amazon to Andes elevational gradient, focussing  
9 on tree seedlings as a key demographic bottleneck for future recruitment.
  - 10
  - 11 Photosynthetic capacity was measured using chlorophyll fluorescence estimated photosynthetic stress experienced by naturally occurring seedlings of seven tree species spanning  
12 a 2800 m elevation plot transect. Physiognomic plant traits were measured to assess the  
13 degree of local acclimatory response to elevationally dependent environmental factors.
  - 14
  - 15 We used linear mixed effects models to compare the effect sizes of canopy layer structural  
16 properties with that of elevation. A matrix of multiple fixed effect mixed models were  
17 compared statistically to ascertain the best combination of predictors affecting seedling  
18 physiognomy and stress metrics.
  - 19
  - 20 Seedlings did not experience photosynthetic stress at higher elevations, with seedlings differ-  
21 ing by species in their acclimatory physiognomic trait response. Canopy structural  
22 properties marginally increased the fit of models predicting photosynthetic efficiency and  
23 physiognomic plant traits. Remotely sensed metrics of forest canopy structure would be  
24 a valuable addition to local elevational range shift models in high value diversity hotspots such as the Andean cloud forests studied here.

25 **1 Introduction**

26 Rapid anthropogenic climate change is causing many species, across a wide range of taxa, to shift  
27 their distributions in space (Chen et al., 2011; Hughes, 2000; Parmesan, 2006). The primary forces  
28 driving this are an increase in temperature and changes in precipitation regime (Corlett and West-  
29 cott, 2013; McCain and Colwell, 2011). Chen et al. (2011) estimates that globally, across a range  
30 of taxonomic groups, species are experiencing mean latitudinal and altitudinal migration rates of  
31  $17.6 \pm 2.9$  km and  $12.2 \pm 1.8$  m per decade, respectively. Previous studies have suggested that the  
32 ability of species to respond to changes in mean annual temperature and precipitation regime will  
33 be important in determining species success over the coming century (Colwell et al., 2008; Chen  
34 et al., 2011; Feeley et al., 2012).

35 Species responses to climate change may occur either in the form of adaptation, *i.e.* changes  
36 in phenology, physiology and morphology, or through range shifts over space (Bellard et al., 2012).

37 Range shifts have been observed in many studies across the world, particularly in temperate, sub-  
38 arctic and montane regions where temperature change is the most extreme (Lenoir and Svenning,  
39 2015). The number of studies documenting adaptational responses to climate change are fewer,  
40 potentially indicating that climate change is occurring so rapidly as to prevent effective adaptational  
41 responses (Mantyka et al., 2012). Range shift rates vary between species depending on their  
42 sensitivity to climate and their fecundity, which affects rate of recruitment into newly suitable areas  
43 (MacLean and Beissinger, 2017; Travis et al., 2013). This asynchronicity has the potential to create  
44 novel species assemblages as species ranges overlap more or less as they shift at different rates, with  
45 unknown consequences for ecosystem functionality (Hobbs et al., 2009). Predicting range shifts  
46 across space has become an active field of research, (see Bellard et al. 2012 and references therein),  
47 and is being used as a tool to inform conservation strategies to mitigate the effects of climate change  
48 on biodiversity and ecosystem functionality (Dawson et al., 2011).

49 The majority of species distribution models used to predict species range shifts as a conservation  
50 tool have used bioclimatic envelopes to constrain species ranges (Pearson and Dawson, 2003; Sinclair  
51 et al., 2010). Bioclimatic envelopes are constructed by correlating current species range extent  
52 with observed environmental conditions within those boundaries, then projecting spatially explicit  
53 climate trends into the future under different climate change scenarios to predict how species range  
54 boundaries will adjust in response (e.g. Araújo et al. 2006; Berry et al. 2002; Peterson et al. 2002;  
55 Thuiller et al. 2005). These models have been criticised often for being overly simplistic, especially  
56 when applied at the local scale (McMahon et al., 2011), where other factors that have not been  
57 considered by the bioclimatic envelope model become important limiting factors for range shifts.  
58 Such factors include unmeasured environmental variables, physical factors such as topography, and  
59 biotic interactions with other species (Davis et al., 1998; Ettinger et al., 2011; Van der Putten et al.,  
60 2010).

61 When range shifts in a rapidly changing climate are driven by a single environmental variable like  
62 mean annual temperature, it is possible that a species will move into an area that is sub-optimal in  
63 other ways than those predicted by the model if range shifts outstrip acclimatory/adaptive potential.  
64 Range shifts into sub-optimal habitats may lead to reductions in local abundance and/or species  
65 richness (Colwell et al., 2008), changes in community composition (Gibson-Reinemeyer et al., 2015),  
66 ecosystem functioning (Bellard et al., 2012), and ecosystem service provision that are not predicted  
67 by bioclimatic envelope models (Dobson et al., 2006; Isbell et al., 2011). In order to accurately  
68 predict range shifts and their consequences for future ecosystem assembly, it is important that  
69 predictive range models be expanded to include variables which describe habitat as well as climate  
70 (Wisz et al., 2013).

71 For sessile taxa such as trees, range shifts occur as a result of differential recruitment and mor-  
72 tality over space, at the leading and trailing edges of their range (Corlett and Westcott, 2013). In  
73 communities of long-lived tree species however, the forest ecosystem may not shift in equilibrium  
74 with the climate as individuals are resilient to gradual changes in climate, developing large root  
75 systems and below-ground water and nutrient reserves to buffer against stressful conditions; adult  
76 trees may persist where more sensitive seedlings perish (Bell et al., 2014; Lenoir et al., 2009). As  
77 tree seedlings recruit upslope into areas that are newly suitable in terms of temperature, they will  
78 encounter novel biotic environments consisting of canopy trees which first recruited into the area  
79 when the climate was different. Forest trees, particularly those in moist tropical forests, often ex-  
80 perience high levels of mortality during the seedling recruitment stage, creating a key demographic  
81 bottleneck that can impact a species' success, potentially limiting upslope migration (Coomes and  
82 Grubb, 2000). Seedling growth is affected by shade regimes created by adult tree canopy gaps.  
83 There is abundant evidence that shading from adult tree canopies reduces seedling growth rate and  
84 thus increases the probability of seedling mortality, with tropical forest tree seedlings frequently  
85 growing into canopy gaps (Valladares et al., 2016). Additionally however, seedlings of many trop-  
86 ical tree species are highly adapted to shade (Matsuraba et al., 2009), meaning that if a seedling

87 germinates under an open space in the canopy, especially in the tropics at a higher elevation, where  
88 UV-B intensity is high, mortality by UV-B and heat damage to photosynthetic machinery is quite  
89 probable (Krause et al., 2001; Li et al., 2010). Many species found at high altitudes have specific  
90 adaptations to avoid UV-B damage to photosynthetic machinery, such as vertically stacked palisade  
91 mesophyll cells and thick cuticles to reduce UV-B absorption, and generally smaller thicker leaves  
92 (Prado et al., 2012). Species found at low altitudes however, are less adapted to high UV-B en-  
93 vironments, instead possessing adaptations to make the most of the diminished light levels found  
94 under thick tree canopy, particularly during the seedling growth stage. If seedlings germinate in  
95 areas that have a different overstorey shade regime and forest structural type to that which they are  
96 adapted to grow in, damage may occur leading to loss of photosynthetic capacity, reducing growth  
97 rates and occasionally resulting in seedling mortality.

98 Montane forest physical structure varies with elevation. Lowland forests often have lower tree  
99 density, with relatively few young trees in the light-deprived understorey, but a higher canopy  
100 cover (). Herbaceous plant cover is generally greater at higher altitudes, with many epiphytic and  
101 ground-level species (Martin et al., 2010). Tree seedlings moving upslope may therefore compete  
102 with existing trees and herbaceous flora for nutrients and rootspace, although there is some separa-  
103 tion between seedling and adult tree rooting depths for most species (Lewis and Tanner, 2000),  
104 especially for the largest trees. These factors which act as limitations to upslope migration of tree  
105 species in tropical montane forests may lead to species' ranges narrowing from the bottom up, with  
106 increased mortality due to temperature at the bottom of the elevational range, but without increased  
107 recruitment at the top end of the elevational range (). This seedling mortality bottleneck provides  
108 a limiting factor to the success of montane tropical forest tree species experiencing range shifts and  
109 raises concern for their conservation as keystone species of these highly biodiverse ecosystems.

110 Andean forests are experiencing warming of between 0.1 °C and 0.6 °C per decade (Marengo  
111 et al., 2011; Vuille et al., 2015) with predicted increases in air temperature of between +1.7°C to  
112 +6.7°C by 2100 (Magrin et al., 2014). In response to these shifts in climate, the Andes has been  
113 projected to experience species turnover of 90% over the next century. However, not all species  
114 follow a predictable upslope migrational trend. In montane tropical forests generally, ~25% of  
115 species showing a downslope movement and ~10% showing no movement (Lenoir et al., 2010).

116 In this study, along a moist tropical forest elevational gradient in the Peruvian Andes, we inves-  
117 tigated the role of biotic effects from existing forest structure on the physiology and physiognomy of  
118 tree seedlings across their elevational ranges, in order to increase our knowledge of the dynamics of  
119 montane cloud forest tree species elevational range shifts. We tested three hypotheses: H<sub>1</sub>) Within  
120 a species, seedlings growing at higher elevations would experience higher levels of photosynthetic  
121 stress than those at lower elevations, H<sub>2</sub>) Species would differ in their degree of acclimation to  
122 variation in adult tree forest structure, and H<sub>3</sub>) A combination of biotic and abiotic explanatory  
123 variables would best explain variation in seedling physiognomic and physiological traits across their  
124 elevational range.

## 125 2 Materials and Methods

### 126 2.1 Study Site

127 Data collection was conducted across 10 permanent 1 ha forest plots in the Kosñipata Valley of Manú  
128 National Park, Peru (-13°N, -71°W, Figure 1, Table 1). The Kosñipata Valley has been identified as  
129 a migration corridor for lowland species to migrate to higher elevations in response to temperature  
130 increase (Feeley et al., 2011) and so is an appropriate location to study range shift drivers (Figure

131 4). Plots are situated between 800 and 3200 m elevation along this migration corridor (Table 1,  
 132 Figure 2). The plots form part of a larger plot network established by the Andes Biodiversity and  
 133 Ecosystem Research Group (ABERG) in 2003 (Malhi et al., 2010; Girardin et al., 2014), and are  
 134 located within the Tropical Andes biodiversity hotspot identified in Myers et al. (2000). The plots  
 135 used in this study contain 719 tree species, and the valley as a whole contains an estimated 1167  
 136 tree species (ABERG unpublished data).

