

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

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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 Photocynthetic 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 com-
16 petition 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 4 bullet points (1) research conducted + rationale, (2) central methods, (3) key results, (4)
21 main conclusions including key points of discussion.

22 **1 Introduction**

23 Rapid anthropogenic climate change is causing many species, across a wide range of taxa, to shift
24 their distributions in space (Hughes, 2000; Parmesan, 2006; Chen et al., 2011). The primary forces
25 driving this are an increase in temperature and changes in precipitation regime (Corlett and West-
26 cott, 2013; ?). Chen et al. (2011) estimates that across a range of taxonomic groups, species are
27 experiencing mean latitudinal and altitudinal migration rates of 17.6 ± 2.9 km and 12.2 ± 1.8 m
28 per decade, respectively. Previous studies have suggested that the ability of tree species to respond
29 to changes in mean annual temperature and precipitation regime will be important in determining
30 species success over the coming century (Colwell et al., 2008; Chen et al., 2011; Feeley et al., 2012).
31 Species responses may occur either in the form of adaptation, *i.e.* changes in phenology, physiology
32 and morphology, or through range shifts over space (Bellard et al., 2012). Range shifts of tree
33 species have been observed in many studies across the world, particularly in temperate, sub-arctic
34 and mountainous regions () where temperature change is the most extreme (). The number of
35 studies documenting adaptational responses are fewer, potentially indicating that climate change
36 is occurring so rapidly as to prevent effective adaptational responses (). Range shift rates vary

37 between tree species. This has the potential to create new species assemblages as species ranges
38 overlap more or less as they shift, with consequences for ecosystem functionality as novel forest
39 assemblages are created. Predicting range shifts across space has become an active field of research,
40 (see Bellard et al. 2012 and references therein). Understanding the drivers of range shifts and their
41 variation between species can aid in the identification of species assemblages at risk of extinction
42 and can inform conservation strategies to mitigate the effects of climate change on biodiversity and
43 ecosystem functionality ().

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

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

65 For sessile taxa such as trees, range shifts occur as a result of differential recruitment and mor-
66 tality over space, at the leading and trailing edges of their range (). In communities of long-lived
67 tree species, the forest ecosystem may not shift in equilibrium with the climate as trees are re-
68 silient to gradual changes in climate, developing large root systems and below-ground water and
69 nutrient reserves to buffer against stressful conditions; adult trees may persist where more sensitive
70 seedlings perish (). Forest trees, particularly those in moist tropical forests, often experience high
71 levels of mortality during the seedling recruitment stage, creating a demographic bottleneck (?).
72 Many seedlings perish due to suboptimal shade regimes created by the arrangement of adult trees
73 creating canopy above them (). The seedlings of many tropical tree species are highly adapted
74 to shade (), meaning that if a seedling germinates in an open space, mortality by UV-B and heat
75 damage to photosynthetic machinery is quite probable (). Seedlings may also compete with adult
76 trees for nutrients (), although there is some separation between seedling and adult tree rooting
77 depths for most species (), especially for the largest trees (). This mortality bottleneck provides a
78 limiting factor to the success of tropical forest tree species experiencing range shifts. If seedlings
79 germinate in areas that are only sparsely shaded but are within temperature boundaries, damage
80 may occur leading to loss of photosynthetic capacity (), reducing growth rates and occasionally
81 resulting in seedling mortality ()�.

82 In montane cloud forests, elevational range shifts are occurring more rapidly than in other areas
83 (). As mean annual temperatures rise, plant species are figuratively pushed up-slope, with higher
84 recruitment at the upslope edge of their range and higher mortality at the downslope edge of
85 their range (). Particularly in the tropics, as altitude increases, UV-B concentration increases,

86 with many species found at high altitudes () having specific adaptations to avoid UV-B damage
87 to photosynthetic machinery, such as vertically stacked palisade mesophyll cells and thick cuticles
88 to reduce UV-B absorption, and generally smaller thicker leaves (). Species found at low altitudes
89 however, are less adapted to high UV-B environments, instead having adaptations to make the
90 most of the diminished light levels found under thick tree canopy, particularly during the seedling
91 growth stage (). Montane forest physical structure also varies with elevation. Lowland forests often
92 have lower tree density, with relatively few young trees in the light-deprived understorey, but a
93 higher canopy cover due to adult trees being larger. Plant ground cover is generally greater at
94 higher altitudes, with many epiphytic and ground-level herbaceous species. It therefore follows
95 that as lowland species move upslope in response to increasing temperature, they may experience
96 increased levels of damaging UV-B radiation as they recruit into areas of forest with thinner canopies.
97 This may lead to species' ranges narrowing from the bottom up, with increased mortality due to
98 temperature at the bottom of the elevational range, but without increased recruitment at the top
99 end of the elevational range due to increased mortality via UV-B exposure.

100 In this study, we investigated the effects of variation in adult tree canopy structure and size
101 distribution on seedling growth form and photosynthetic stress, across an elevational gradient in
102 the Peruvian Andes, spanning lowland wet forest and montane cloud forest. Our aim was to
103 assess the role of biotic effects from the existing forest structure on the potential growth of tree
104 seedlings, in order to increase our knowledge of the dynamics of montane cloud forest tree species
105 elevational range shifts. We tested three hypotheses: 1) Within a species, seedlings growing at higher
106 elevations would experience higher levels of photosynthetic stress than those at lower elevations, 2)
107 Species would differ in their degree of acclimation to variation in adult tree canopy structure and
108 size distribution, 3) A combination of biotic and abiotic explanatory variables would best explain
109 variation in seedling physiognomic and physiological traits across their elevational range.

110 2 Materials and Methods

111 2.1 Study Site

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

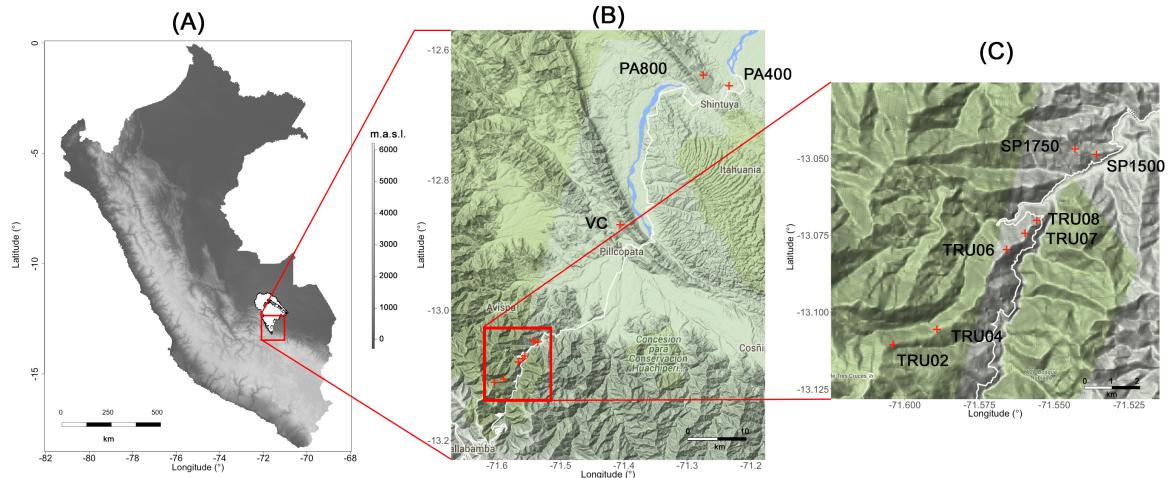


Figure 1: Maps showing the location of the study area and plot locations. (A) The site location within Peru with elevation shading, showing the proximity to Manú National Park (white area). (B) The location of the 1 ha plots within the Kosñipata Valley. (C) An enlargement of the Trocha Union and San 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.

