

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 4 bullet points (1) research conducted + rationale, (2) central methods, (3) key results, (4)
8 main conclusions including key points of discussion.

9 **1 Introduction**

10 Rapid anthropogenic climate change is causing many species, across a wide range of taxa, to shift
11 their distributions in space (Hughes, 2000; Parmesan, 2006; Chen et al., 2011). The primary forces
12 driving this are an increase in temperature and changes in precipitation regime (Corlett & West-
13 cott, 2013; ?). Chen et al. (2011) estimates that across a range of taxonomic groups, species are
14 experiencing mean latitudinal and altitudinal migration rates of 17.6 ± 2.9 km and 12.2 ± 1.8 m
15 per decade, respectively. For sessile taxa such as trees, range shifts occur as a result of differential
16 recruitment and mortality over space, at the leading and trailing edges of their range (). In communi-
17 ties of long-lived tree species, the forest ecosystem may not shift in equilibrium with the climate
18 as trees are resilient to gradual changes in climate, developing large root systems and below-ground
19 water and nutrient reserves to buffer against stressful conditions; adult trees may persist where
20 more sensitive seedlings perish (). Previous studies have suggested that the ability of tree species
21 to respond to changes in mean annual temperature and precipitation regime will be important in
22 determining species success over the coming century (Colwell et al., 2008; Chen et al., 2011; Feeley
23 et al., 2012). Species responses may occur either in the form of adaptation, *i.e.* changes in phenol-
24 ogy, physiology and morphology, or through range shifts over space (Bellard et al., 2012). Range
25 shifts of tree species have been observed in many studies across the world, particularly in temperate,
26 sub-arctic and mountainous regions () where temperature change is the most extreme (), while the
27 number of studies documenting adaptational responses are few, potentially indicating that climate
28 change is occurring so rapidly as to prevent effective adaptational responses (). Predicting range
29 shifts across space has become an active field of research, (see Bellard et al. 2012 and references
30 therein). Understanding species range shifts can aid in the identification of species assemblages at
31 risk of extinction and can inform conservation strategies to mitigate the effects of climate change
32 on biodiversity and ecosystem functionality ().

33 The majority of species distribution models used to predict species range shifts as a conservation
34 tool have used bioclimatic envelopes to constrain species' ranges (Pearson & Dawson, 2003; Sinclair
35 et al., 2010). Bioclimatic envelopes are constructed by correlating current species range extent

36 with observed environmental conditions within those boundaries, then projecting spatially explicit
37 climate trends into the future under different climate change scenarios to predict how species range
38 boundaries will adjust in response (e.g. Berry et al. 2002; Peterson et al. 2002; Thuiller et al.
39 2005; Araújo et al. 2006). These models have been criticised often for being overly simplistic,
40 especially when applied at the local scale (), where other factors that have not been considered by
41 the bioclimatic envelope model become important limiting factors for a species. Such factors include
42 unmeasured environmental variables, physical factors such as topography, and biotic interactions
43 with other species (Davis et al., 1998; Van der Putten et al., 2010; Ettinger et al., 2011). When range
44 shifts in a rapidly changing climate are driven by a single environmental variable like mean annual
45 temperature, it is possible that a species will move into an area that is sub-optimal in other ways than
46 those predicted by the model if range shifts outstrip acclimatory/adaptive potential (). Range shifts
47 into sub-optimal habitats may lead to reductions in local species abundance and/or richness (Colwell
48 et al., 2008), changes in community composition (), ecosystem functioning (Bellard et al., 2012),
49 and ecosystem service provision that are not predicted by bioclimatic envelope models (Dobson
50 et al., 2006; Isbell et al., 2011). In order to accurately predict range shifts and their consequences
51 for future ecosystem assembly, it is important that predictive range models be expanded to include
52 variables which describe habitat as well as climate, and consider ecosystem level effects rather than
53 simply species level effects ().

54 Forest trees, particularly those in moist tropical forests, often experience high levels of mortality
55 during the seedling recruitment stage, creating a demographic bottleneck (?). Many seedlings perish
56 due to suboptimal shade regimes created by the arrangement of adult trees creating canopy above
57 them (). The seedlings of many tropical tree species are highly adapted to shade (), meaning that
58 if a seedling germinates in an open space, mortality by UV-B and heat damage to photosynthetic
59 machinery is quite probable (). Seedlings may also compete with adult trees for nutrients (),
60 although there is some separation between seedling and adult tree rooting depths for most species
61 (), especially for the largest trees (). This mortality bottleneck provides a limiting factor to the
62 success of tropical forest tree species experiencing range shifts. If seedlings germinate in areas that
63 are only sparsely shaded, damage may occur leading to loss of photosynthetic capacity (), reducing
64 growth rates and occasionally resulting in seedling mortality ().

65 In montane cloud forests, elevational range shifts are occurring more rapidly than in other
66 areas (). As mean annual temperatures rise, plant species are figuratively pushed up-slope, with
67 higher recruitment at the upslope edge of their range and higher mortality at the downslope edge
68 of their range (). Particularly in the tropics, as altitude increases, UV-B concentration increases,
69 with many species found at high altitudes () having specific adaptations to avoid UV-B damage
70 to photosynthetic machinery, such as vertically stacked palisade mesophyll cells and thick cuticles
71 to reduce UV-B absorption, and generally smaller thicker leaves (). Species found at low altitudes
72 however, are less adapted to high UV-B environments, instead having adaptations to make the most
73 of the diminished light levels found under thick tree canopy, particularly during the seedling growth
74 stage (). Montane forest physical structure also varies with elevation. Lowland forests often have
75 lower tree density, with relatively few young trees in the light-deprived understorey, but a higher
76 canopy cover due to adult trees being larger. Plant ground cover is generally greater at higher
77 altitudes, with many epiphytic and ground-level herbaceous. It therefore follows that as lowland
78 species move upslope in response to increasing temperature, they may experience increased levels
79 of damaging UV-B radiation as they recruit into areas of forest with thinner canopies. This may
80 lead to species' ranges narrowing from the bottom up, with increased mortality due to temperature
81 at the bottom of the elevational range, but without increased recruitment at the top end of the
82 elevational range due to increased mortality via UV-B exposure.