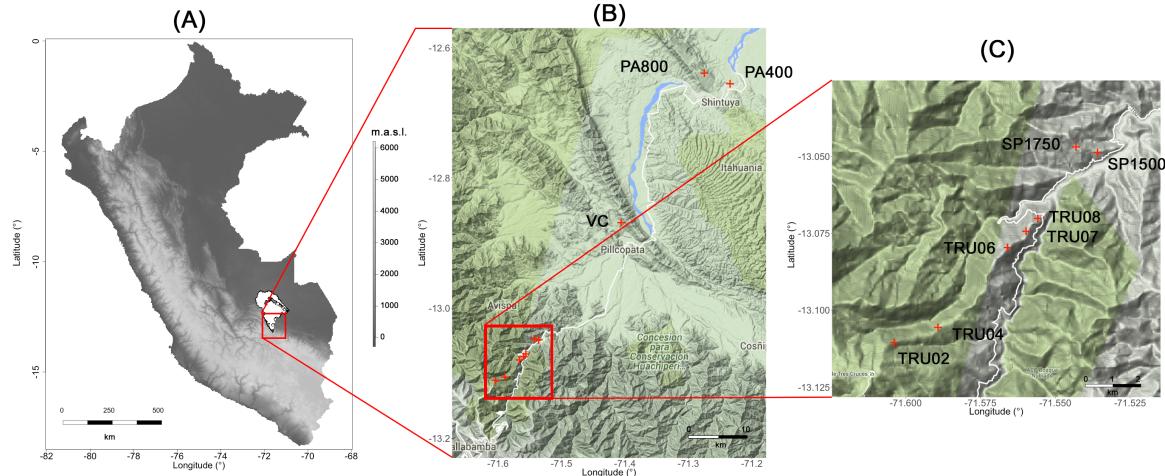


Figure 1: Maps showing the location of the study area and plot locations. (A) The site location within Peru with elevation shading, showing the proximity to Manú National Park on the eastern flank of the Andes (white area). (B) The location of the 1 ha plots within the Kosñipata Valley. (C) An enlargement of the Trocha Union (TU) and San Pedro (SP) 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	Total_C	Total_N	Soil_pH	trees_ha
PA400	406						475
PA800	822						690
VC	861	3087	20.7	16	1.4	3.8	645
SP1500	1497	2631	17.4	10.5	1	4	860
SP1750	1770	2631	15.8	26	1.8	4.2	887
TRU08	1839	2472	16	31	2	4.3	954
TRU07	2135	1827		37	2.1	4	1060
TRU06	2281		14.9				1101
TRU04	2733	2318	11.1	28.5	1.8	3.9	1287
TRU02	3213		8.9	44.5	2.6	3.8	1417

137 Add something about the environmental variation within the elevational gradient, presence of  
 138 cloud zone etc.

139 **2.2 Study species**

140 We chose seven tree species for comparison from a total of 719 identified species within the 9 study  
 141 plots. Species were selected according to their contrasting ranges (Figure 2), differences in genus  
 142 migratory pattern (Feeley et al., 2011) (Figure 4), and because each species is dominant across its  
 143 range in the Kosñipata Valley (ABERG, unpublished data) (Figure 3). Seedlings of *Myrcia* spp.  
 144 (MS) are difficult to reliably identify to species in the field due to similar morphology and were  
 145 instead sampled as a composite of three potential species: *Myrcia splendens*, *M. fallax*, and *M.*  
 146 *rostrata*, the only *Myrcia* species known to be present in our plots from previous ABERG censuses.  
 147 They are referred to as *Myrcia* spp. from here onwards.

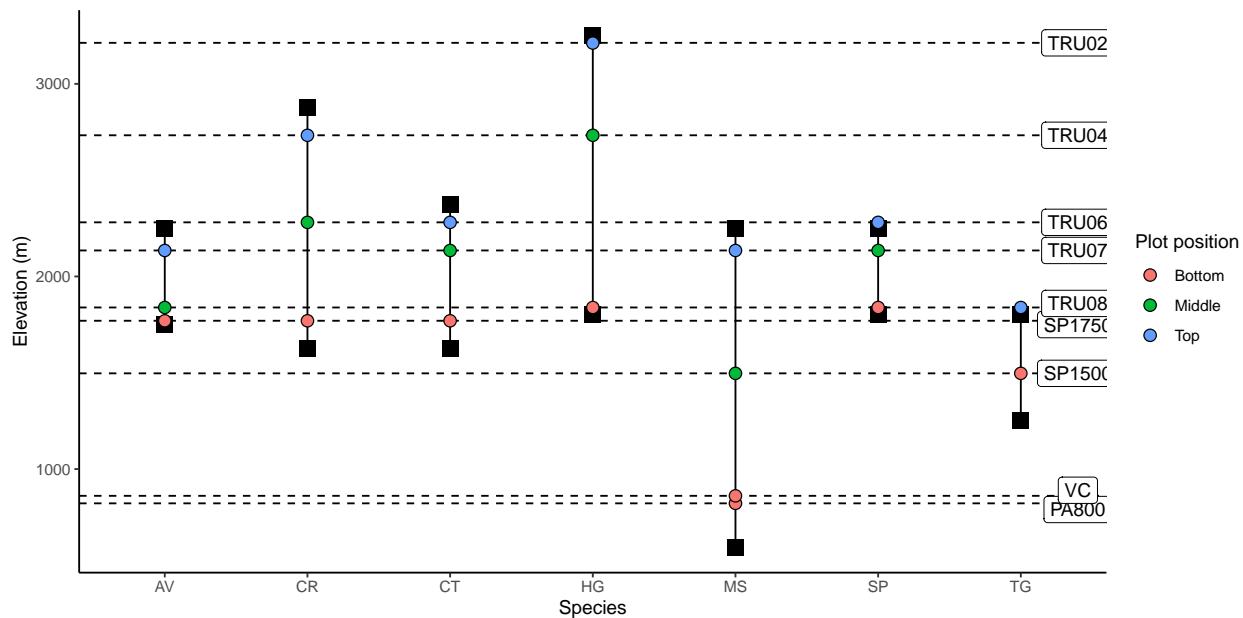


Figure 2: Elevations of study plots for each species (coloured points) with the upper and lower range extents for each species (black squares). Plot elevations are marked as dashed lines and labelled. See Table 2 for full species names.

Table 2

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

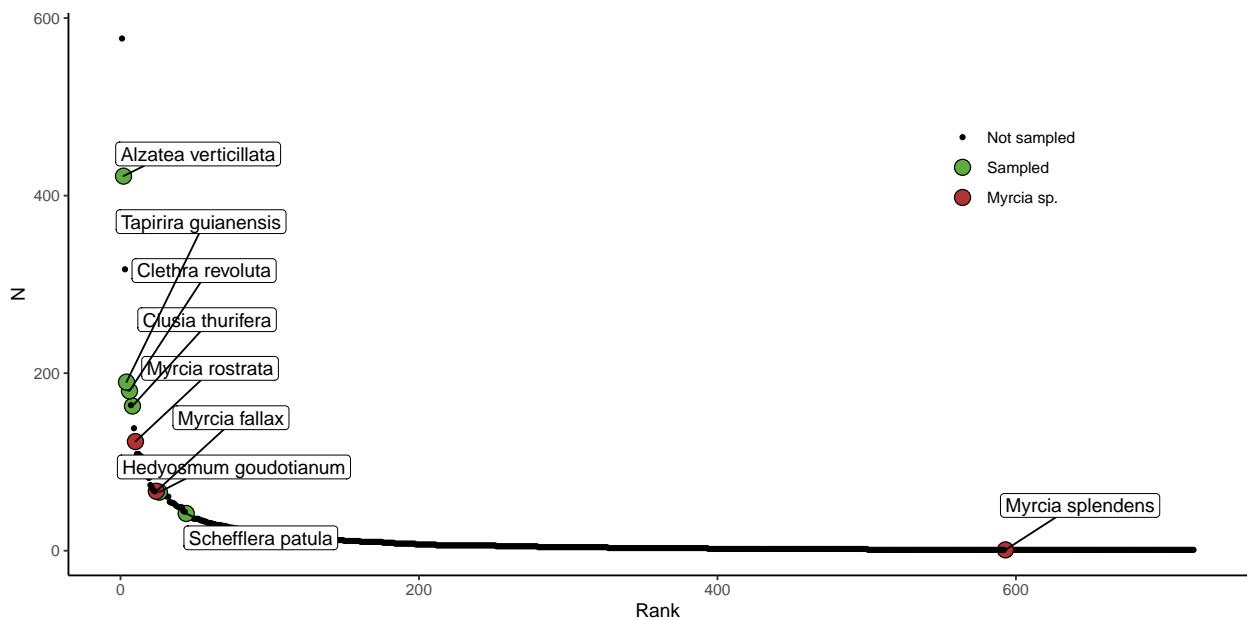


Figure 3: Rank abundance curve of all individuals >10 cm DBH of all species found in the plots measured in this study. Census data from 2014 (ABERG, unpublished data). Species sampled as part of this study are highlighted in red. *Myrcia* species which form the composite *Myrcia* spp. (MS) are highlighted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

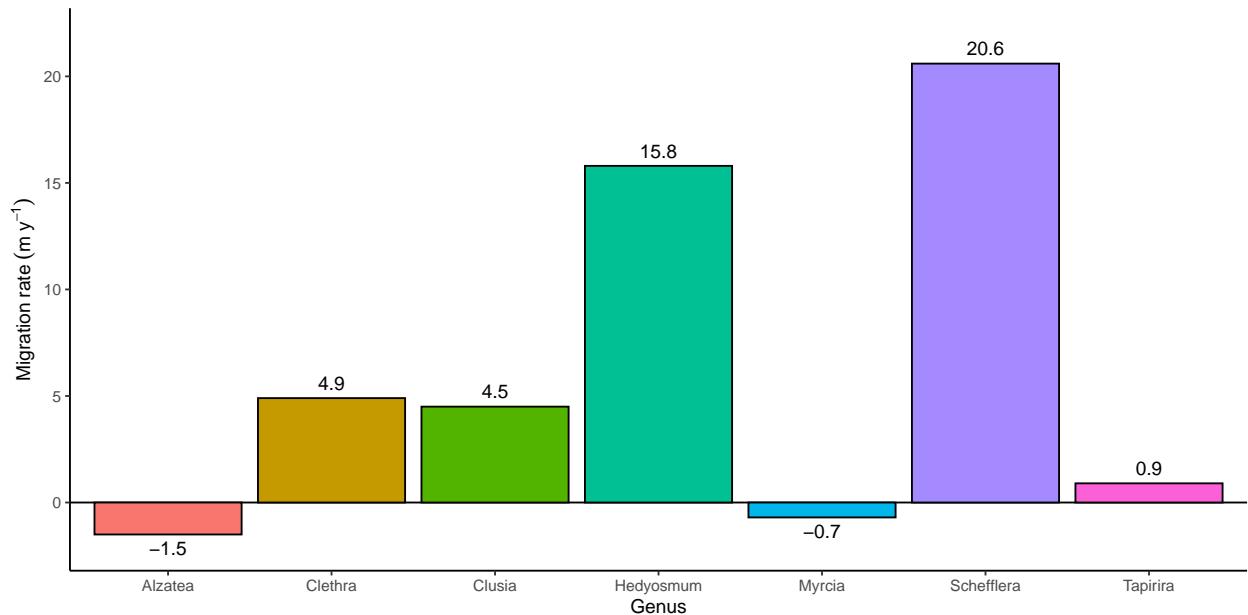


Figure 4: Estimated elevational migration rates within the Kosñipata valley for genera sampled in this study. Migration rates are estimated using shifts in the centre of gravity of tree basal area as measured in the ABERG 1 ha plot network. Adapted from (Whitaker et al., 2014).

## 148 2.3 Sampling and Measurement

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

152 another sampled seedling were excluded from the analysis, as it could not be guaranteed that the  
153 stems were not connected by a stolon or rhizome. It also ensured that canopy layer structural  
154 measurements were truly independent. Within a cluster of seedlings within 5 m of each other, each  
155 seedling was assigned a number and a random number generator was used to choose a single seedling  
156 for measurement.