122 2.2 Study species

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

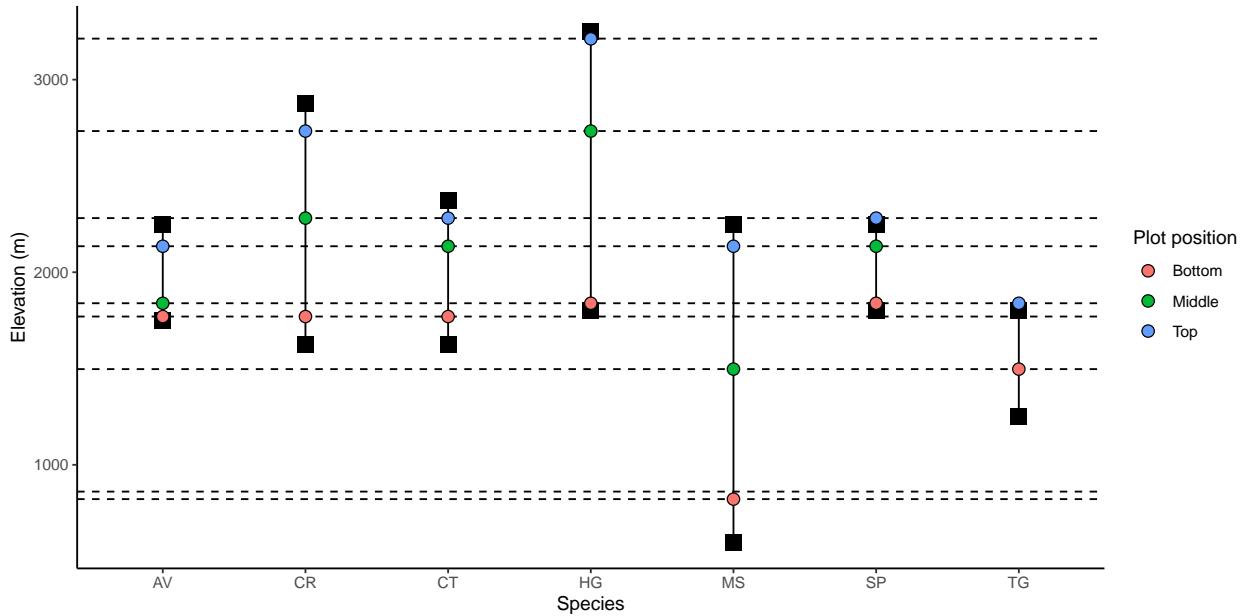


Figure 2: Elevation of study plots for each species (coloured points) with the upper and lower range extents for each species (black squares). Plot elevations are marked as dashed lines.

Table 1

Species code	Species	Bottom	Middle	Top
AV	<i>Alzatea verticillata</i>	SP1750=7	TRU08=5	TRU07=6
CR	<i>Clethra revoluta</i>	TRU08/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

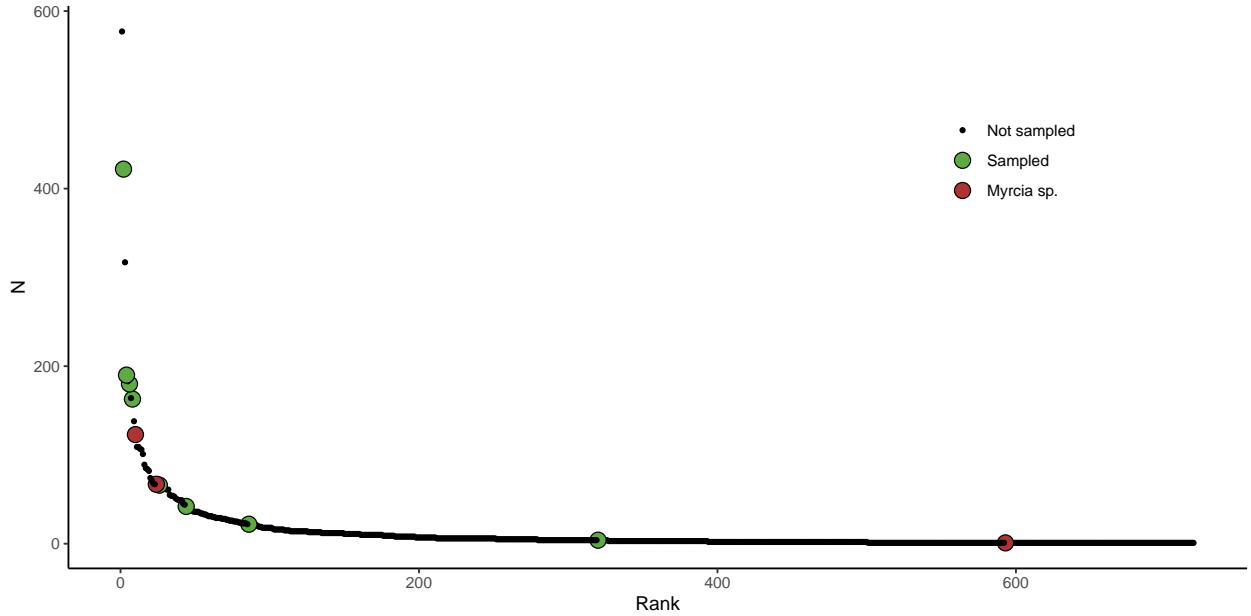


Figure 3: Rank abundance curve of all individuals >10 cm DBH of all species found in the plots measured in this study. Census data from 2014 (ABERG, unpublished data). Species sampled as part of this study are highlighted in red. *Myrcia* species which form the composite *Myrcia* spp. are highlighted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

131 2.3 Sampling and Measurement

132 Species were sampled in three plots representing the top, middle and bottom elevational extents of
 133 their ranges (Figure 2). Within each plot, a maximum of 10 seedlings were sampled. To minimise
 134 the chance of pseudo-replication of sampled seedlings, seedlings closer than 10 m to another sampled
 135 seedling were excluded from the analysis, as it could not be guaranteed that the stems were not
 136 connected by a stolon or rhizome. It also ensured that competition measurements were truly
 137 independent. Within a cluster of seedlings within 5 m of each other, each seedling was assigned a
 138 number and a random number generator was used to choose a single seedling for measurement.

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

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

145 Where F_m is the maximal fluorescence in the dark and F_o is the minimal fluorescence in the
 146 dark (Maxwell and Johnson, 2000). Fluorescence measurements were taken after exposing the
 147 seedling to 30 minutes of total darkness, to ensure complete dark adaptation (Campbell et al.,
 148 2007). Dark-adapted F_v/F_m measures the photosynthetic capacity of the leaf by relaxing the
 149 reaction centres prior to the fluorescence measurement. F_v/F_m is preferable to other chlorophyll
 150 fluorescence measures as it removes the noise created by environmental conditions at the time of
 151 measurement, instead providing a measure of the underlying photosynthetic capacity. A reduction

152 in F_v/F_m is indicative of plant stress. Here, individuals with F_v/F_m values <0.7 are considered to
153 be experiencing stress (Maxwell and Johnson, 2000).