83 In this study, we investigated the effects of variation in adult tree canopy structure and size
84 distribution on seedling growth form and photosynthetic stress, across an elevational gradient in
85 the Peruvian Andes, spanning lowland wet forest and montane cloud forest. Our aim was to assess

86 the role of biotic effects of the existing forest structure on the potential recruitment probability
 87 of tree seedlings, in order to increase our knowledge of the dynamics of montane cloud forest tree
 88 species elevational range shifts. We tested three hypotheses: 1) Within a species, seedlings growing
 89 at higher elevations would experience higher levels of photosynthetic stress than those at lower
 90 elevations, 2) Species would differ in their degree of acclimation to variation in adult tree canopy
 91 structure and size distribution, 3) A combination of biotic and abiotic explanatory variables would
 92 best explain variation in seedling morphological and physiological traits across their elevational
 93 range.

94 2 Materials and Methods

95 2.1 Study Site

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

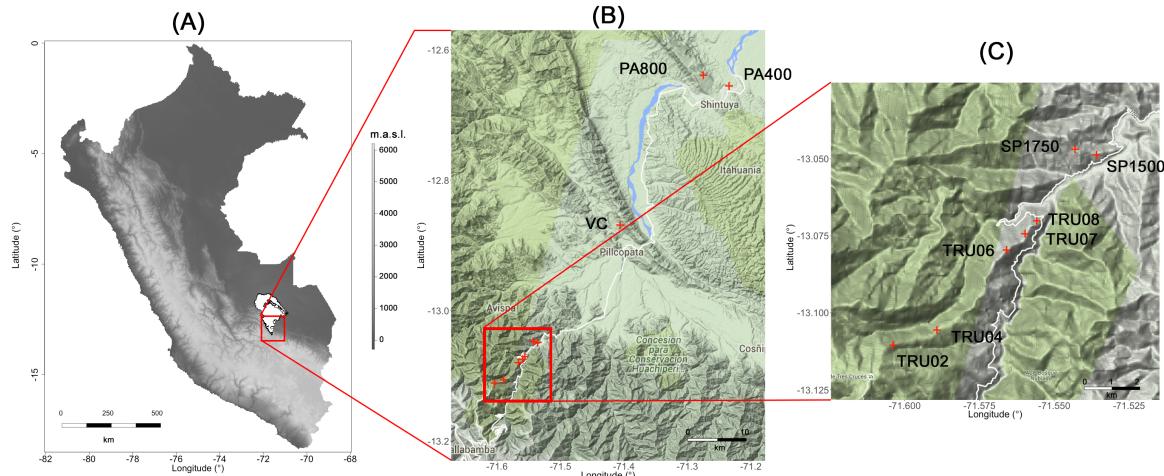


Figure 1: Maps showing the location of the study area and plot locations. (A) The site location within Peru with elevation shading, showing the proximity to Manú National Park (white area). (B) The location of the 1 ha plots within the Kosñipata Valley. (C) An enlargement of the Trocha Union and San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

105 **2.2 Study species**

106 We chose nine tree species for comparison from a total of 719 identified species within the 10 study
 107 plots. Species were selected according to their contrasting ranges (Figure ??), differences in genus
 108 migratory pattern (Feeley et al., 2011), and because each species is dominant across its range in the
 109 Kosñipata Valley (ABERG, unpublished data, [Appendix VI](#)). Despite having no quantitative range
 110 shift prediction information, *Iriartea deltoidea* and *Dictyocaryum lamarckianum* were included in
 111 order to observe potential differences in response between monocot and dicot species, as both are
 112 monocots. Both *I. deltoidea* and *D. lamarckianum* are large-seeded palm species, as such, they are
 113 expected to be migrating upslope, similar to other large-seeded palms (Hillyer & Silman, 2010).
 114 Seedlings of *Myrcia spp.* are difficult to reliably identify to species in the field due to similar
 115 morphology and were thus sampled as a composite of three potential species: *Myrcia splendens*,
 116 *M. fallax*, and *M. rostrata*, the only *Myrcia* species known to be present in our plots from ABERG
 117 censuses. They are referred to as *Myrcia spp.* from here on.