157 Proxies for photosynthetic capacity were measured on the highest fully-expanded leaf of each  
158 seedling to assess seedling stress. Seedlings under physiological stress may deactivate or lose chloro-  
159 phyll photo-centres, lowering photosynthetic capacity. Chl<sub>a</sub> fluorescence was measured to estimate  
160 photosynthetic capacity using a Walz Mini-PAM II (Walz Effeltrich, Germany), on a randomly  
161 selected area of adaxial leaf surface, avoiding prominent leaf veins. These measurements were used  
162 to calculate  $F_v/F_m$  according to Genty et al. (1989):

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

163 Where  $F_m$  is the maximal fluorescence in the dark and  $F_o$  is the minimal fluorescence in the dark  
164 (Maxwell and Johnson, 2000). Fluorescence measurements were taken after exposing the seedling  
165 to 30 minutes of total darkness by covering with an opaque black bag, to ensure complete dark  
166 adaptation (Campbell et al., 2007). Dark-adapted  $F_v/F_m$  measures the photosynthetic capacity of  
167 the leaf by relaxing the photo-centres prior to the fluorescence measurement.  $F_v/F_m$  is preferable to  
168 other chlorophyll fluorescence measures to estimate underlying physiological stress as it removes the  
169 noise created by environmental conditions at the time of measurement, instead providing a measure  
170 of the underlying photosynthetic capacity. A reduction in  $F_v/F_m$  is indicative of plant stress. Here,  
171 individuals with  $F_v/F_m$  values <0.7 are considered to be experiencing stress (Maxwell and Johnson,  
172 2000).

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

$$Chl_a = 117.1 \times \frac{\overline{SPAD}}{148.84 - \overline{SPAD}} \quad (2)$$

## 180 2.4 Leaf and whole-plant morphological measurements

181 After leaf physiological measurements, the same upper-most expanded leaf was removed from the  
182 seedling and hydrated for a minimum of 48 hours to reverse any leaf curling or contraction in thick-  
183 ness due to dessication. With the petiole removed, each leaf was photographed with a scale and  
184 the projected lead area was calculated using ImageJ Version 1.51 (Schneider et al., 2012). Mean  
185 leaf thickness was calculated using a digital micrometer (0-25 mm, Precision Technologies Interna-  
186 tional, Tamworth, Staffordshire, UL) on three random points on the leaf, avoiding the midvein and  
187 prominent leaf veins. To quantify whole-seedling physiognomic characteristics we measured stem  
188 diameter below the lowest set of leaves using the digital micrometer and counted the number of  
189 fully expanded leaves (excluding cotyledons). We also measured seedling height from the base of  
190 the stem to the tip of the upper-most fully expanded leaf. Stem volume was calculated from stem

width and seedling height assuming a cylinder of constant diameter (). To account for differences in seedling growth stage and to reduce the number of collinear variables in statistical analyses, stem height and number of leaves was expressed as the ratio of number of leaves per unit stem height.

## 2.5 Forest canopy structural measurements

To assess adult-seedling interactions we used two metrics, Leaf Area Index of canopy foliage, and a metric approximating the degree of crowding from surrounding adult trees. Leaf Area Index (LAI) was calculated from hemispherical photographs of the forest canopy above each seedling. Photographs were captured under uniformly overcast cloudy conditions to avoid lens flare and to aid in delineation of foliage from sky during processing (Frazer et al., 2001). Images were taken with a Coolpix 4500 compact camera, with a Nikon FC-E8 hemispherical fisheye converter lens. Images were constrained to a 60° circular azimuthal field of view in order to restrict LAI calculations to the part of the sky where the majority of photosynthetically active radiation penetrates the canopy (Jupp et al., 2008; Jonckheere et al., 2004). Images were then converted to 8-bit grayscale and binarized manually in ImageJ 1.51 to separate sky from plant material. Binarized images were then analyzed using *Hemiphot* (ter Steege, 2018) in R to estimate LAI as the projected leaf area per unit ground area ( $\text{m}^2 \text{ m}^{-2}$ ).

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

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

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. An iterative selection method for competitive trees assumes that if the path between two trees is blocked by some obstacle, e.g. another tree, the intensity of competition between them will be greatly reduced (Gadow and Hui, 1999). The radius around the seedling is divided into 12 30° sectors, where only the nearest tree >10 cm DBH within each sector is measured (Figure 5). The size of the Competition Radius ( $C_R$ ) is defined as:

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

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 interpolate the value of  $C_R$  for plot VC, for which no stand density data exists. We fitted a linear regression between the elevation and trees  $\text{ha}^{-1}$  of each plot, and interpolated the trees  $\text{ha}^{-1}$  of plot VC using the regression fit (Figure 6).  $C_R$  was rounded to the nearest metre for ease of measurement (Table 3).

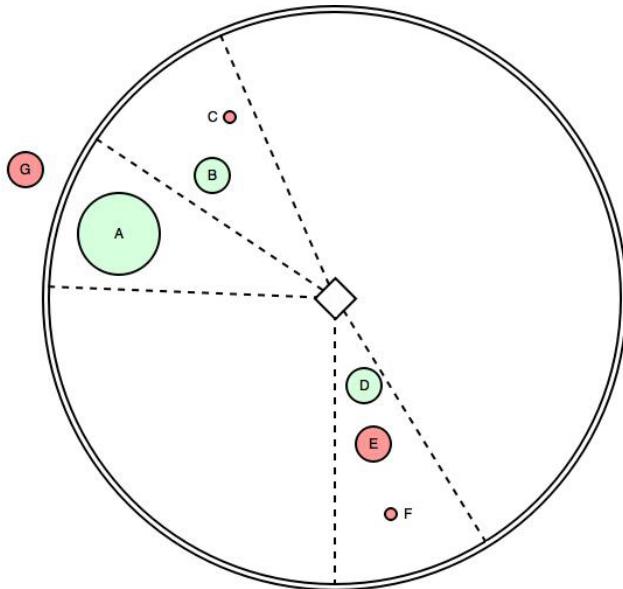


Figure 5: Schematic diagram showing the iterative selection of active competitor trees for the Iterative Seedling Index (ISI) (Equation 3). Trees marked in green (A, B, D) are active competitors for the tree of interest (black diamond). Trees marked in red (C, E, F, G) are non-active competitors, coloured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

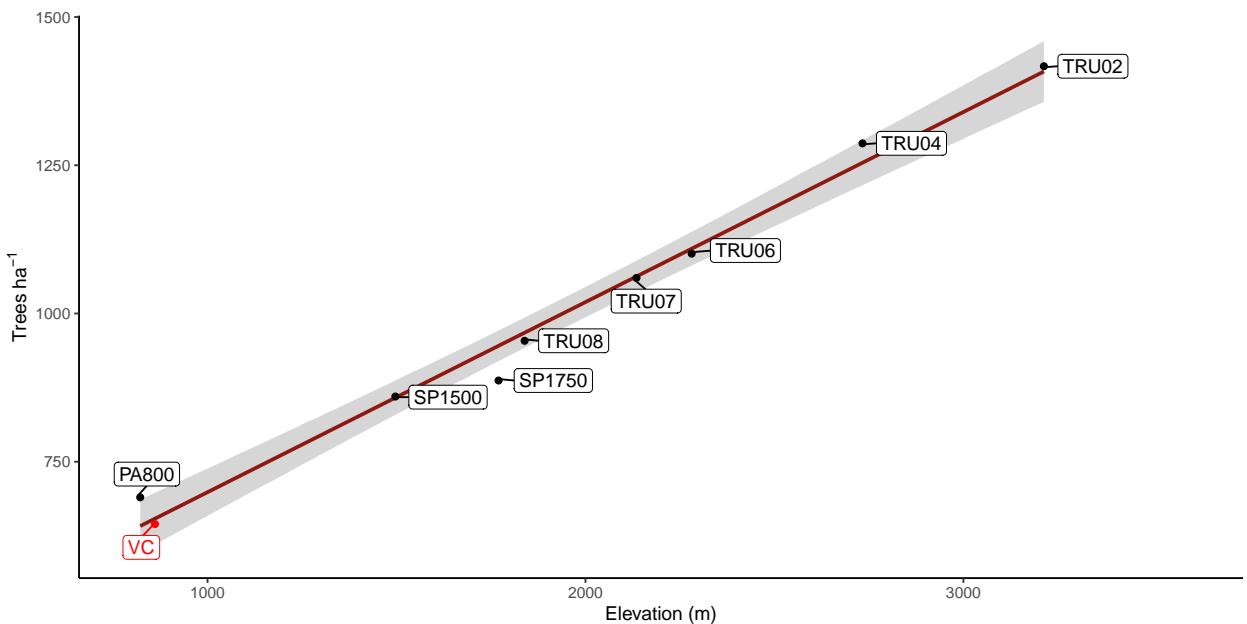


Figure 6: Linear regression with 95% confidence interval of number of trees per hectare across elevation for each site, used to estimate number of trees per hectare for site VC.  $R^2 = 0.896$ ,  $F_{(1,7)} = 579.5$ ,  $p < 0.001$ .

Table 3

site	trees_ha	c_r
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

## 228 2.6 Statistical Analysis

229 A matrix of single predictor linear mixed effects models were compared to test for the presence and  
 230 strength of the causal relationship between each of the two forest canopy layer structure variables  
 231 and each of the six plant traits. The fixed effect of elevation was also included in this comparison  
 232 in order to compare the effects of canopy layer structure to that of other unmeasured elevationally  
 233 dependent environmental effects. All fixed effects were standardised and rescaled with a mean of 0  
 234 and a standard deviation of 1 to allow easy comparison of effect sizes, according to (Gruber et al.,  
 235 2011). Comparison of models with different single fixed effects was performed on models fitted  
 236 using Maximum Likelihood (ML) estimates (Bolker et al., 2008). Model quality was assessed using  
 237 Akaike Information Criteria ( $AIC$ ) (Akaike, 1992),  $\delta AIC_r$  against a random effects model, and fixed  
 238 effect marginal pseudo-R<sup>2</sup> values ( $R_M^2$ ) using *r.squared.GLM()* from the *MuMIn* package (Bartoń,  
 239 2019). Models using different fixed effects were compared using an approximation of the variance  
 240 explained by the model ( $R_C^2$ ) using *r.squared.GLM()* (Bartoń, 2019), and slope coefficients (Figure  
 241 12) to compare their relative effect on plant traits. Random effects of site and species were added  
 242 to the models. Site was added as a random intercept effect to account for pseudo-replication in site  
 243 characteristics within which multiple seedlings per site were sampled. Tree species was added as a  
 244 random slope effect to account for differences in morphology and physiology between seedlings and  
 245 to allow for comparison of model slopes between species. As there were multiple species sampled  
 246 within a single plot, but not all plots contained all species, these models have a partially crossed  
 247 random effects structure. Single fixed effect model structures were as follows:

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

248 where  $Y_{ij}$  is the response variable of species  $i$  at site  $j$ ,  $X_{ij}$  is the fixed effect value of species  
 249  $i$  in site  $j$ . The random intercept grouping effect of site was used in all models to account for  
 250 pseudo-replication in site characteristics for seedlings sampled along the elevation gradient.

251 To better understand the multiplicative effects of canopy layer structure and other elevationally  
 252 dependent environmental variables on plant traits we also compared linear mixed effects models  
 253 with combinations of fixed effects, using  $AIC$ ,  $W_i$  and  $R_C^2$ , to find the model which best explained  
 254 variation in each plant trait. These models used the same basic model specification as the single  
 255 fixed effect models shown above, except with multiple additive fixed effects. To ensure all models  
 256 converged, these more complicated models used random intercept effects for both species and sites.  
 257 For initial model comparison, these models were fitted using Maximum Likelihood. All statistical  
 258 analyses were conducted using R, version 3.2.4 (R Core Team, 2019). Linear mixed effects models

259 were fitted using the *lme4* package (Bates et al., 2015). The best fitting models for each physiological  
260 and physiognomic plant trait were refitted using Restricted Maximum Likelihood (REML) in order  
261 to assess fixed effect slopes.