154 In addition to F_v/F_m , leaf chlorophyll content was measured using a multi-spectral SPAD-meter
155 (Minolta SPAD-502Plus, Spectrum Technologies, Plainfield, Illinois, USA). To account for variation
156 in chlorophyll content across the leaf (), SPAD measurements were taken at three random points on
157 the leaf. The leaf midvein, other prominent veins, and areas of obvious leaf necrosis were avoided
158 in these measurements. The mean of the SPAD values was used to calculate an estimate leaf
159 chlorophyll content using the conversion factor outlined in for tropical broadleaf tree species:

$$Chl_{\alpha} = 0.53e^{0.0364 \times SPAD} \quad (2)$$

160 2.4 Leaf and whole-plant morphological measurements

161 2.5 Competition measurements

162 To assess adult-seedling competition interactions we used two metrics, Leaf Area Index of canopy
163 foliage, and a metric approximating the degree of crowding from surrounding adult trees. Leaf
164 Area Index (LAI) was calculated from hemispherical photographs of the forest canopy above each
165 seedling. Photographs were captured under uniformly overcast cloud conditions to avoid lens flare
166 and to aid in delineation of foliage from sky during processing (?). Images were taken with a
167 Coolpix 4500 compact camera, with a Nikon FC-E8 hemispherical fisheye converter lens. Images
168 were constrained to a 60° circular azimuthal field of view in order to restrict LAI calculations to
169 the part of the sky where the majority of photosynthetically active radiation penetrates the canopy
170 (??). Images were then converted to 8-bit grayscale and binarized manually in ImageJ Version 1.51
171 () to separate sky from plant material. Binarized images were then analyzed using Hemiphot () in
172 R to estimate LAI as the projected leaf area per unit ground area ($m^2 m^{-2}$).

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

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

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

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

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 ha^{-1} of each plot, and interpolated the trees ha^{-1} of plot VC using the regression fit (Figure ??). C_R was rounded to the nearest metre for ease of measurement (Table ??).

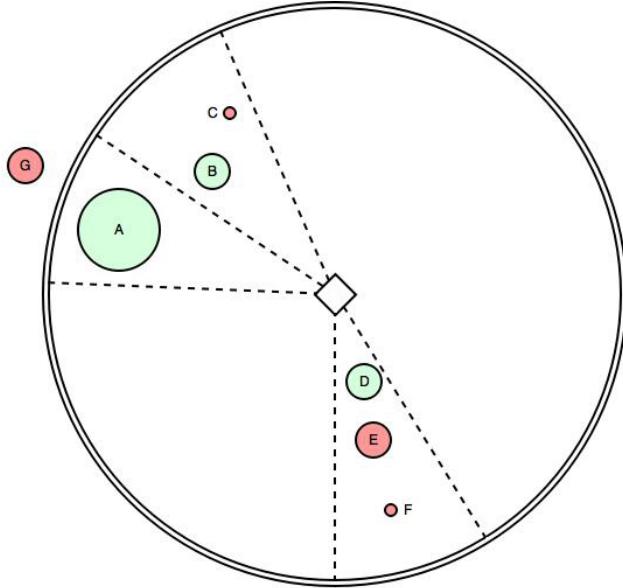


Figure 4: Schematic diagram showing the iterative selection of active competitor trees for the Iterative Seedling Index (ISI) (Equation 3). Trees marked in green (A, B, D) are active competitors for the tree of interest (black diamond). Trees marked in red (C, E, F, G) are non-active competitors, coloured 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).

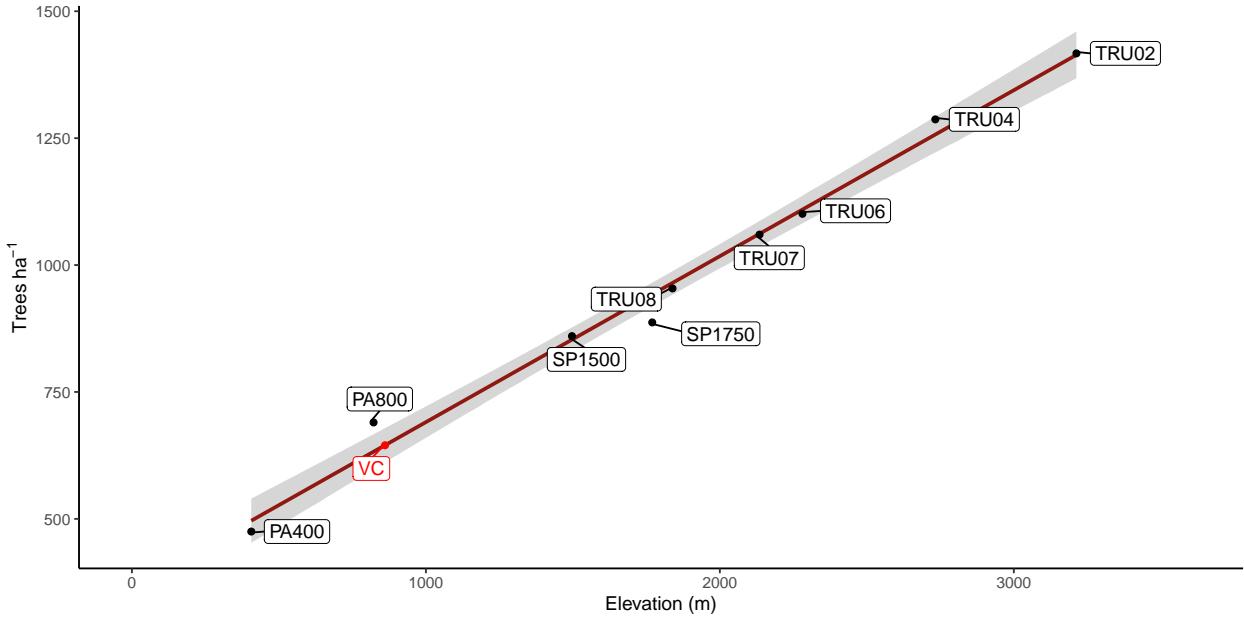


Figure 5: Linear regression with 95% confidence interval of number of trees per hectare for each site, used to estimate number of trees per hectare for site VC. $R^2 = 0.896$, $F_{(1,7)} = 579.5$, $p < 0.001$.