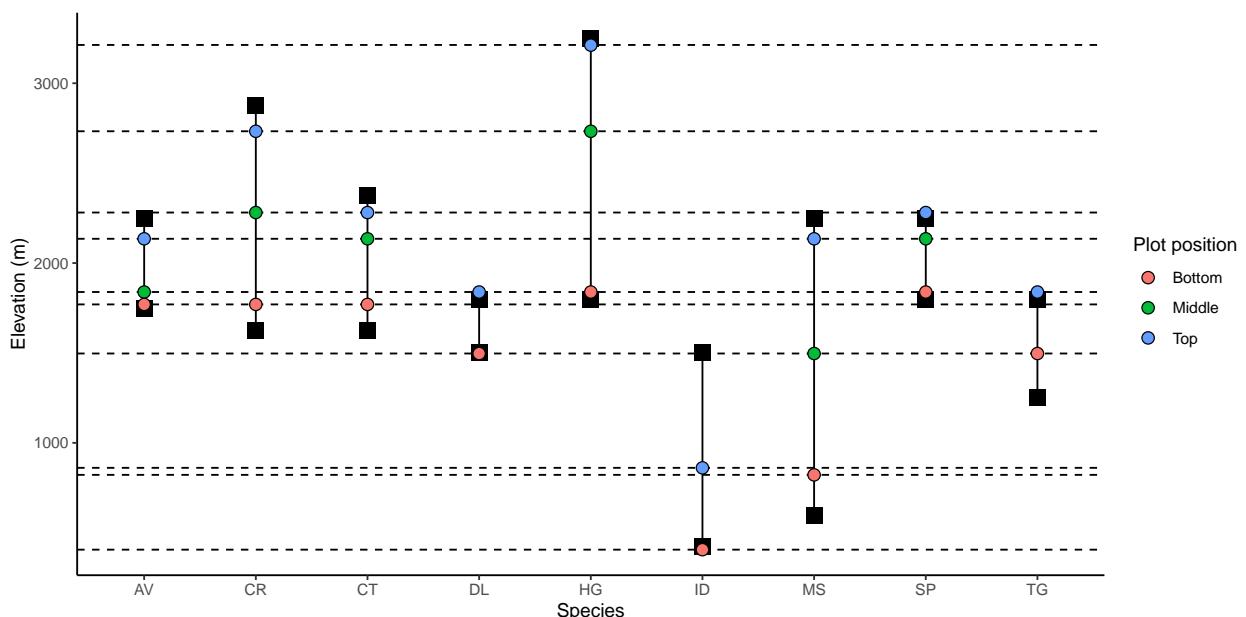


Figure 2: Elevation of study plots for each species (coloured points) with the upper and lower range extents for each species (black squares). Plot elevations are marked as dashed lines.

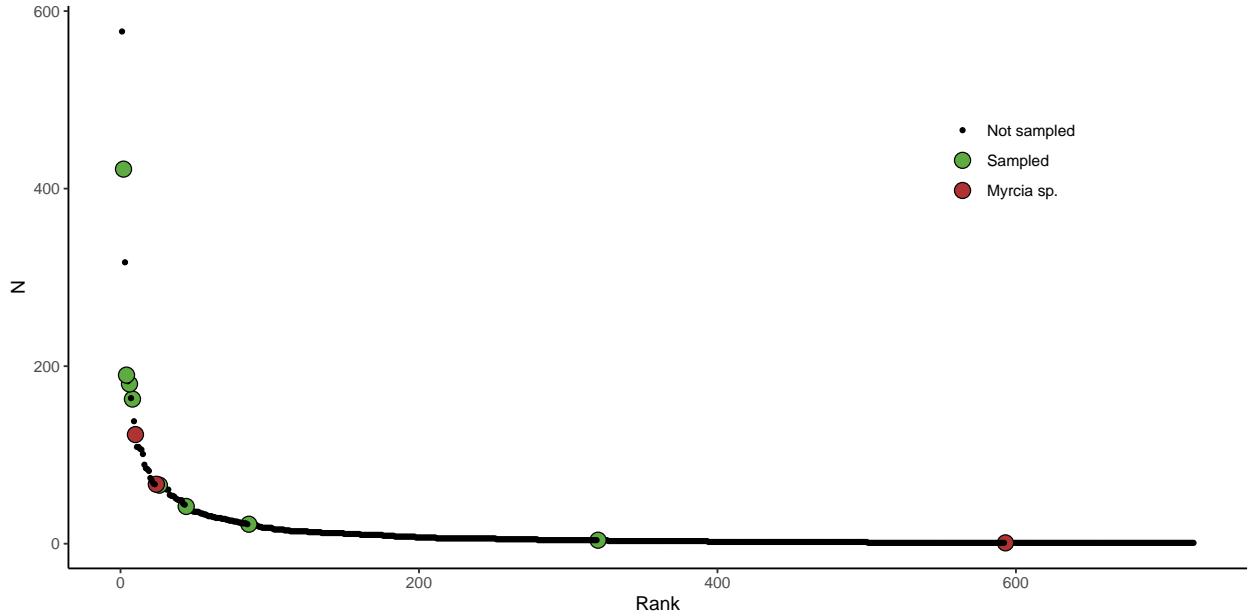


Figure 3: Rank abundance curve of all individuals >10 cm DBH of all species found in the plots measured in this study. Census data from 2014 (ABERG, unpublished data). Species sampled as part of this study are highlighted in red. *Myrcia* species which form the composite *Myrcia* spp. are highlighted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

118 2.3 Sampling and Measurement

119 Species were sampled in three plots representing the upper, middle and lower elevational extents
120 of their ranges (Figure 2). Within each plot, a maximum of 10 seedlings were sampled. Seedling
121 mortality creates a narrow bottleneck for tree survival in closed canopy tropical forests, seedlings
122 are particularly sensitive to environment stress. To minimise the chance of pseudo-replication of
123 sampled seedlings, seedlings closer than 10 m to another sampled seedling were excluded from the
124 analysis, as it could not be guaranteed that the stems were not connected by a stolon or rhizome.
125 It also ensured that competition radius measurements were truly independent. Within a cluster
126 of seedlings within 5 m of each other, each seedling was assigned a number and a random number
127 generator was used to choose a single seedling for measurement.

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

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

134 Where F_m is the maximal fluorescence in the dark and F_o is the minimal fluorescence in the dark
135 (Maxwell & Johnson, 2000). Fluorescence measurements were taken after exposing the seedling to 30
136 minutes of total darkness, to ensure complete dark adaptation (Campbell et al., 2007). Dark-adapted
137 F_v/F_m measures the photosynthetic efficiency of the leaf by relaxing the reaction centres prior to
138 the fluorescence measurement. F_v/F_m is preferable to other chlorophyll fluorescence measures as
139 it removes the noise created by environmental conditions at the time of measurement, instead

140 providing a measure of the underlying photosynthetic efficiency. A reduction in F_v/F_m is indicative
141 of plant stress. Here, individuals with F_v/F_m values <0.7 are considered to be experiencing stress
142 (Maxwell & Johnson, 2000).