## 262 3 Results

### 263 3.1 Variation in plant traits across elevation

264 All species except *Myrcia* spp. (MS) showed a general positive trend in photosynthetic efficiency  
265 ( $F_v/F_m$ ) across their respective elevational ranges, though the spread of  $F_v/F_m$  within species  
266 was small, though with some distinct outliers. *Myrcia* spp. did not meaningfully vary over their  
267 elevational range. Random effect slopes of photosynthetic efficiency over elevation showed that none  
268 of the species level regressions dipped below the critical stress threshold of 0.7. Of the 151 measured  
269 seedlings, 12 had an  $F_v/F_m$  below 0.7. Of those 12 seedlings, 4 were *Alzatea verticillata* (AV), 4  
270 were *Hedyosmum goudotianum*, 2 were *Clethra revoluta* (CR) and 1 each from *Clusia thurifera* (CT)  
271 and *Myrcia* spp. (MS) (Figure 11).

272 Chl $\alpha$  generally decreased with elevation, with negative trends in *A. verticillata* (AV), *C. thurifera*  
273 (CT), *Myrcia* spp. (MS), *Schefflera patula* (SP) and *Tapirira guianensis* (TG). *C. revoluta* (CR)  
274 and *Hedyosmum goudotianum* (HG) had positive trends (Figure 9). Variation was high within  
275 species sample locations however, with the distribution of Chl $\alpha$  being generally right-skewed within  
276 each species sample.

277 The relationship between physiognomic plant traits and elevation varied between species. Leaf:height  
278 ratio generally decreased with increasing elevation, with seedlings becoming less leafy as elevation in-  
279 creased, except for *A. verticillata* (AV) which showed a U-shaped relationship, and *H. goudotianum*  
280 (HG) which showed a hump-shaped relationship (Figure 8). Leaf area did not vary meaningfully  
281 across elevation except in *S. patula* (SP) where it decreased and *T. guianensis* (TG) where it  
282 increased. Leaf thickness generally increased or remained the same with elevation, except in *C.*  
283 *thurifera* (CT), which had a weak negative relationship, with some individuals at the lower end  
284 of the elevational range having particularly thick leaves. Stem volume was similarly unaffected by  
285 elevation, except in *S. patula* (SP), where it decreased with elevation and in *H. goudotianum* (HG)  
286 where it increased, driven by very large seedlings at the top end of the elevation gradient.

287 Species with restricted elevational ranges were more likely to have steeper relationships of both  
288 physiological and physiognomic plant traits across elevation, e.g. *A. verticillata* (AV), *C. thurifera*  
289 (CT), *S. patula* (SP) and *T. guianensis* (TG). These species with restricted elevational ranges also  
290 inhabit the cloud zone of the forest elevational gradient (Figure 14).

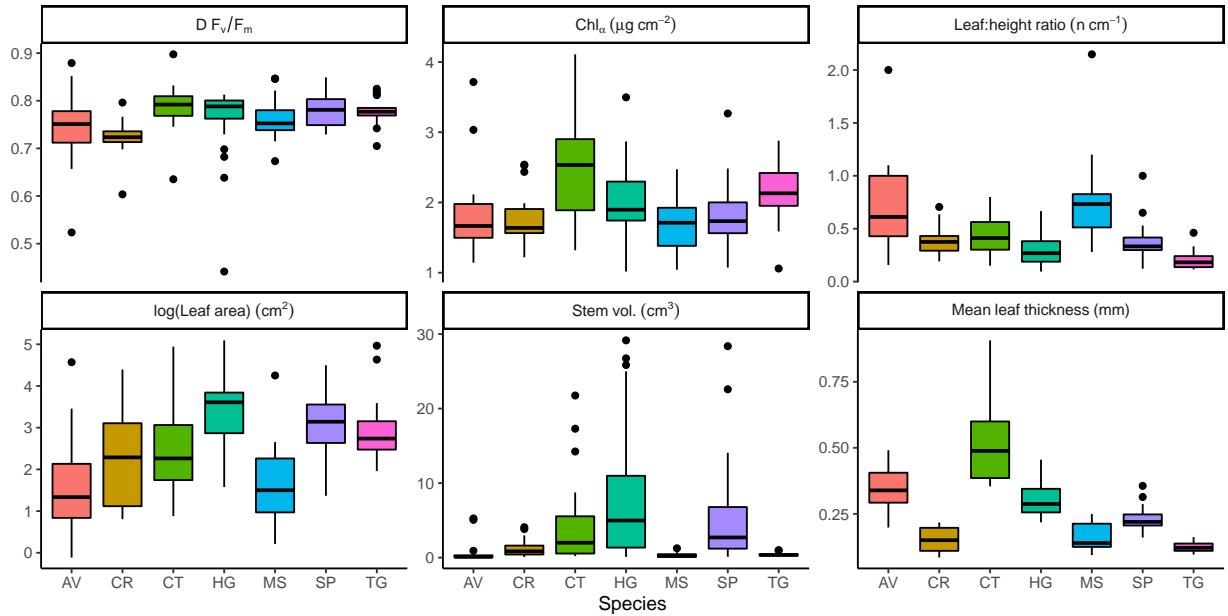


Figure 7: Box plots showing the variation in plant trait values within each species. Thick black lines show the median value for each species, boxes indicate the interquartile range of values, lines show the 95% quantile and points show outliers outwith the 95% quantile range.

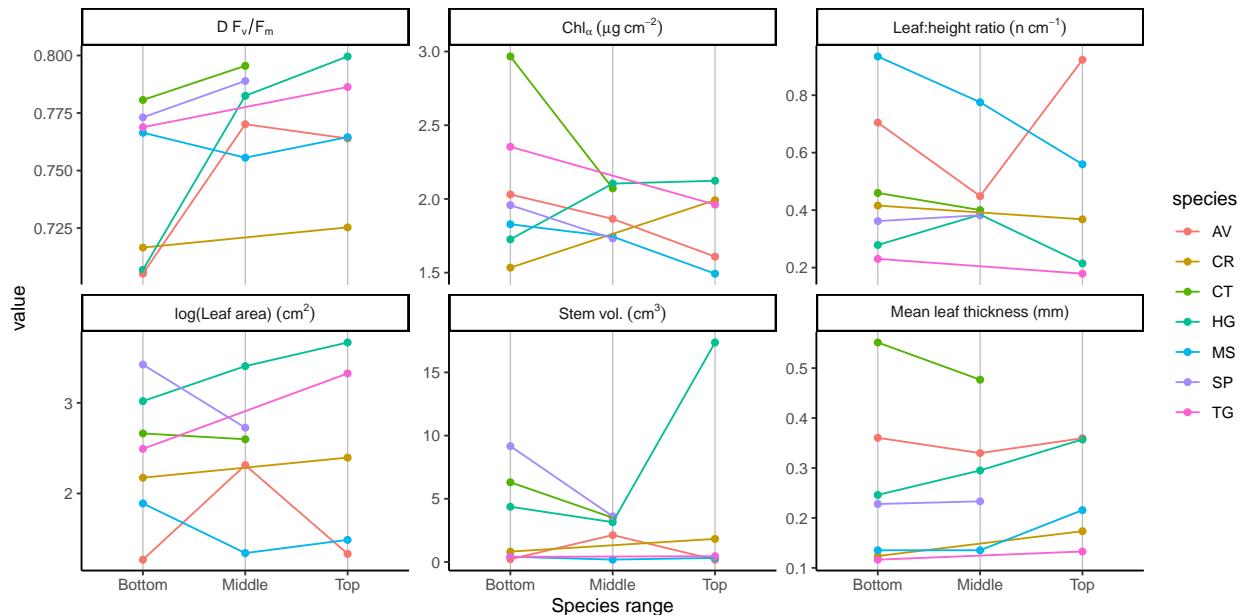


Figure 8: Interaction plots showing the variation in plant trait values within each species.

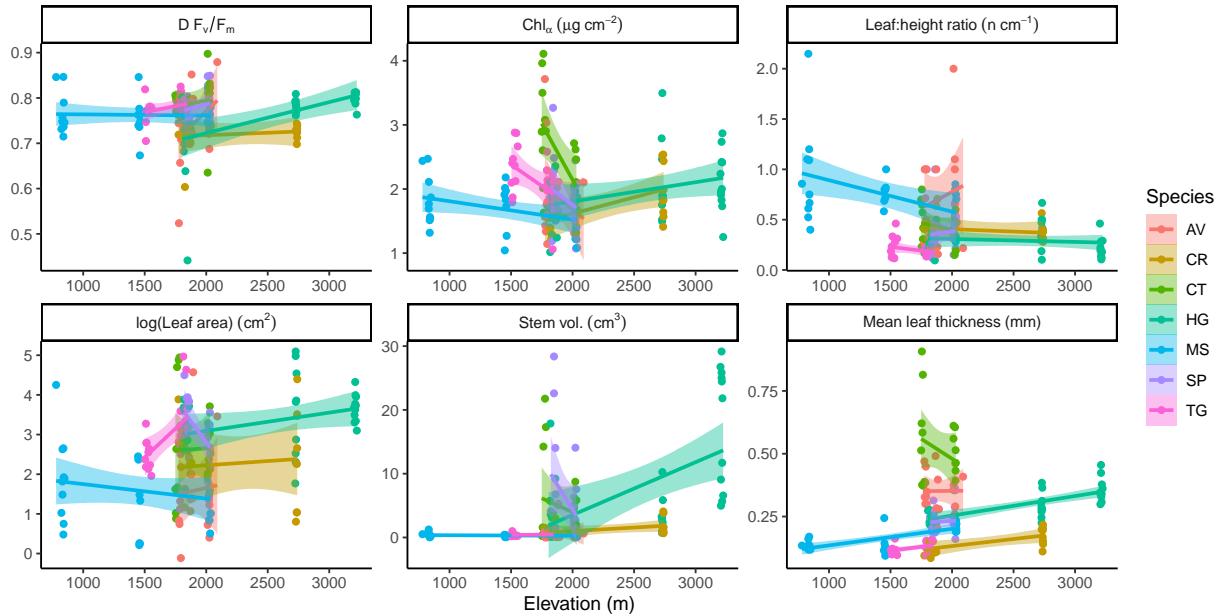


Figure 9: Scatter plots with linear model fits for each species, showing the variation in plant stress variables and plant traits across elevation.