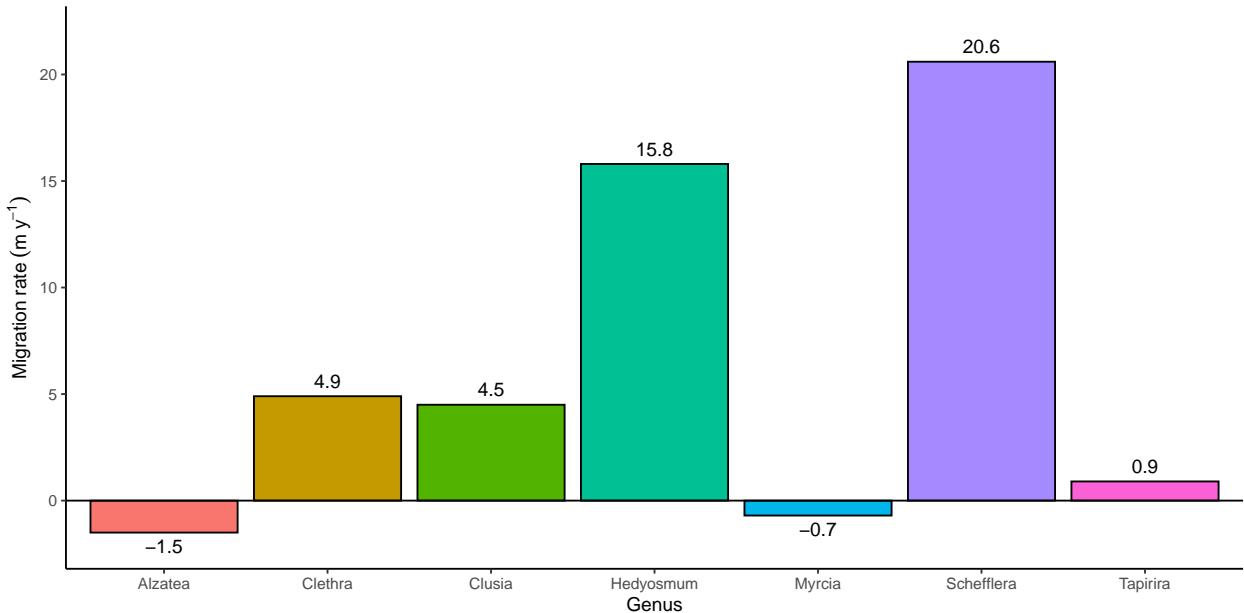


Figure 6: Estimated elevational migration rates within the Kosñipata valley for selected genera of which species are studied here. Migration rates are estimated using shifts in the centre of gravity of tree basal area as measured in the ABERG 1 Ha plot network.

192 2.6 Statistical Analysis

193 A matrix of single predictor linear mixed effects models were compared to test for the presence and
 194 strength of the causal relationship between each of the two competition variables and each of the
 195 six plant traits. The fixed effect of elevation was also included in order to compare the effects of
 196 competition to that of elevation. All fixed effects were standardised to allow easy comparison of
 197 effect sizes, according to (Gruber et al., 2011; ?). Model comparison was performed on models

198 fitted using Maximum Likelihood (ML) estimates (?). Model quality was compared using Akaike
199 Information Criteria (AIC) (Akaike, 1992), Akaike weights (W_i), and fixed effect marginal pseudo-
200 R^2 values (R_M^2).

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

209 The best quality single fixed effect models (using either independent intercepts or slopes for each
210 species) were compared using ΔAIC_r against a random effects model, the variance explained by the
211 whole model (R_C^2) and the fixed effects (R_M^2) using the *MuMin* package (?), and slope coefficients
212 (Figure ??, Figure ??) to compare their relative effect on plant traits.

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

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

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

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

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

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

225 3 Results

226 3.1 Variation in plant traits across elevation

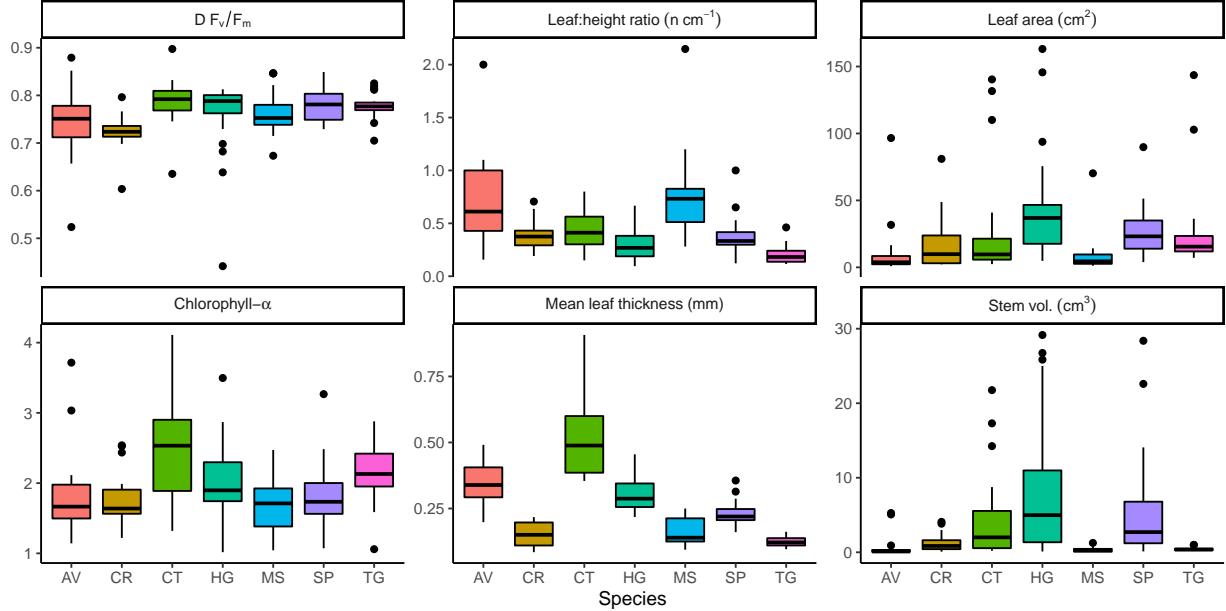


Figure 7: Box plots showing the variation in plant trait values within each species.

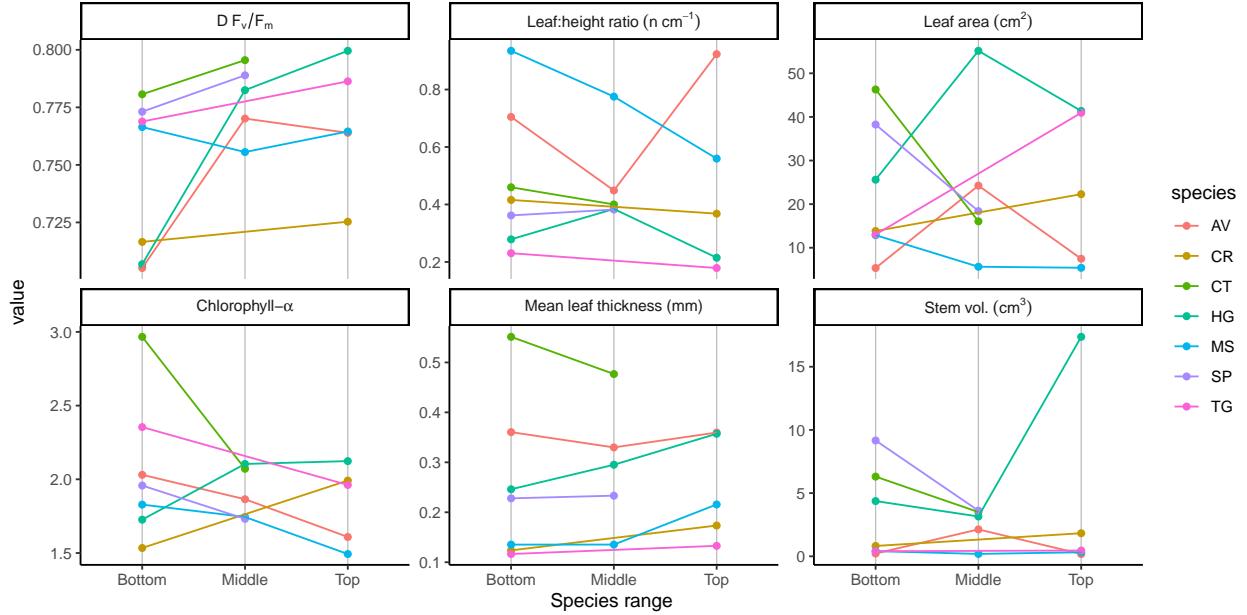


Figure 8: Interaction plots showing the variation in plant trait values within each species.