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

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

150 2.4 Leaf and whole-plant morphological measurements

151 2.5 Competition measurements

152 To assess adult-seedling competition interactions we used to metrics, Leaf Area Index of canopy
153 foliage, and a calculation approximating the degree of crowding from adult trees. Leaf Area Index
154 (LAI) was calculated from hemispherical photographs of the forest canopy above each seedling.
155 Photographs were captured under uniformly overcast cloud conditions to avoid lens flare and to aid
156 in delineation of foliage from sky (?). Images were taken with a Coolpix 4500 compact camera,
157 with a Nikon FC-E8 hemispherical fisheye converter lens. Images were constrained to a 60° circular
158 azimuthal field of view, WHY. Images were then converted to 8-bit grayscale and binarized manually
159 in ImageJ version () to separate sky from plant material. Binarized images were then analyzed using
160 Hemiphot () in R to estimate LAI as the projected leaf area per unit ground area ($m^2 m^{-2}$).

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

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

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

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

where N is the number of trees >10 cm DBH per ha (stand density). Stand density data was taken from ABERG census data within each plot (ABERG unpublished data) and used to interpolate values C_R for plot VC, for which no stand density data exists, by fitting the elevation of the plot to a linear regression between elevation and trees ha^{-1} for the remaining plots (Figure S1). C_R was rounded to the nearest metre for ease of measurement (Table ??).

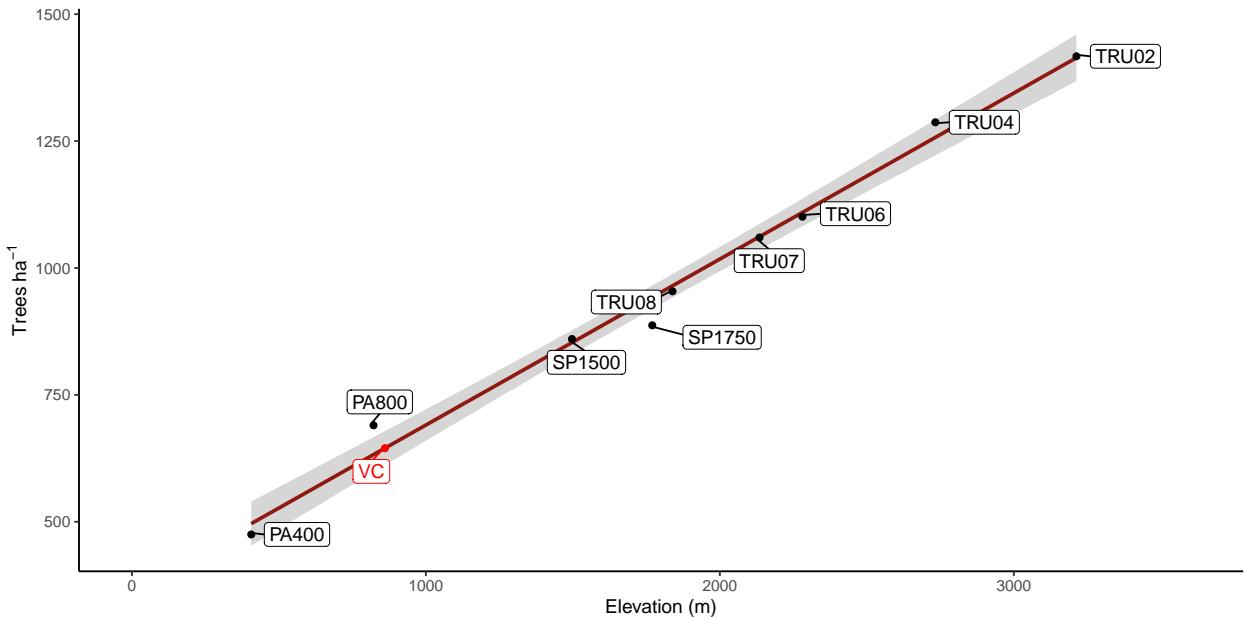


Figure 4: Linear regression with 95% confidence interval of number of trees per hectare for each site, used to estimate number of trees per hectare for site VC. $R^2 = 0.896$, $F_{(1,7)} = 579.5$, $p < 0.001$.