### 291 3.2 Variation of forest canopy structure with elevation

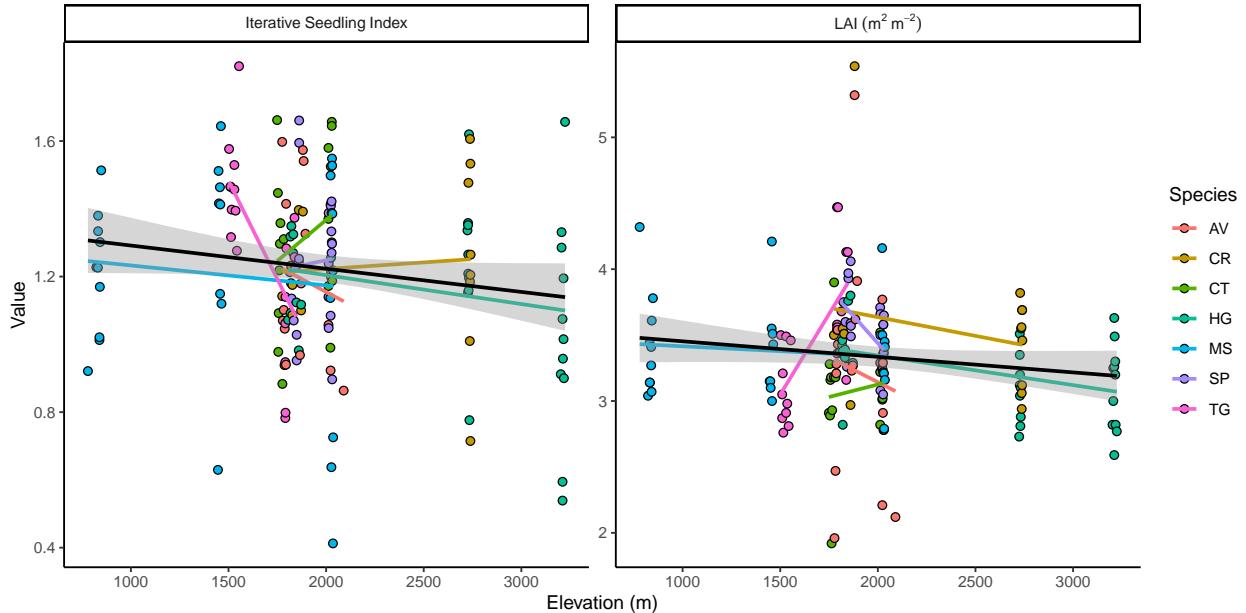


Figure 10: Scatter plots with linear model fits showing the variation in forest canopy structural measurements across elevation. Points are coloured by the species of seedling around which the measurement was taken. Coloured lines show linear model fits for each species. The thick black line shows a general linear model across all species, with a 95% confidence interval. It is important to note that this variation in forest canopy structural properties does not necessarily reflect the average value of the variable across elevation, rather the average value of the variable where seedlings were found to be growing.

292 Proxies of tree canopy structural variation did not vary significantly with elevation. LAI and ISI  
 293 both showed weak negative correlations with elevation (LAI:  $t = -1.66(1,149)$ ,  $p = 0.099$ ; ISI:  $t =$   
 294  $-1.85(1,149)$ ,  $p = 0.066$ ). The highest LAI values occurred near the top of the cloud forest zone at  
 295 1881 m in site TU08, however the lowest LAI values also occurred in the cloud forest zone at 1763  
 296 m in site SP1750.

### 297 3.3 Directional effects of forest canopy layer structure on plant traits

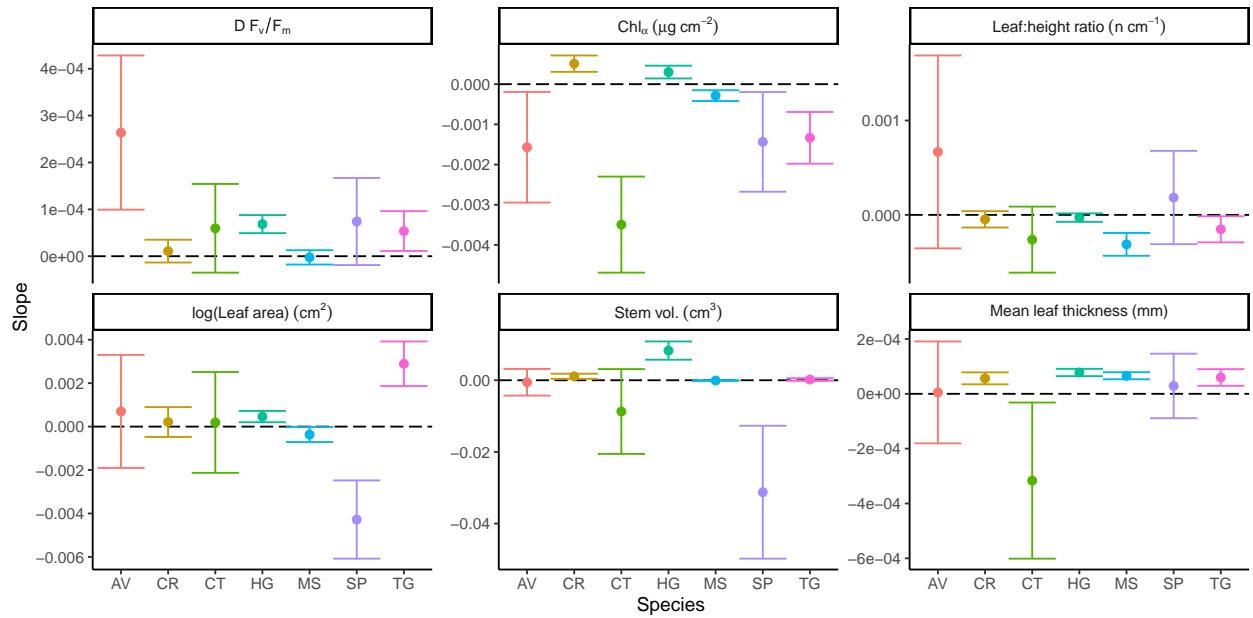


Figure 11: Interval plots showing the effect sizes (slopes) of each species in single fixed effect linear mixed effects models of plant traits against elevation variables. Error bars show the 95% confidence interval of the linear relationship.

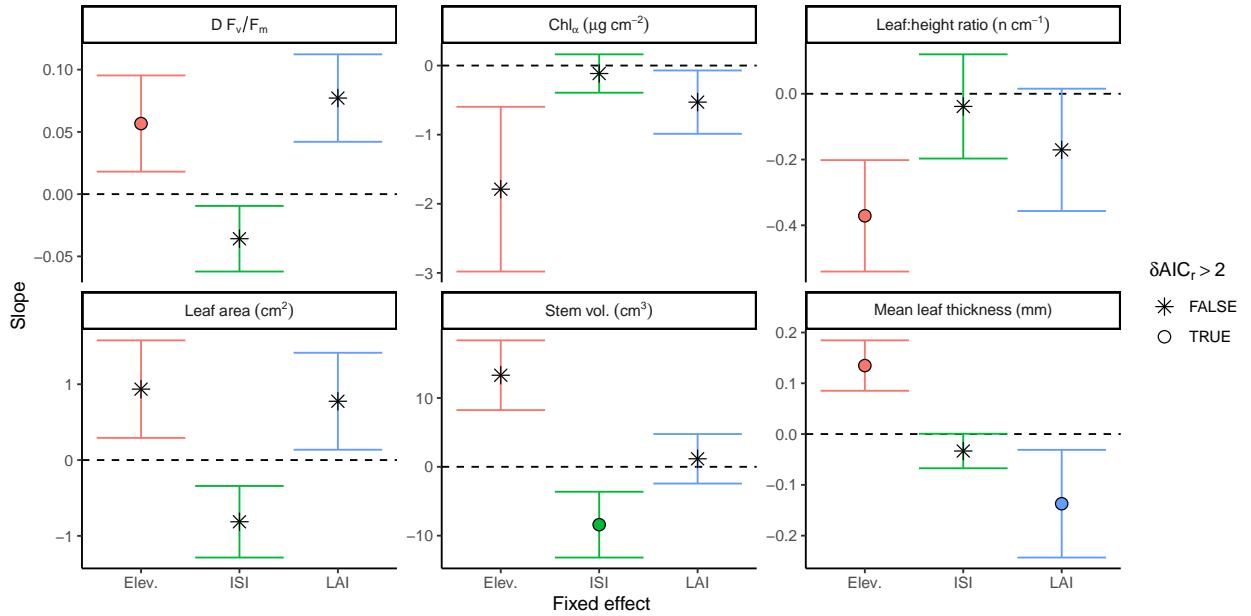


Figure 12: Model slopes for each single fixed effect model of plant traits predicted by elevation and forest canopy structure variables. Error bars are  $\pm 1$  standard error. Models where  $\delta AIC_r$  was less than two and therefore not appreciably better than an equivalent random effects models are shown as asterisks.

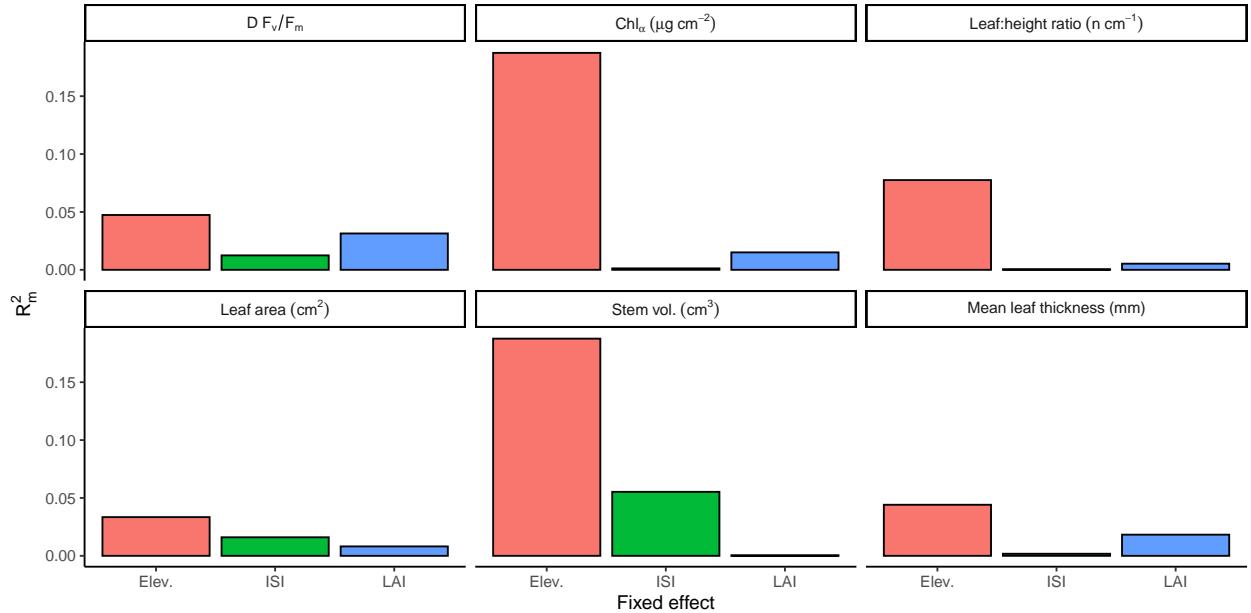


Figure 13: The approximation of marginal  $R^2$  explained by the fixed effect of each single fixed effect model.