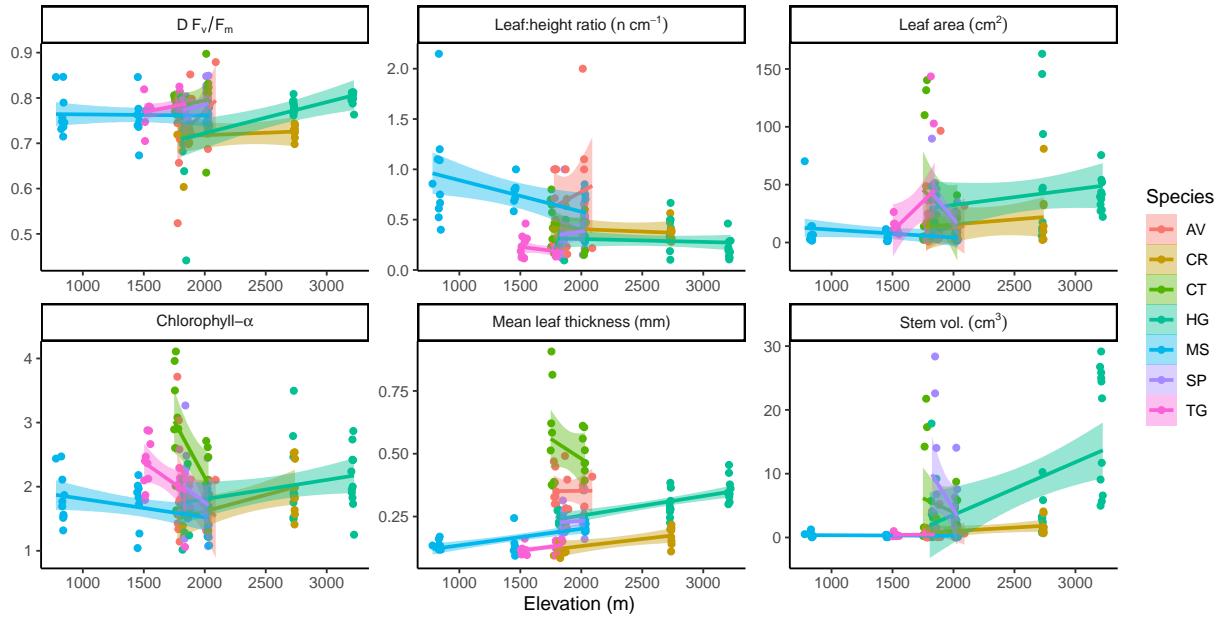


Figure 9: Scatter plots with linear model fits for each species, showing the variation in plant stress variables and plant traits across elevation.

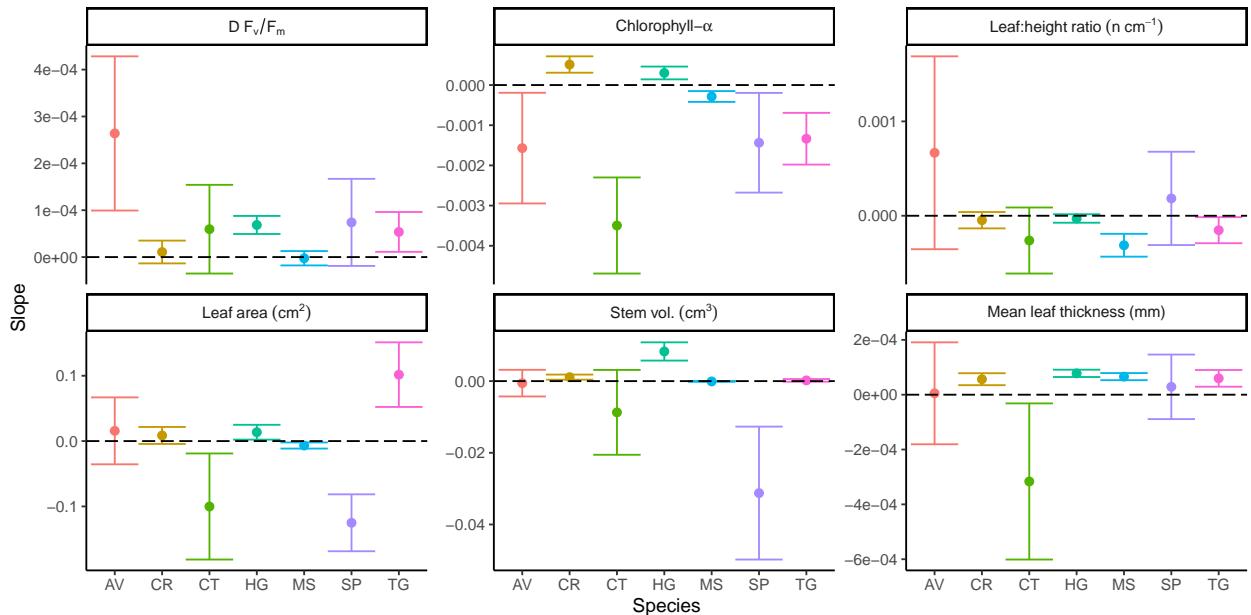


Figure 10: Interval plots showing the effect sizes (slopes) of each fixed effect in single fixed effect linear mixed effects models of plant traits against forest structure variables and elevation, for comparison.

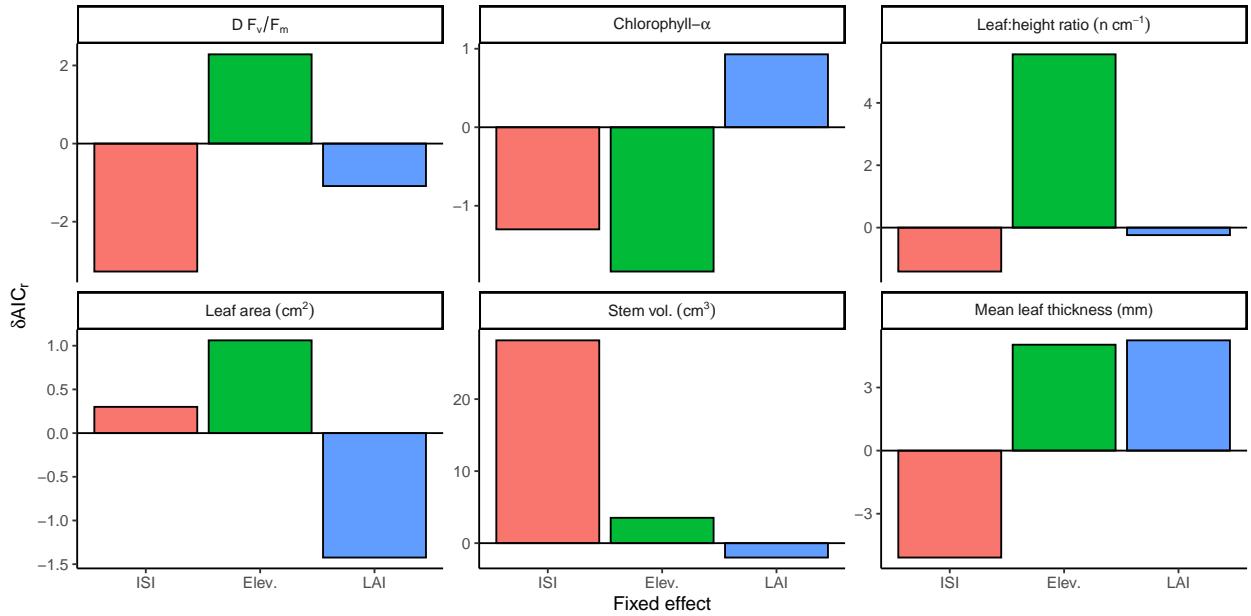


Figure 11: The difference in AIC values between each single fixed effect model and a corresponding random effects model using no fixed effects. A higher ΔAIC_r means the model is of higher quality than the random effects model. Horizontal dashed red line indicates the level at which a model is not appreciably better quality than the corresponding random effects model.