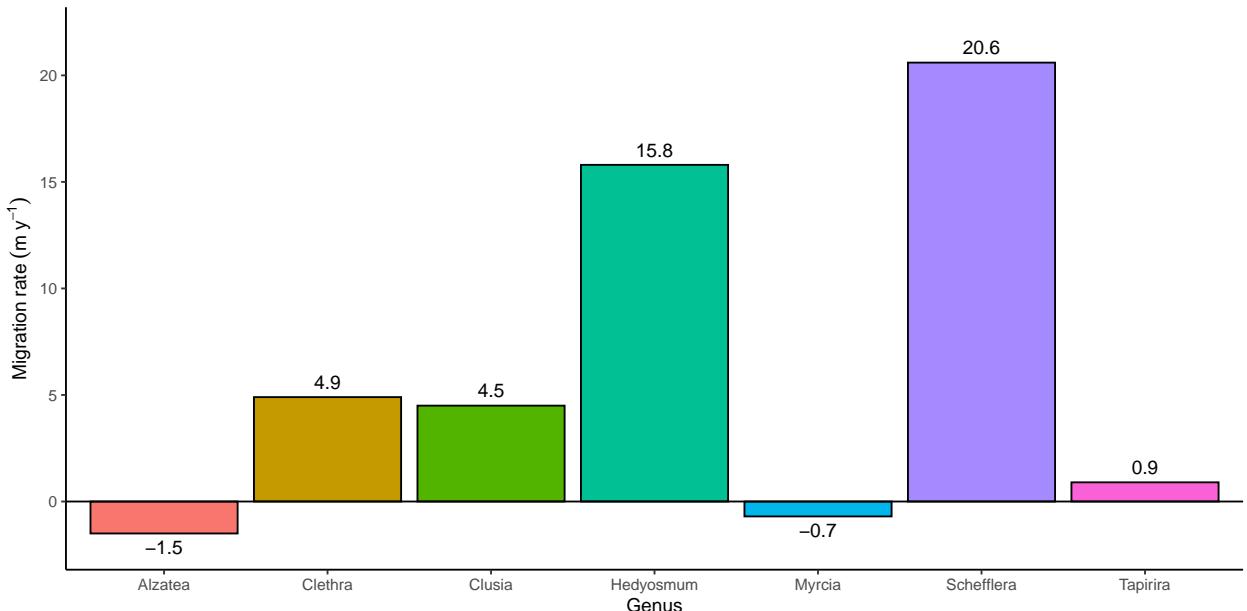


Figure 5: Estimated elevational migration rates of selected genera of which species are studied here. Migration rates are estimated using shifts in the centre of gravity of basal area as measured in the ABERG 1 Ha plot network.

179 **2.6 Statistical Analysis**

180 A matrix of single predictor linear mixed effects models were compared to test for the presence and
181 strength of the causal relationship between each competition variable and each plant trait. All model
182 variables were standardised to allow easy comparison of effect sizes, according to (?Gruber et al.,
183 2011; ?). Model comparison was performed on models fitted using Maximum Likelihood (ML)
184 estimates according to. Model quality was compared using Akaike Information Criteria (*AIC*)
185 (Akaike, 1992), Akaike weights (W_i), and fixed effect marginal pseudo-R² values (R_M^2).

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

190 Add linear mixed model set up as an equation or schematic diagram or something

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

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

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

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

207 **3 Results**

208 **3.1 Variation in plant traits across elevation**

209 Physiological leaf trait models were not of a better quality when species were given their own slopes.
210 All morphological traits had at least one model where a random slope structure for species produced
211 a model of better quality. Leaf area was better using a random slope for all except herbaceous plant
212 abundance.

213 Within each species, the degree to which plant traits varied over their elevational range differed
214 significantly according to linear models of the effect of species on plant trait slope **WHAT IS THE**
215 **LINEAR MODEL RESULT? VARIANCE EXPLAINED** (Figure 7, Figure ??).

216 Single fixed effect mixed effects models were better than random effects models in 15/24 cases
 217 ($\Delta AIC_{r,\zeta} < 2$) (Figure ??). However, competition variables account for only a small percentage of the
 218 variance in each plant trait, with the highest R^2_M being ISI predicting stem volume ($R^2_M = 4.3\%$)
 219 (Figure ??). Elevation has a greater influence over plant traits than any competition variable in all
 220 cases.

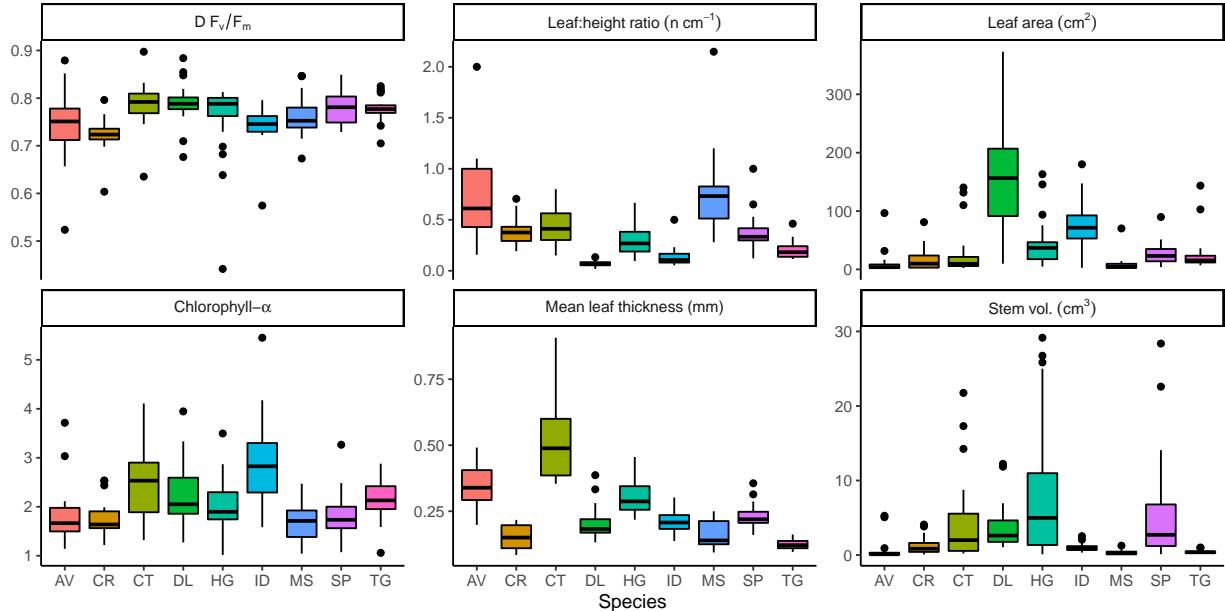


Figure 6: Box plots showing the variation in plant trait values within each species.