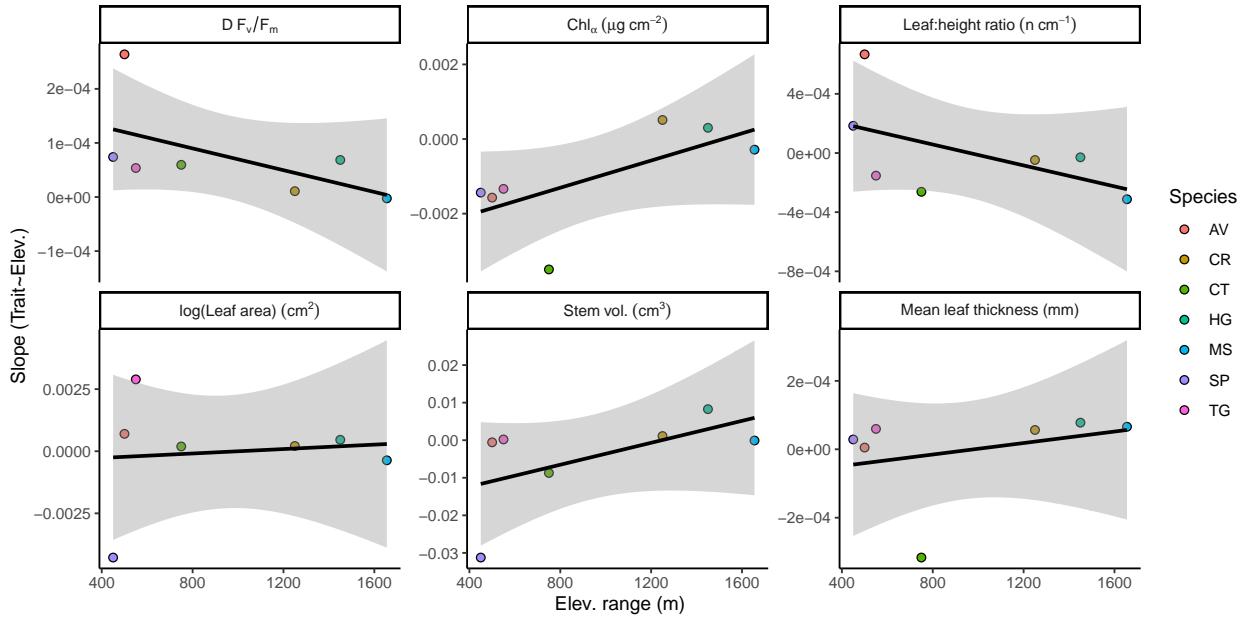


Figure 14: Relationship between model slope and species elevational range, for linear models between seedling traits and elevation of measurement, for each species. Shaded areas show the regression 95% confidence interval.

298 Across species, models with single fixed effects poorly estimated variation in plant traits. Models  
 299 with the fixed effect of elevation explained the greatest amount of variation in plant traits, notably  
 300 stem volume and Chlorophyll- $\alpha$ , but neither of these models were appreciably better than a random  
 301 effects model including only the effects of site and species (Figure 13). Models with ISI vs. stem  
 302 volume and LAI vs. leaf thickness were the only two single fixed effect models using canopy structure  
 303 variables which provided adequate model fit, estimated via  $\delta AIC_r$ , slope coefficients and  $R_m^2$  (Figure  
 304 13). ISI caused a decrease in stem volume, LAI caused a decrease in leaf thickness.

305 Table 4 shows the fixed effects and model fit measures from the best fitting multiple fixed effect  
 306 models used to predict plant traits. All of the best multiple predictor mixed effects models included  
 307 elevation as a fixed effect. All of the best models, except the model predicting leaf Chl $\alpha$ , included  
 308 both adult canopy structure variables, ISI and LAI, alongside that of elevation (Figure 15). The  
 309 variance explained by these best multiple predictor mixed effects models was higher than that for  
 310 the single fixed effects models but the variance accounted for by the fixed effects remained low, the  
 311 highest being for stem volume, with an  $R_m^2$  of 0.23.  $F_v/F_m$ , Leaf:height ratio, Stem volume and  
 312 Leaf thickness had models which were better than a random effects model with  $\delta AIC_r > 2$ . In the  
 313 best fitting multiple fixed effect model for  $F_v/F_m$ , ISI and LAI had contrasting effects. An increase  
 314 in ISI led to a decrease in  $F_v/F_m$  while an increase in LAI led to an increase in  $F_v/F_m$ .

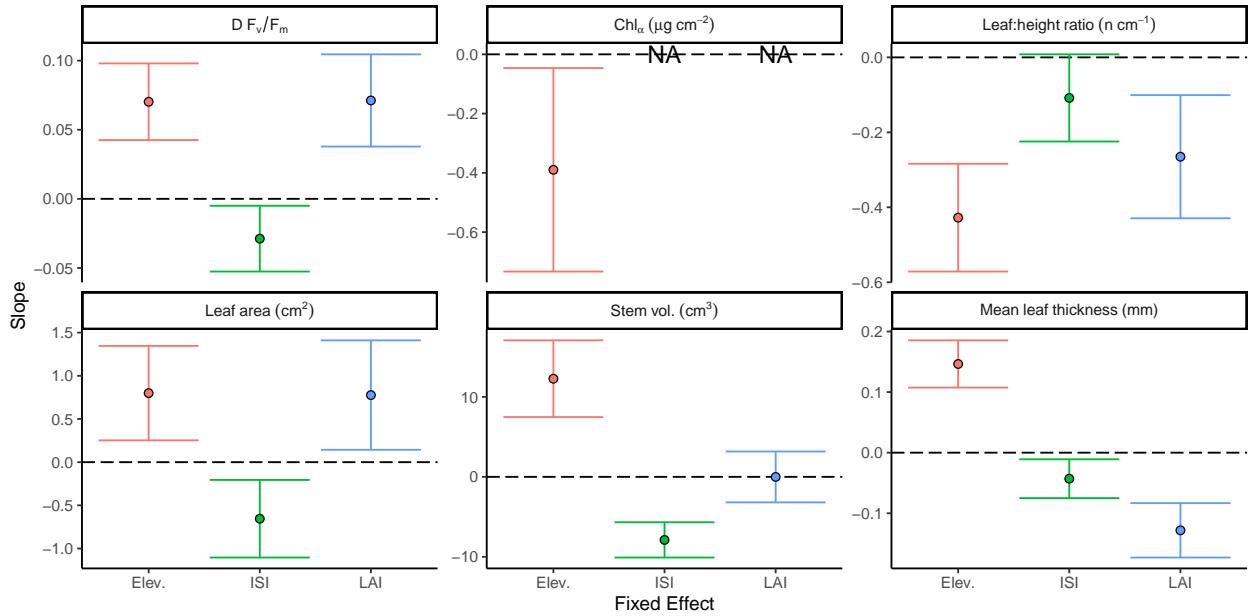


Figure 15

Table 4

response	fixed_eff	daicr	r2c	r2m
d_fvfm	elev_scale.comp_adult_metric_log_scale.lai_scale	-4.82	0.29	0.1
leaf_chl	lai_scale	0.73	0.28	0.01
leaf_height_ratio	elev_scale.comp_adult_metric_log_scale.lai_scale	-4.31	0.37	0.1
leaf_area_cm2_log	elev_scale.comp_adult_metric_log_scale.lai_scale	-0.06	0.31	0.05
stem_vol_cm3	elev_scale.comp_adult_metric_log_scale.lai_scale	-11.6	0.57	0.23
leaf_thick_mean_mm	elev_scale.comp_adult_metric_log_scale.lai_scale	-12.59	0.78	0.08

## 315 Discussion

316 This study aimed to: (a) determine whether tree seedling physiological and physiognomic plant  
 317 traits were affected by tree canopy structure across an elevation gradient, (b) assess how the effects  
 318 of canopy structure compared to that of elevation, and (c) assess the degree to which plant trait-  
 319 elevation relationships vary among species. It was found that forest canopy structure variables  
 320 never influence a given plant trait more than elevation, but that combinations of elevation and  
 321 canopy structure variables predict variation in plant traits marginally better than elevation alone.  
 322 Canopy structure variables were not correlated with elevation, and instead reflected variation in  
 323 habitat, with forest canopy structure becoming highly spatially variable within the cloud forest  
 324 zone. Tree species with more restricted elevational ranges, which inhabit the cloud zone of the  
 325 elevational gradient were more sensitive to variation in canopy structural factors. Interestingly  
 326 however, according to  $F_v/F_m$  chlorophyll fluorescence measurements, seedlings did not experience  
 327 greater physiological stress at higher elevations, instead all species exhibited model slopes  $>0$  or  
 328 approaching 0.

329 **3.4 Photosynthetic efficiency -  $F_v/F_m$  and Chl $\alpha$**

330 Estimates of photosynthetic efficiency using  $F_v/F_m$  and leaf Chl $\alpha$  concentration suggest that seedlings  
331 are not stressed at any point along their current elevational range, and thus are acclimating to their  
332 environment. Seedlings had lower  $F_v/F_m$  at the base of their elevational ranges. This suggests that  
333 if climate warming were to continue seedling mortality may occur at the base of the species eleva-  
334 tional range, but that further upslope migration is not limited. Species with restricted elevational  
335 ranges, found in the cloud zone ~1500-1800 m had steeper relationships of  $F_v/F_m$  and elevation,  
336 which suggests that these species may be the most vulnerable to continued warming. This raises  
337 concerns for the cloud forest zone as a unique ecosystem, as species turnover is high within this zone,  
338 with high biodiversity across multiple taxonomic groups (Ledo et al., 2012). Continued warming  
339 may lead to a reduction of cloud forest specialist tree species, which instead may be replaced by  
340 generalist lowland species which have a competitive advantage at the top end of their elevational  
341 range (Valladares and Niinemets, 2008; Nicotra et al., 2010). **citet A paper which suggests cloud**  
342 **forest vulnerability.**

343 It was predicted that seedlings at the upper limits of their elevational range would have lower  
344 photosynthetic efficiency due to increased exposure to damaging UV-B rays, however this was not  
345 observed and so H<sub>1</sub> can be rejected. If this effect does exist, it may not have been observed in  
346 this study as we located existing seedlings in their natural habitat, which presumably were located  
347 in suitably shaded areas in order that they avoid UV-B damage. Certainly, above-seedling LAI  
348 measurements and ISI values only decreased marginally over the entire elevational transect (Figure  
349 10). Therefore, upslope migration of seedlings may not be limited by existing forest canopy effects,  
350 due to adequate spatial heterogeneity of canopy structure.

351 Mixed effects models with multiple fixed effects used to predict variation in  $F_v/F_m$  were of better  
352 quality when forest canopy structure variables were included, though this increase in model fit was  
353 small and so H<sub>3</sub> should not be accepted unequivocally. As elevation and the forest canopy structure  
354 variables were not correlated, this implies that predictions of seedling stress can be improved by  
355 adding measurements tree canopy layer structural properties to models in addition to elevationally  
356 dependent abiotic environmental factors.

357 Data on tree canopy layer structure was collected laboriously by hand for this study. Given the  
358 relatively minor increase in model fit, it may not be practical to include canopy layer structural prop-  
359 erties in larger scale models predicting elevational range shifts. In some cases though, for example  
360 when predicting changes within the highly sensitive and inherently valuable cloud forest ecosystem,  
361 it may be desirable. There is also promise that canopy structural data could be collected using  
362 remote sensing methods to reduce labour in data collection while achieving a more representative  
363 estimate of forest structural properties at the landscape scale **has somebody done this already?**

364 **Write about why Chlorophyll-a had a poor relationship with elevation and canopy variables.**

365 **3.5 Plant trait response to elevation**

366 **intro, variation in physiognomy denotes acclimation**

367 Tree species varied in seedling physiognomic acclimatory responses to elevation. As with pho-  
368 tosynthetic efficiency measurements, species with narrow elevational ranges were more sensitive to  
369 elevational variation. *S. patula* (SP) grew smaller leaves and smaller stems with increasing ele-  
370 vation. This can be interpreted as a conservative response to increasingly stressful environmental  
371 conditions at higher elevations. Similarly, the succulent leaved *C. thurifera* had thinner leaves at

372 higher elevations, possibly a conservative or stress response to higher elevations. As the standard  
373 error of the model slope was large however, the apparent trend may have been driven by a few  
374 seedlings with particularly thick leaves, possibly as a result of high soil moisture content (Figure 7).  
375 *C. thurifera* is a succulent.