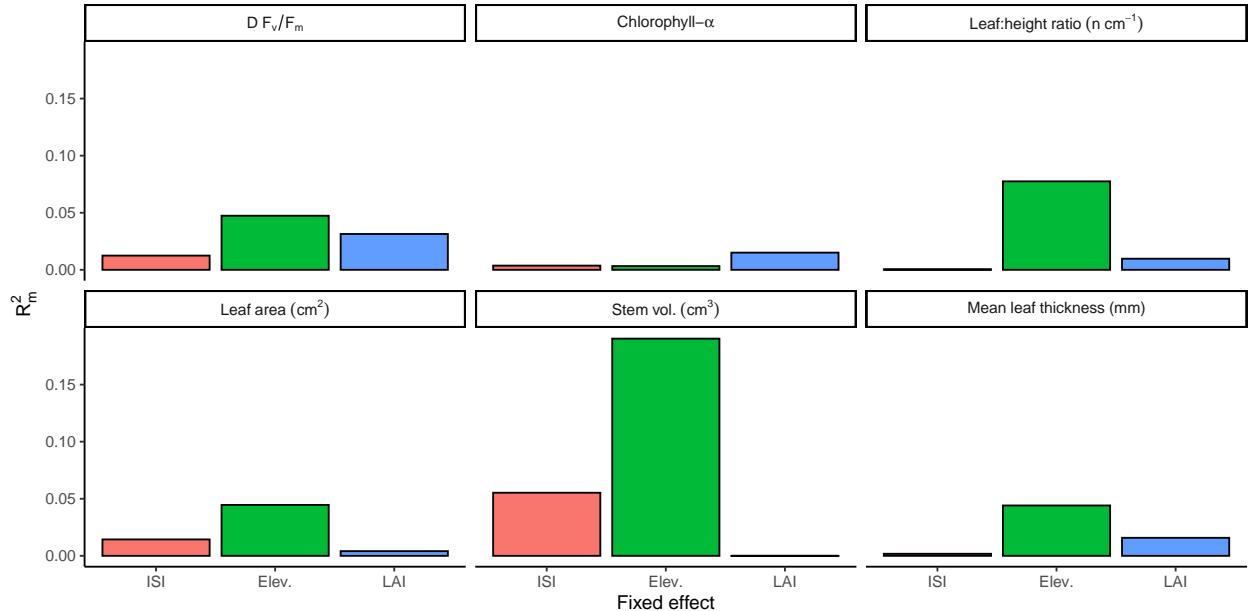


Figure 12: The variance explained by each single fixed effect model. The pale bars indicate the variance explained by the whole model while the bold bars indicate the variance explained just by the fixed effect in the model.

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

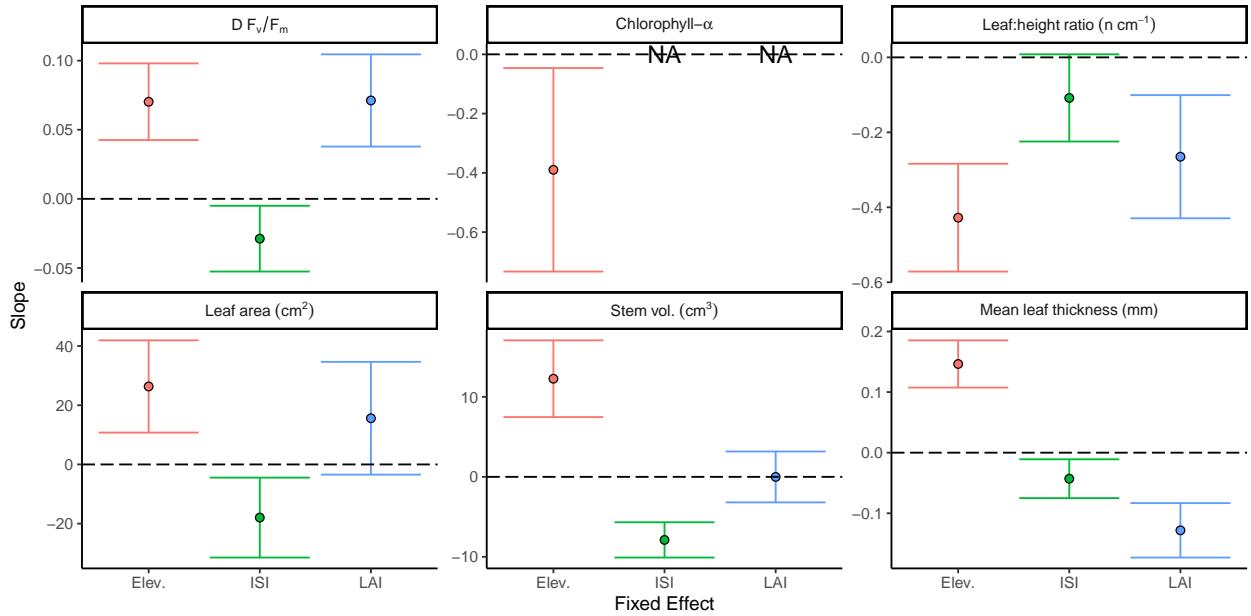


Figure 13

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

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

242 3.2 Effects of competition on plant traits

243 Linear mixed effect models of the relationship between adult tree competition variables and plant
 244 traits outperformed equivalent random effect models in 15/24 cases, *i.e.* those with a $\Delta\text{AIC}_r < 2$.
 245 However, the competition variables only accounted for a small percentage of the variance in each
 246 plant trait. The highest R^2_M in these single fixed effects models was the effect of Iterative
 247 Seedling Index on stem volume ($R^2_M = 4.3\%$), despite the model as a whole explaining 56% of
 248 the variation in stem volume. A similar effect is seen in all the other single fixed effect models,
 249 suggesting that unmeasured site specific effects are responsible for a large portion of the variation
 250 in plant traits.

251 The best fitting multiple fixed effect models all included the effects of elevation, Iterative Seedling
 252 Index and Leaf Area Index to explain variation in plant traits, except leaf chlorophyll content, which
 253 only included Leaf Area Index.