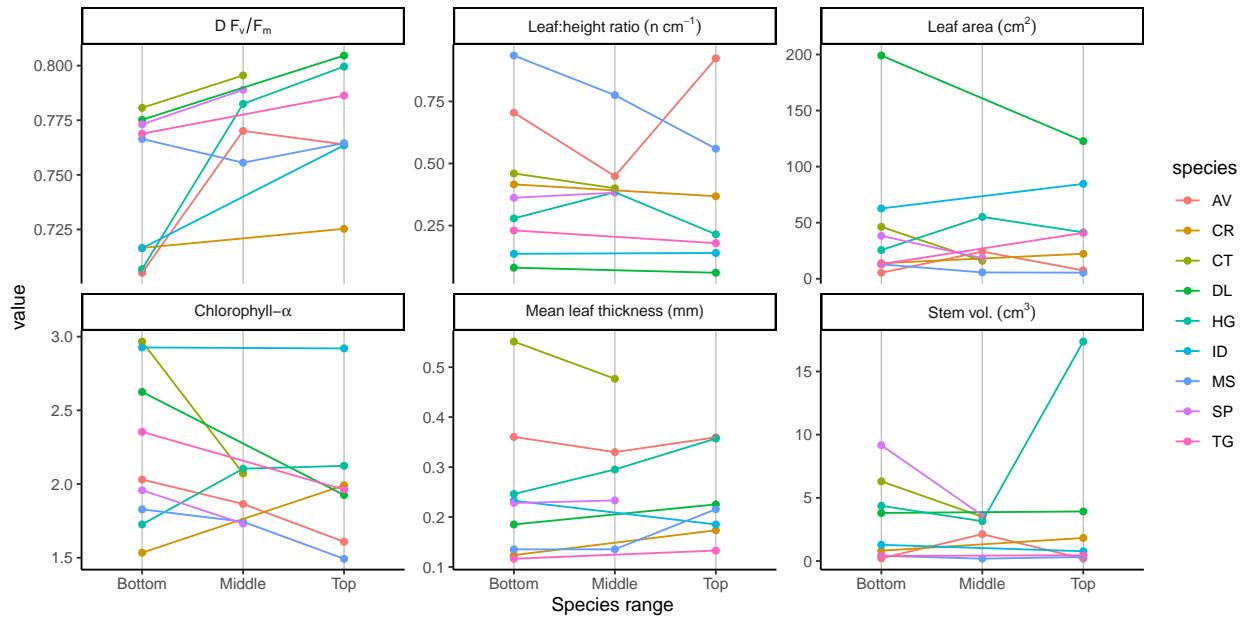


Figure 7: Interaction plots showing the variation in plant trait values within each species.

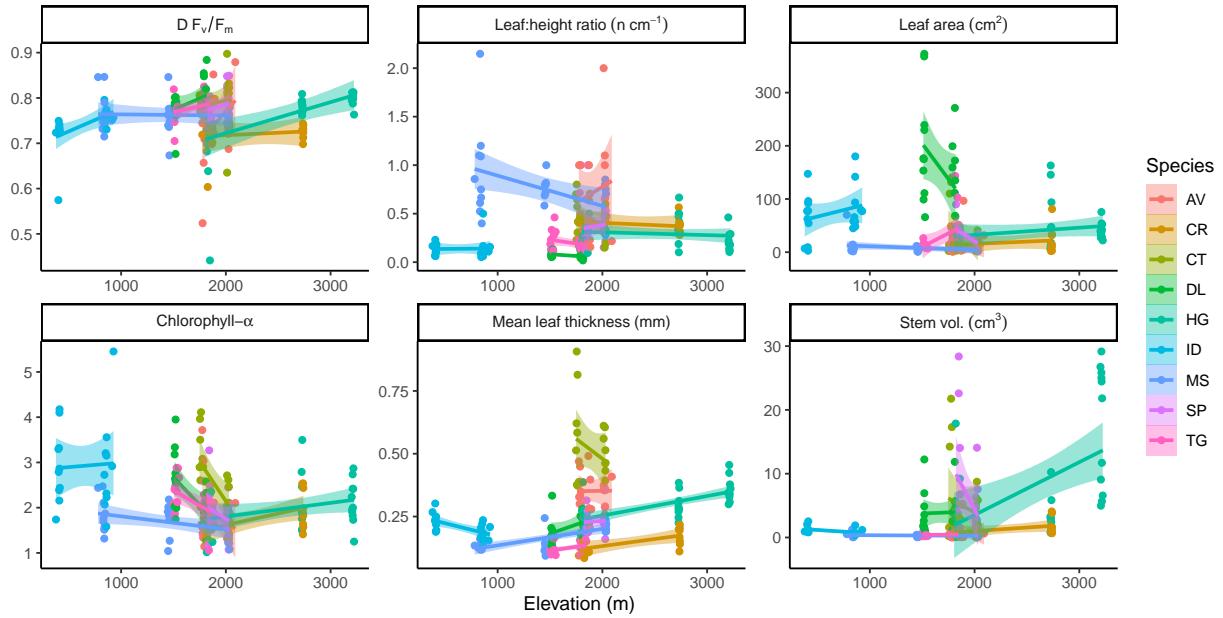


Figure 8: Scatter plots with linear model fits for each species, showing the variation in plant stress variables and plant traits across elevation.