### 376 3.6 Species rarity, specialists and generalists

377 Nine tree species were selected for this study. Although these species are common in the areas we  
378 sampled (Appendix VI), there are many other species which may react more or less to the biotic  
379 environment. There is evidence that rare species (small population) are more sensitive to variation  
380 in environmental factors, (Lyons et al., 2005; Mouillot et al., 2013). Rare species are more likely  
381 to occupy specialist niches, which occur over a narrower geographic range than those of generalist  
382 species (Boulangeat et al., 2012). The evolutionary histories of specialists means they are less likely  
383 to be able to acclimate to novel environments (). Compared to the common species studied here,  
384 rare species will not have such a large direct effect on globally significant ecosystem services such as  
385 carbon sequestration, albedo, and drainage. This does not mean however, that rare species do not  
386 have the potential to heavily influence ecosystem services indirectly. Lyons and Schwartz (2001),  
387 and Lyons et al. (2005) found that less common species play vital supporting roles in maintaining  
388 ecosystem functions such as enhancing invasion resistance and making limiting resources available  
389 to other species.

### 390 3.7 Future studies

391 This study is deliberately wide in its scope, using proxies for forest canopy structure in order to  
392 infer the influences of multiple ecosystem processes such as nutrient competition, and shading. By  
393 not explicitly testing the effects of these mechanistic processes, which are complex in their effects,  
394 we cannot determine the relative contribution of each process implicit in the measured proxies.  
395 It is recommended therefore that experiments under constant environmental conditions explicitly  
396 test the effect of variation in specific ecosystem processes such as shading and nutrient availability.  
397 Understanding the specific mechanisms which drive the trends seen in this study will help to identify  
398 elevation dependent thresholds which may act as a barrier to seedling growth in the future under  
399 continued elevational range shifts.

400 Here, we focussed on tree seedlings as a key demographic bottleneck for tree survival, however,  
401 continued climate change over the long term may also lead to changes in the survival of existing adult  
402 trees, with further consequences for ecosystem structure and function. One of the key limiting factor  
403 for large tropical forest trees is water availability. In the Central Andes, precipitation is predicted  
404 to reduce by ~15% by 2100 (Lewis et al., 2011). In order to determine whether changes in elevation  
405 dependent environmental variables also affect adult trees along our elevational gradient, similar  
406 studies to ours could be performed on adult trees. Seed production of adult trees in the tropics is  
407 often reduced under stress conditions (Klimas et al., 2012; Muller-Landau, 2010). By understanding  
408 how climate change affects seed production the accuracy of local species range-shift models could  
409 be improved by adding spatially explicit demographic terms.

410

## 411 Conclusion

412 **References**

- 413 Akaike, H. (1992), ‘Information theory and an extension of the maximum likelihood principle’,  
414 *Breakthroughs in Statistics* pp. 610–624.
- 415 Araújo, M. B., Thuiller, W. and Pearson, R. G. (2006), ‘Climate warming and the decline of  
416 amphibians and reptiles in europe’, *Journal of Biogeography* **33**, 1712–1728.
- 417 Bartoń, K. (2019), *MuMIn: Multi-Model Inference*. R package version 1.43.6.
- 418 Bates, D., Mächler, M., Bolker, B. M. and Walker, S. C. (2015), ‘Fitting linear mixed-effects models  
419 using lme4’, *Journal of Statistical Software* **67**(1), 1–48.
- 420 Bell, D. M., Bradford, J. B. and Lauenroth, W. K. (2014), ‘Early indicators of change: diversgent  
421 climate envelopes between tree life stages imply range shifts in the western united states’, *Global  
422 Ecology and Biogeography* **23**, 168–180.
- 423 Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. and Courchamp, F. (2012), ‘Impacts of  
424 climate change on the future of biodiversity’, *Ecology Letters* **15**, 365–377.
- 425 Berry, P. M., Dawson, T. P., Harrison, P. A. and Pearson, R. G. (2002), ‘Modelling potential impacts  
426 of climate change on the bioclimatic envelope of species in britain and ireland’, *Global Ecology &  
427 Biogeography* **11**, 453–462.
- 428 Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H.  
429 and White, J. S. (2008), ‘Generalized linear mixed models: a practical guide for ecology and  
430 evolution’, *Trends in Ecology and Evolution* **24**(3), 127–135.
- 431 Boulangeat, I., Lavergne, S., Van Es, J., Garraud, L. and Thuiller, W. (2012), ‘Niche breadth, rarity  
432 and ecological characteristics within a regional flora spanning large environmental gradients’,  
433 *Journal of Biogeography* **39**, 204–214.
- 434 Campbell, C., Atkinson, L., Zaragoza-Castells, J., Lundmark, M., Atkin, O. and Hurry, V. (2007),  
435 ‘Acclimation of photosynthesis and respiration is asynchronous in response to changes in temper-  
436 ature regardless of plant functional group’, *New Phytologist* **176**, 375–389.
- 437 Chen, I., Hill, J. K., Ohlemüller, R., Roy, D. B. and Thomas, C. D. (2011), ‘Rapid range of species  
438 associated with high levels of climate warming’, *Science* **333**, 1024–1026.
- 439 Colwell, R. K., Brehm, G., Cardelís, C. L., Gilman, A. C. and Longino, J. T. (2008), ‘Global  
440 warming, elevational range shifts and lowland biotic attrition in the wet tropics’, *Science* **322**, 258–  
441 261.
- 442 Coomes, D. A. and Grubb, P. J. (2000), ‘Impacts of root competition in forests and woodlands: a  
443 theoretical framework and review of experiments’, *Ecological Monographs* **70**(2), 171–207.
- 444 Corlett, R. T. and Westcott, D. A. (2013), ‘Will plant movemenets keep up with climate change’,  
445 *Trends in Ecology & Evolution* **28**(8), 482–488.
- 446 Coste, S., Baraloto, C., Leroy, C., Marcon, É., Renaud, A., Richardson, A. D., Roggy, J., Schimann,  
447 H., Uddling, J. and Hérault, B. (2010), ‘Assessing foliar chlorophyll contents with the spad-502  
448 chlorophyll meter: a calibration test with thirteen tree species of tropical rainforest in french  
449 guiana’, *Annals of Forest Science* **67**(6), 607–607.
- 450 Davis, M. A., Wrage, K. J. and Reich, P. B. (1998), ‘Competition between tree seedlings and  
451 herbaceous vegetation: support for a theory of resource supply and demand’, *Journal of Ecology*  
452 **86**, 652–661.

- 453 Dawson, T. P., Jackson, S. T., House, J. I., Prentice, I. C. and Mace, G. M. (2011), 'Beyond  
454 predictions: biodiversity conservation in a changing climate', *Science* **332**, 53–58.
- 455 Dobson, A., Lodge, D., Alder, J., Cumming, G. S., Keymer, J., McGlade, J., Mooney, H., Rusak,  
456 J. A., Sala, O., Wolters, V., Wall, D., Winfree, R. and Xenopoulos, M. A. (2006), 'Habitat loss,  
457 trophic collapse, and the decline of ecosystem services', *Ecology* **87**(8), 1915–1924.
- 458 Ettinger, A. K., Ford, K. R. and HilleRisLambers, J. (2011), 'Climate determines upper, but not  
459 lowe, altitudinal range limits of pacific northwest conifers', *Ecology* **92**(6), 1323–1331.
- 460 Feeley, K. J., Malhi, Y., Zelazowski, P. and Silman, M. R. (2012), 'The relative importance of defor-  
461 estation, precipitation change, and temperature sensitivity in determining the future distributions  
462 and diversity of amazonian plant species', *Global Change Biology* **18**, 2636–2647.
- 463 Feeley, K. J., Silman, M. R., Bush, M. B., Farfan, W., Cabrera, K. G., Malhi, Y., Meir, P., Revilla,  
464 N. S., Quisiyupanqui, M. N. R. and Saatchi, S. (2011), 'Upslope migration of andean trees',  
465 *Journal of Biogeography* **38**, 783–791.
- 466 Frazer, G. W., Fournier, R. A., Trofymow, J. A. and Hall, R. J. (2001), 'A comparison of digital  
467 and film fisheye photography for analysis of forest canopy structure and gap light transmission',  
468 *Agricultural and Forest Meteorology* **109**, 249–263.
- 469 Gadow, K. V. and Hui, G. (1999), *Modelling Forest Development*, Springer, The Netherlands.
- 470 Genty, B., Briantais, J. and Baker, N. R. (1989), 'The relationship between the quantum yield  
471 of photosynthetic electron transport and quenching of chlorophyll fluorescence', *Biochimica et  
472 Biophysica Acta* **990**, 87–92.
- 473 Gibson-Reinemer, D. K., Sheldon, K. S. and Rahel, F. J. (2015), 'Climate change creates rapid  
474 species turnover in montane communities', *Ecology and Evolution* **5**(12), 2340–2347.
- 475 Girardin, C. A. J., Espejob, J. E. S., Doughty, C. E., Huasco, W. H., Metcalfe, D. B., Durand-Baca,  
476 L., Marthews, T. R., Aragao, L. E. O. C., Farfán-Rios, W., García-Cabrera, K., Halladay, K.,  
477 Fisher, J. B., Galiano-Cabrera, D. F., Huaraca-Quispe, L. P., Alzamora-Taype, I., Eguiluz-Mora,  
478 L., Salinas-Revilla, N., Silman, M. R., Meir, P. and Malhi, Y. (2014), 'Productivity and carbon  
479 allocation in a tropical montane cloud forest in the peruvian andes', *Plant Ecology & Diversity*  
480 **7**(1-2), 107–123.
- 481 Gruber, C. E., Nakagawa, S., Laws, R. J. and Jamieson, I. G. (2011), 'Multimodel inference in  
482 ecology and evolution: challenges and solutions', *Journal of Evolutionary Biology* **24**, 699–711.
- 483 Hegyi, F. (1974), A simulation model for managing jack-pine stands, in 'Royal College of Forestry,  
484 editor', Royal College of Forestry, Stockholm, Sweden, pp. 74–90.
- 485 Hobbs, R. J., Higgs, E. and Harris, J. A. (2009), 'Novel ecosystems: implications for conservation  
486 and restoration', *Trends in Ecology and Evolution* **24**(11), 599–605.
- 487 Hughes, L. (2000), 'Biological consequences of global warming: is the signal already apparent?',  
488 *Trends in Ecology and Evolution* **15**(2), 56–61.
- 489 Isbell, F., Calcagno, V., Hector, A., Connolly, J., Harpole, W. S., Reich, P. B., Scherer-Lorenzen, M.,  
490 Schmid, B., Tilman, D., van Ruijven, J., Weigelt, A., Wilsey, B. J., Zavaleta, E. S. and Loreau,  
491 M. (2011), 'Hugh plant diversity is needed to maintain ecosystem services', *Nature* **477**, 199–203.
- 492 Jonckheere, I., Fleck, S., Nackaerts, K., Muys, B., Coppin, P., Weiss, M. and Baret, F. (2004),  
493 'Review of methods for in situ leaf area index determination part i. theories, sensors and hemi-  
494 spherical photography', *Agricultural and Forest Meteorology* **121**, 19–35.