254 **Discussion**

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

261 **4 Effect of competition and elevation on plant traits**

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

266 **Leaf physiology**

267 Together, SPAD and F_v/F_m are useful measures of a plant's health and the integrity of its photo-
268 synthetic apparatus (?). SPAD is used as a proxy for leaf chlorophyll content (?), while F_v/F_m
269 measures the efficiency with which a leaf can utilise light for photosynthesis (Maxwell and Johnson,
270 2000). This study found contrasting effects of elevation on SPAD and F_v/F_m . As elevation in-
271 creased, photosynthetic efficiency increased but chlorophyll content decreased slightly (Figure ??).
272 There is however, large variation in SPAD within sites and elevation explains little of the variance
273 in SPAD (Figure ??), meaning this relationship may be erroneous. Competition variables explained
274 comparatively little variation in F_v/F_m or SPAD compared to morphological leaf traits (Figure
275 ??b).

276 **Photosynthetic efficiency**

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

291 Canopy density decreases with elevation (Figure ??), though this trend may be the result of

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

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

In contrast to the effects of LAI, ISI caused a decrease in photosynthetic efficiency. This suggests that the mechanisms by which LAI may affect photosynthetic efficiency (shading, temperature regulation) differ from those of ISI (nutrient competition, water competition, predation mutualisms) (?). 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

340 this optimum is likely to vary markedly among species and has been criticised as yet another
341 arbitrary threshold for a dynamic phenomenon (?). As a conservative estimate, here plants are
342 defined as experiencing physiological stress when $F_v/F_m < 0.7$. Figure ?? shows that only a few
343 individuals fall below this threshold, suggesting that few individuals along the elevational gradient
344 are experiencing stress. Only *C. revoluta* features reduced photosynthetic capacity with elevation.
345 *C. revoluta* also has the most individuals below the 0.7 threshold. This could be evidence that *C.*
346 *revoluta* individuals experience greater stress at increasing elevations, but the relationship shown
347 here is not strong enough to be conclusive, with large variation within each plot that *C. revoluta*
348 seedlings were sampled. Alternatively other species which feature an increase in photosynthetic
349 efficiency may be experiencing stress at lower elevations, giving support for the hypothesis given
350 by Campbell et al. (2007), in which species ranges contract from the bottom up. Temperature
351 increase is the most likely source of this increased stress at the lower limits of species ranges,
352 though stress induced by antagonistic interactions from previously lower elevation species that have
353 shifted upslope faster is also possible. Herbivores for example are expected to move upslope faster
354 than tree species due to their mobility and shorter life-cycles (Chen et al., 2011).

355 SPAD

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

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

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

370 Summary

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

379 Leaf and plant morphology

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

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

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

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

416 Summary

417 Stem volume was the only morphological plant trait that showed clear variation with a competition
418 variable (ISI), therefore H_{n1} is accepted for all other morphological plant traits. All morpholog-
419 ical plant traits were best explained by a multiple fixed effect model including elevation and a
420 combination of competition variables, therefore H_{n2} is accepted for all morphological plant traits.
421 Morphological plant traits varied across elevation in a manner similar to that identified by previous
422 studies, responding to elevation dependent abiotic environmental variables such as temperature and
423 nutrient availability. The strength of the relationships seen here is not as great as that demonstrated

424 by other studies, possibly because of the comparatively low sample size per species in this study
425 compared to larger reviews and the presence of confounding environmental variables that were not
426 accounted for in statistical analysis.

427 5 Variation in plant traits with elevation

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

436 Variation among species

437 Species varied largely in the direction, magnitude and variance of their plant trait response to
438 elevation (Figure ??), therefore H_{n5} is rejected. Variation among species in slope implies that species
439 differ in their sensitivity to changing environmental conditions across elevation. *D. lamarckianum*
440 and *I. deltoidea*, the two monocot species, show no similarity in their plant trait response to elevation,
441 often having different slope directions for a given plant trait. Together, *D. lamarckianum* and *I. deltoidea*
442 show no difference to dicot species in terms of their plant trait-elevation relationship.
443 *A. verticillata* has a comparatively large variance for all trait-elevation relationships except stem
444 volume. This implies that *A. verticillata* is either more sensitive to changes in climate, or that it
445 has a larger acclimatory range than other species; both may be true. *A. verticillata* has a very small
446 elevational range (Figure ??) but is also one of the most common tree species found along this set of
447 plots (Appendix VI). This supports the theory that common species have a wider acclimatory range
448 and that species with small ranges are sensitive to environmental variation. In contrast, *Myrcia*
449 spp. has little variation in plant traits compared to other species but has the largest elevational
450 range, the *Myrcia* spp. species sampled are among the rarer species sampled.

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

465 **Summary**

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

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

480 **6 Predictions for future species migration**

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

493 Most species featured a decrease in photosynthetic efficiency at the bottom of their elevational
494 ranges. This implies that these species may experience progressively greater plant stress at the
495 bottom of their ranges as temperature increases, and the bottom of their range will continue to
496 shift upslope as a result. This study cannot infer whether the contraction of species' lower range
497 limits will be faster or slower than the expansion of the upper range limit, though other studies
498 have suggested that lower range limits will shift upslope faster than upper limits (Campbell et al.,
499 2007), owing to climate change proceeding faster than micro-evolutionary processes to adapt to
500 higher elevations. This will lead to an overall reduction in range size for many species.

501 **7 Limitations of this study**

502 This study sampled seedling physiology over a narrow time period. While F_v/F_m and SPAD are
503 unlikely to vary on a daily basis, they may do over the course of a season (?). Seedlings are likely to
504 alter their leaf physiology and morphology in response to a temporally heterogeneous environment
505 throughout the course of their life. As canopy gaps open and close the light and precipitation

506 regime will change. The measured physiological responses of individuals therefore may not be
507 representative of its physiology over a lifetime. Furthermore, this study only measured seedlings,
508 ignoring other life stages. This means the results of this study cannot be used to directly infer
509 the effects of biotic interactions on plant traits across entire populations. It is likely however, that
510 established adult trees will be less sensitive to competition from other adult trees and completely
511 insensitive to competition from seedlings (?).

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

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

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

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

540 8 Further research

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

547 In order to determine whether changes in competition intensity also affect adult trees, and thus
548 recruitment, similar studies should be performed on adult trees. This would help to improve the

549 accuracy of species range-shift models by adding the potential variation found within populations
550 and allowing demographically explicit models.

551 Conclusion

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

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

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

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

574 Forest structure based competition affects physiological stress independently of elevation

575 References

- 576 Akaike, H. (1992), ‘Information theory and an extension of the maximum likelihood principle’,
577 *Breakthroughs in Statistics* pp. 610–624.
- 578 Araújo, M. B., Thuiller, W. and Pearson, R. G. (2006), ‘Climate warming and the decline of
579 amphibians and reptiles in europe’, *Journal of Biogeography* **33**, 1712–1728.
- 580 Bates, D., Mächler, M., Bolker, B. M. and Walker, S. C. (2015), ‘Fitting linear mixed-effects models
581 using lme4’, *Journal of Statistical Software* **67**(1), 1–48.
- 582 Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. and Courchamp, F. (2012), ‘Impacts of
583 climate change on the future of biodiversity’, *Ecology Letters* **15**, 365–377.
- 584 Berry, P. M., Dawson, T. P., Harrison, P. A. and Pearson, R. G. (2002), ‘Modelling potential impacts
585 of climate change on the bioclimatic envelope of species in britain and ireland’, *Global Ecology &*
586 *Biogeography* **11**, 453–462.