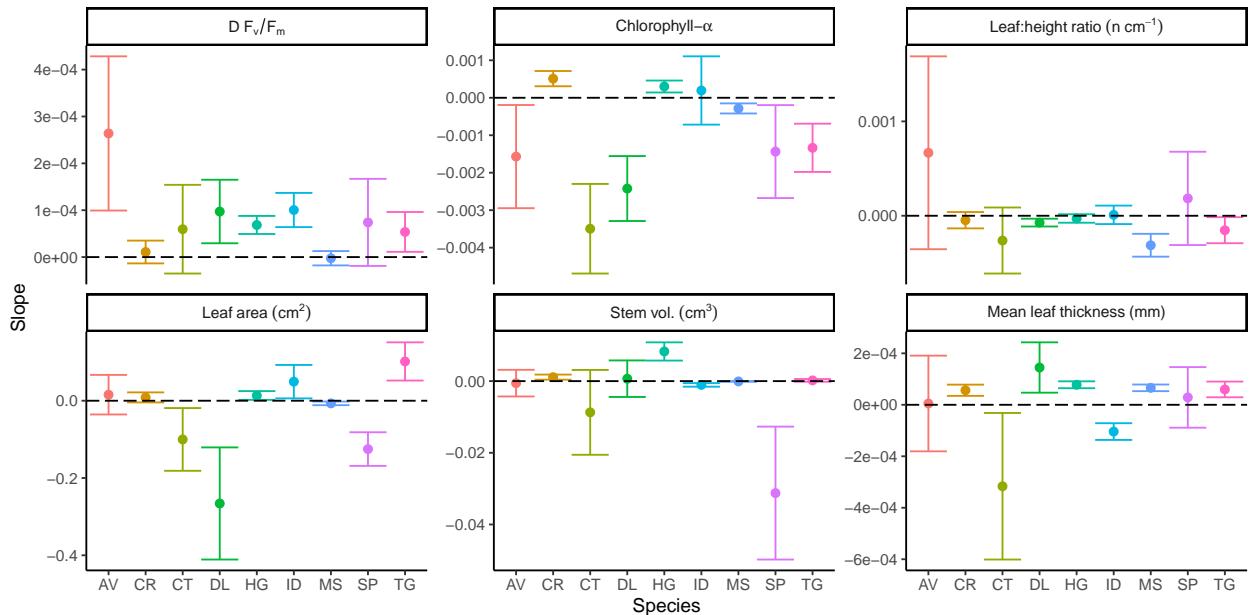


Figure 9: Interval plots showing the effect sizes (slopes) of each fixed effect in single fixed effect linear mixed effects models of plant traits against forest structure variables and elevation, for comparison.

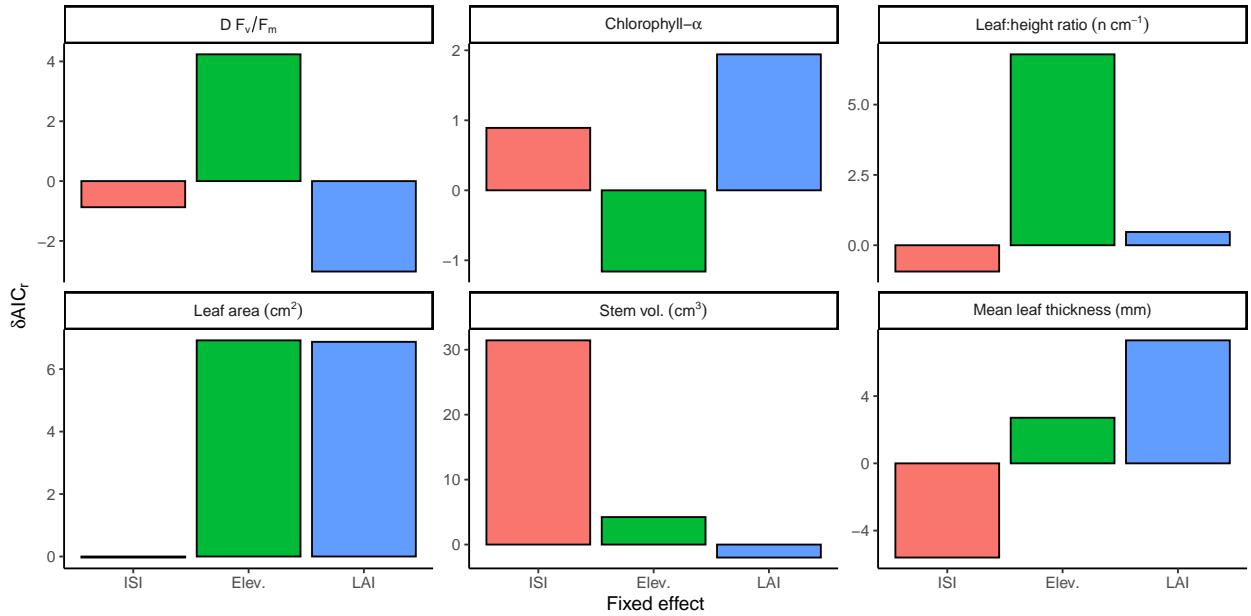


Figure 10: The difference in AIC values between each single fixed effect model and a corresponding random effects model using no fixed effects. A higher ΔAIC_r means the model is of higher quality than the random effects model. Horizontal dashed red line indicates the level at which a model is not appreciably better quality than the corresponding random effects model.