- 495 Jupp, D. L. B., Culvenor, D. S., Lovell, J. L., Newnham, G. J., Strahler, A. H. and Woodcock,  
496 C. E. (2008), 'Estimating forest lai profiles and structural parameters using a ground-based laser  
497 called 'echidna'', *Tree Physiology* **29**, 171–181.
- 498 Klimas, C. A., Kainer, K. A., Waft, L. H., Staudhammer, C. L., Rigamonte-Azevedo, V., Correia,  
499 M. F. and Lima, L. M. S. (2012), 'Control of *Carapa guianensis* phenology and seed production at  
500 multiple scales: a five-year study exploring the influences of tree attributes, habitat heterogeneity  
501 and climate cues', *Journal of Tropical Ecology* **28**.
- 502 Krause, G. H., Koroleva, O. Y., Dalling, J. W. and Winter, K. (2001), 'Acclimation of tropical tree  
503 seedlings to excessive light in simulated tree-fall gaps', *Plant, Cell and Environment* **24**, 1245–  
504 1352.
- 505 Ledo, A., Condés, S. and Alberdi, I. (2012), 'Forest biodiversity assessment in peruvian andean  
506 montane cloud forest', *Journal of Mountain Science* **9**, 372–384.
- 507 Lee, W., von Gadow, K., Chung, D., Lee, J. and Shin, M. (2004), 'Dbh growth model for *Pinus*  
508 *densiflora* and *Quercus variabilis* mixed forests in central korea', *Ecological Modelling* **176**, 187–  
509 200.
- 510 Lenoir, J., Gégout, J., Guisan, A., Vittoz, P., Wohlgemuth, T., Zimmermann, N. E., Dullinger, S.,  
511 Pauli, H., Willner, W. and Svenning, J. (2010), 'Going against the flow: potential mechanis,s for  
512 unexpected downslope range shifts in a warming climate', *Ecography* **33**, 295–303.
- 513 Lenoir, J., Gégout, J., Pierrat, J., Bontemps, J. and Dhôte, J. (2009), 'Differences between tree  
514 species seedling and adult altitudinal distribution in mountain forests during the recent warm  
515 period (1986–2006)', *Ecography* **32**, 765–777.
- 516 Lenoir, J. and Svenning, J. C. (2015), 'Climate-related range shifts - a global multidimensional  
517 synthesis and new research directions', *Ecography* **38**, 15–28.
- 518 Lewis, S. L., Brando, P. M., Phillips, O. L., van der Heijden, G. and Nepstad, D. (2011), 'The 2010  
519 amazon drought', *Science* **331**(6017), 554.
- 520 Lewis, S. L. and Tanner, E. V. J. (2000), 'Effects of above- and belowground competition on growth  
521 and survival of rain forest tree seedlings', *Ecology* **81**(9), 2525–2538.
- 522 Li, F., Peng, S., Chen, B. and Hou, Y. (2010), 'A meta-analysis of the responses of woody and  
523 herbaceous plants to elevated ultraviolet-b radiation', *Acta Oecologia* **36**, 1–9.
- 524 Lyons, K. G., Brigham, C. A., Traut, B. H. and Schwartz, M. W. (2005), 'Rare species and ecosystem  
525 functioning', *Conservation Biology* **19**, 1019–1024.
- 526 Lyons, K. G. and Schwartz, M. W. (2001), 'Rare species loss alters ecosystem function - invasion  
527 resistance', *Ecology Letters* **4**, 358–265.
- 528 MacLean, S. A. and Beissinger, S. R. (2017), 'Species' traits as predictors of range shifts under  
529 contemporary climate change: a review and meta-analysis', *Global Change Biology* **23**, 4094–  
530 4105.
- 531 Magrin, G. O., Marengo, J. A., Boulanger, J., Buckeridge, M. S., Castellano, E., Poveda, G.,  
532 Scarano, F. R. and Vicuña, S. (2014), 'Central and south america'.
- 533 Malhi, Y., Silman, M., Salinas, N., Bush, M., Meir, P. and Saatchi, S. (2010), 'Introduction: ele-  
534 vation gradients in the tropics: laboratories for ecosystem ecology and global change research',  
535 *Global Change Biology* **16**, 3171–3175.
- 536 Mantyka, C. S., Martin, T. G. and Rhodes, J. R. (2012), 'Interactions between climate and habi-  
537 tatt loss effects on biodiversity: a systematic review and meta-analysis', *Global Change Biology*  
538 **18**, 1239–1252.

- 539 Marengo, J. A., Pabón, J., Díaz, A., Rosas, G., Ávalos, G., Montealegre, E., Villacis, M., Solman,  
540 S. and Rojas, M. (2011), Climate change: Evidence and future scenarios for the andean region, *in*  
541 S. K. Herzog, R. Martinez, P. M. Jørgensen and H. Tiessen, eds, ‘Climate change and Biodiversity  
542 in the Tropical Andes’, Inter-American Institute for Bloal Change Research (IAI) and Scientific  
543 Committee on Problems of the Environment (SCOPE), pp. 110–127.
- 544 Martin, P. H., Fahey, T. J. and Sherman, R. E. (2010), ‘Vegetation zonation in a neotropical  
545 montane forest: environment, disturbance and ecotones’, *Biotropica* **43**(5), 533–543.
- 546 Matsuraba, S., Krause, G. H., Aranda, J., Virgo, J., Beisel, K. G., Jahns, P. and Winter, K. (2009),  
547 ‘Sun-shade patterns of leaf carotenoid composition in 86 species of neotropical forest plants’,  
548 *Functional Plant Biology* **36**, 20–36.
- 549 Maxwell, K. and Johnson, G. N. (2000), ‘Chlorophyll fluorescence - a practical guide’, *Journal of*  
550 *Experimental Botany* **51**(345), 659–668.
- 551 McCain, C. M. and Colwell, R. K. (2011), ‘Assessing the threat to montane biodiversity from discordant  
552 shifts in temperature and precipitation in a changing climate’, *Ecology Letters* **14**, 1236–1245.
- 553 McMahon, S. M., Harrison, S. P., Armbruster, W. C., Bartlein, P. J., Beale, C. M., Edwards,  
554 M. E., Kattge, J., Midgley, G., Morin, X. and Prentice, I. C. (2011), ‘Improving assessment and  
555 modelling of climate change impacts on global terrestrial biodiversity’, *Trends in Ecology and*  
556 *Evolution* **26**(5), 249–259.
- 557 Mouillot, D., Bellwood, D. R., Baraloto, C., Chave, J., Galzin, R., Harmelin-Vivien, M., Kulbicki,  
558 M., Lavergne, S., Lavorel, S., Mouquet, N., Pain, C. E. T., Renaud, J. and Thuiller, W. (2013),  
559 ‘Rare species support vulnerable functions in high-diversity ecosystems’, *PLoS Biology* **11**(5), 1–  
560 11.
- 561 Muller-Landau, H. C. (2010), ‘The tolerance-fecundity trade-off and the maintenance of diversity  
562 in seed size’, *Proceedings of the National Academy of Sciences* **107**(9), 4242–4247.
- 563 Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B. and Kent, J. (2000),  
564 ‘Biodiversity hotspots for conservation priorities’, *Nature* **403**, 853–858.
- 565 Nicotra, A. B., Atkin, O. K., Bonser, S. P., Davidson, A. M., Finnegan, E. J., Mathesius, U.,  
566 Poot, P., Purugganan, M. D., Richards, C. L., Valladares, F. and van Kleunen, M. (2010), ‘Plant  
567 phenotypic plasticity in a changing climate’, *Trends in Plant Science* **15**(12), 684–692.
- 568 Parmesan, C. (2006), ‘Ecological and evolutionary responses to recent climate change’, *Annual*  
569 *Review of Ecology, Evolution and Systematics* **37**, 637–669.
- 570 Pearson, R. G. and Dawson, T. P. (2003), ‘Predicting the impacts of climate change on the distribution  
571 of species: are bioclimate envelope models useful?’, *Global Ecology & Biogeography*  
572 **12**, 361–371.
- 573 Peterson, A. T., Ball, L. G. and Cohoon, K. P. (2002), ‘Predicting distributions of mexican birds  
574 using ecological niche modelling methods’, *Ibis* **144**, E27–E32.
- 575 Prado, F. E., Rosa, M., Prado, C., Podazza, G., Interdonato, R., González, J. A. and Hilal, M.  
576 (2012), Uv-b radiation, its effects and defense mechanisms in terrestrial plants, *in* P. Ahmad and  
577 M. Prasad, eds, ‘Environmental Adaptations and Stress Tolerance of Plants in the Era of Climate  
578 Change’, Springer, New York, USA, pp. 57–83.
- 579 R Core Team (2019), *R: A Language and Environment for Statistical Computing*, R Foundation for  
580 Statistical Computing, Vienna, Austria.
- 581 Schneider, C. A., Rasband, W. S. and Eliceiri, K. W. (2012), ‘Nih image to imagej: 25 years of  
582 image analysis’, *Nat Methods* **9**(7), 671–675.

- 583 Seifert, T., Seifert, S., Seydack, A., Durrheim, G. and von Gadow, K. (2014), 'Competition effects  
584 in an afrotropical forest', *Forest Ecosystems* **1**(13), 1–15.
- 585 Serrano, L. (2008), 'Effects of leaf structure on reflectance estimates of chlorophyll content', *International  
586 Journal of Remote Sensing* **29**, 17–18.
- 587 Sinclair, S. J., White, M. D. and Newell, G. R. (2010), 'How useful are species distribution models  
588 for managing biodiversity under future climates?', *Ecology and Society* **15**(1), 1–13.
- 589 ter Steege, H. (2018), *Hemiphot.R: Free R scripts to analyse hemispherical photographs for canopy  
590 openness, leaf area index and photosynthetic active radiation under forest canopies*, Leiden, The  
591 Netherlands. Unpublished report.
- 592 Thuiller, W., Richardson, D. M., Pyšek, P., Midgley, G. F., Hughes, G. O. and Rouget, M. (2005),  
593 'Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale',  
594 *Global Change Biology* **11**, 2234–2250.
- 595 Travis, J. M. J., Delgado, M., Bocedi, G., Baguette, M., Bartoń, K., Bonte, D., Boulangeat, I.,  
596 Hodgson, J. A., Kubisch, A., Penteriani, V., Saastamoinen, M., Stevens, V. M. and Bullock,  
597 J. M. (2013), 'Dispersal and species' responses to climate change', *Oikos* **122**, 1532–1540.
- 598 Valladares, F., Laanisto, L., Niinemets, Ü. and Zavala, M. A. (2016), 'Shedding light on shade:  
599 ecological perspectives of understorey plant life', *Plant Ecology & Diversity* **9**(3), 237–251.
- 600 Valladares, F. and Niinemets, Ü. (2008), 'Shade tolerance, a key plant feature of complex nature  
601 and consequences', *Annual Review of Ecology, Evolution and Systematics* **39**, 237–257.
- 602 Van der Putten, W. H., Macel, M. and Visser, M. E. (2010), 'Predicting species distribution and  
603 abundance responses to climate change: why it is essential to include biotic interactions across  
604 trophic levels', *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**, 2025–  
605 2034.
- 606 Vuille, M., Franquist, E., Garreaud, R., Casimiro, W. S. L. and Cáceres, B. (2015), 'Impact of the  
607 global warming hiatus on andean temperature', *Journal of Geophysical Research: Atmospheres*  
608 **120**, 3745–3757.
- 609 Whitaker, J., Ostle, N., Nottingham, A. T., Ccahuana, A., Salinas, N., Bardgett, R. D., Meir,  
610 P. and McNamara, N. P. (2014), 'Microbial community composition explains soil respiration  
611 responses to changing carbon inputs along an andes-to-amazon elevation gradient', *Journal of  
612 Ecology* **102**, 1052–1071.
- 613 Wisz, M. S., Pottier, J., Kissling, W. D., Pellissier, L., Lenoir, J., Damgaard, C. F., Dormann,  
614 C. F., Forchhammer, M. C., Grytnes, J., Guisan, A., Heikkinen, R. K., Hoye, T. T., Kähn,  
615 I., Luoto, M., Maiorano, L., Nilsson, M., Normand, S., Öckinger, Schmidt, N. M., Termansen,  
616 M., Timmermann, A., Wardle, D. A., Aastrup, P. and Svenning, J. (2013), 'The role of biotic  
617 interactions in shaping distributions and realised assemblages of species: implications for species  
618 distribution modelling', *Biological Reviews* **88**, 15–30.