- 587 Campbell, C., Atkinson, L., Zaragoza-Castells, J., Lundmark, M., Atkin, O. and Hurry, V. (2007),
 588 ‘Acclimation of photosynthesis and respiration is asynchronous in response to changes in temper-
 589 ature regardless of plant functional group’, *New Phytologist* **176**, 375–389.
- 590 Chen, I., Hill, J. K., Ohlemüller, R., Roy, D. B. and Thomas, C. D. (2011), ‘Rapid range of species
 591 associated with high levels of climate warming’, *Science* **333**, 1024–1026.
- 592 Colwell, R. K., Brehm, G., Cardelús, C. L., Gilman, A. C. and Longino, J. T. (2008), ‘Global
 593 warming, elevational range shifts and lowland biotic attrition in the wet tropics’, *Science* **322**, 258–
 594 261.
- 595 Corlett, R. T. and Westcott, D. A. (2013), ‘Will plant movements keep up with climate change?’,
 596 *Trends in Ecology & Evolution* **28**(8), 482–488.
- 597 Davis, M. A., Wrage, K. J. and Reich, P. B. (1998), ‘Competition between tree seedlings and
 598 herbaceous vegetation: support for a theory of resource supply and demand’, *Journal of Ecology*
 599 **86**, 652–661.
- 600 Dobson, A., Lodge, D., Alder, J., Cumming, G. S., Keymer, J., McGlade, J., Mooney, H., Rusak,
 601 J. A., Sala, O., Wolters, V., Wall, D., Winfree, R. and Xenopoulos, M. A. (2006), ‘Habitat loss,
 602 trophic collapse, and the decline of ecosystem services’, *Ecology* **87**(8), 1915–1924.
- 603 Ettinger, A. K., Ford, K. R. and HilleRisLambers, J. (2011), ‘Climate determines upper, but not
 604 lowe, altitudinal range limits of pacific northwest conifers’, *Ecology* **92**(6), 1323–1331.
- 605 Feeley, K. J., Malhi, Y., Zelazowski, P. and Silman, M. R. (2012), ‘The relative importance of defor-
 606 estation, precipitation change, and temperature sensitivity in determining the future distributions
 607 and diversity of amazonian plant species’, *Global Change Biology* **18**, 2636–2647.
- 608 Feeley, K. J., Silman, M. R., Bush, M. B., Farfan, W., Cabrera, K. G., Malhi, Y., Meir, P., Revilla,
 609 N. S., Quisiyupanqui, M. N. R. and Saatchi, S. (2011), ‘Upslope migration of andean trees’,
 610 *Journal of Biogeography* **38**, 783–791.
- 611 Gelman, A. and Su, Y.-S. (2018), *arm: Data analysis using regression and multilevel/hierarchical
 612 models*. R package version 1.10-1.
 613 **URL:** <https://CRAN.R-project.org/package=arm>
- 614 Girardin, C. A. J., Espejob, J. E. S., Doughty, C. E., Huasco, W. H., Metcalfe, D. B., Durand-Baca,
 615 L., Marthews, T. R., Aragao, L. E. O. C., Farfán-Rios, W., García-Cabrera, K., Halladay, K.,
 616 Fisher, J. B., Galiano-Cabrera, D. F., Huaraca-Quispe, L. P., Alzamora-Taype, I., Egiluz-Mora,
 617 L., Salinas-Revilla, N., Silman, M. R., Meir, P. and Malhi, Y. (2014), ‘Productivity and carbon
 618 allocation in a tropical montane cloud forest in the peruvian andes’, *Plant Ecology & Diversity*
 619 **7**(1-2), 107–123.
- 620 Gruber, C. E., Nakagawa, S., Laws, R. J. and Jamieson, I. G. (2011), ‘Multimodel inference in
 621 ecology and evolution: challenges and solutions’, *Journal of Evolutionary Biology* **24**, 699–711.
- 622 Hegyi, F. (1974), A simulation model for managing jack-pine stands, in ‘Royal College of Forestry,
 623 editor’, Royal College of Forestry, Stockholm, Sweden, pp. 74–90.
- 624 Hillyer, R. and Silman, M. R. (2010), ‘Changes in species interactions across a 2.5 km elevation gra-
 625 dient: effects on plant migration in response to climate change’, *Global Change Biology* **16**, 3205–
 626 3214.
- 627 Hughes, L. (2000), ‘Biological consequences of global warming: is the signal already apparent?’,
 628 *Trends in Ecology and Evolution* **15**(2), 56–61.

- 629 Isbell, F., Calcagno, V., Hector, A., Connolly, J., Harpole, W. S., Reich, P. B., Scherer-Lorenzen, M.,
630 Schmid, B., Tilman, D., van Ruijven, J., Weigelt, A., Wilsey, B. J., Zavaleta, E. S. and Loreau,
631 M. (2011), 'Hugh plant diversity is needed to maintain ecosystem services', *Nature* **477**, 199–203.
- 632 Lee, W., von Gadow, K., Chung, D., Lee, J. and Shin, M. (2004), 'Dbh growth model for *Pinus*
633 *densiflora* and *Quercus variabilis* mixed forests in central korea', *Ecological Modelling* **176**, 187–
634 200.
- 635 Malhi, Y., Silman, M., Salinas, N., Bush, M., Meir, P. and Saatchi, S. (2010), 'Introduction: ele-
636 vation gradients in the tropics: laboratories for ecosystem ecology and global change research',
637 *Global Change Biology* **16**, 3171–3175.
- 638 Maxwell, K. and Johnson, G. N. (2000), 'Chlorophyll fluorescence - a practical guide', *Journal of*
639 *Experimental Botany* **51**(345), 659–668.
- 640 Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B. and Kent, J. (2000),
641 'Biodiversity hotspots for conservation priorities', *Nature* **403**, 853–858.
- 642 Parmesan, C. (2006), 'Ecological and evolutionary responses to recent climate change', *Annual*
643 *Review of Ecology, Evolution and Systematics* **37**, 637–669.
- 644 Pearson, R. G. and Dawson, T. P. (2003), 'Predicting the impacts of climate change on the dis-
645 tribution of species: are bioclimate envelope models useful?', *Global Ecology & Biogeography*
646 **12**, 361–371.
- 647 Peterson, A. T., Ball, L. G. and Cohoon, K. P. (2002), 'Predicting distributions of mexican birds
648 using ecological niche modelling methods', *Ibis* **144**, E27–E32.
- 649 R Core Team (2019), *R: A Language and Environment for Statistical Computing*, R Foundation for
650 Statistical Computing, Vienna, Austria.
651 **URL:** <https://www.R-project.org/>
- 652 Seifert, T., Seifert, S., Seydack, A., Durrheim, G. and von Gadow, K. (2014), 'Competition effects
653 in an afrotropical forest', *Forest Ecosystems* **1**(13), 1–15.
- 654 Sinclair, S. J., White, M. D. and Newell, G. R. (2010), 'How useful are species distribution models
655 for managing biodiversity under future climates?', *Ecology and Society* **15**(1), 1–13.
- 656 Thuiller, W., Richardson, D. M., Pyšek, P., Midgley, G. F., Hughes, G. O. and Rouget, M. (2005),
657 'Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale',
658 *Global Change Biology* **11**, 2234–2250.
- 659 Van der Putten, W. H., Macel, M. and Visser, M. E. (2010), 'Predicting species distribution and
660 abundance responses to climate change: why it is essential to include biotic interactions across
661 trophic levels', *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**, 2025–
662 2034.