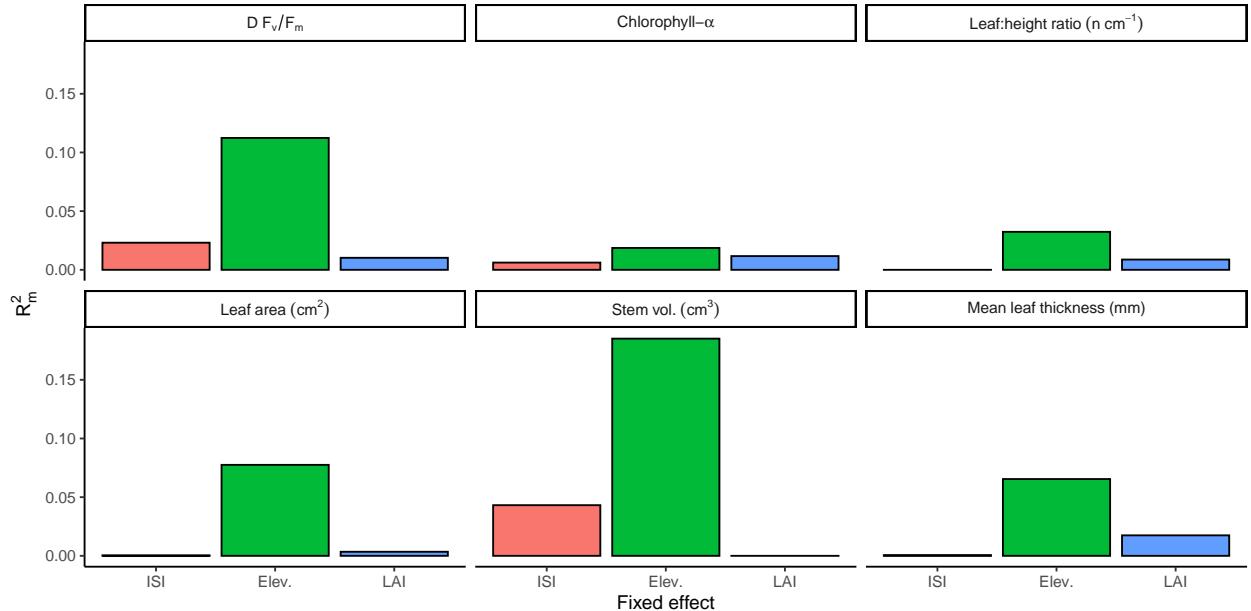


Figure 11: The variance explained by each single fixed effect model. The pale bars indicate the variance explained by the whole model while the bold bars indicate the variance explained just by the fixed effect in the model.

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.

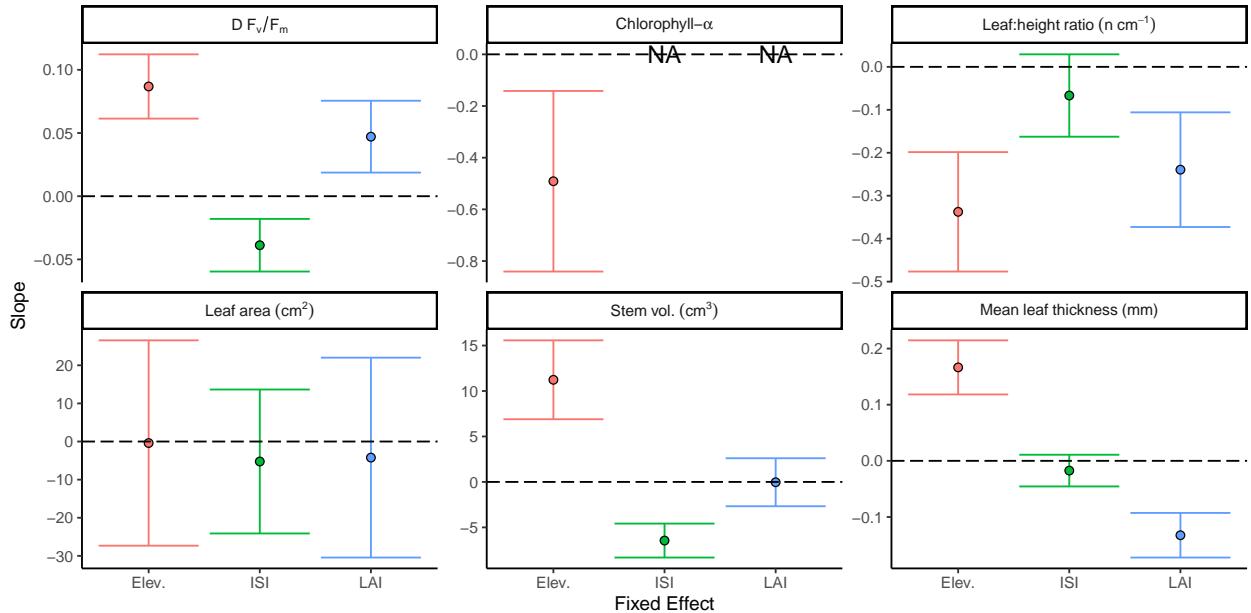


Figure 12

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

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

236 3.2 Effects of competition on plant traits

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

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

248 **Discussion**

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

255 **4 Effect of competition and elevation on plant traits**

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

260 **Leaf physiology**

261 Together, SPAD and F_v/F_m are useful measures of a plant's health and the integrity of its photo-
262 synthetic apparatus (?). SPAD is used as a proxy for leaf chlorophyll content (?), while F_v/F_m
263 measures the efficiency with which a leaf can utilise light for photosynthesis (Maxwell & Johnson,
264 2000). This study found contrasting effects of elevation on SPAD and F_v/F_m . As elevation in-
265 creased, photosynthetic efficiency increased but chlorophyll content decreased slightly (Figure ??).
266 There is however, large variation in SPAD within sites and elevation explains little of the variance
267 in SPAD (Figure ??), meaning this relationship may be erroneous. Competition variables explained
268 comparatively little variation in F_v/F_m or SPAD compared to morphological leaf traits (Figure
269 ??b).

270 **Photosynthetic efficiency**

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

285 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 & Johnson (2000) suggest that generally, optimum F_v/F_m is ~ 0.83 , and that if F_v/F_m falls below ~ 0.8 , it is indicative of some kind of plant stress. It is important to note however, that this

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

349 SPAD

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

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

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

364 Summary

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

373 Leaf and plant morphology

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

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

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

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

410 Summary

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

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

421 5 Variation in plant traits with elevation

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

430 Variation among species

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

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

459 **Summary**

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

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

474 **6 Predictions for future species migration**

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

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

495 **7 Limitations of this study**

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

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

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

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

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

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

534 8 Further research

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

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

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

545 Conclusion

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

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

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

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

568 Forest structure based competition affects physiological stress independently of elevation

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