Leaf-level photosynthetic capacity in lowland Amazonian and high-elevation, Andean tropical moist forests of Peru

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Summary

- We examined whether variations in photosynthetic capacity are linked to variations in the environment and/or associated leaf traits for tropical moist forest (TMFs) in the Andes/western-Amazon regions of Peru.
- We compared photosynthetic capacity (V_{cmax} and J_{max}), leaf mass, nitrogen and phosphorus per unit leaf area (M_a, N_a and P_a respectively), and chlorophyll from 210 species at 18 field sites along a 3,300-m elevation gradient. Western-blots were used to quantify abundance of the CO_2-fixing enzyme, Rubisco.
- Area- and N-based rates of photosynthetic capacity at 25˚C were higher in upland- than lowland-TMFs, underpinned by greater investment of N in photosynthesis in high-elevation trees. Soil [P] and leaf P_a were key explanatory factors for models of area-based V_{cmax} and J_{max} but did not account for variations in photosynthetic N-use efficiency. At any given N_a and P_a, the fraction of N allocated to photosynthesis was higher in upland than lowland species. For a small subset of lowland TMF trees examined, a substantial fraction of Rubisco was inactive.
- These results highlight the importance of soil- and leaf-phosphorus in defining photosynthetic capacity of TMFs, with variations in N allocation and Rubisco activation state further influencing photosynthetic rates and N-use efficiency of these critically important forests.

Keywords: Elevation, carboxylation capacity, leaf traits, nitrogen, phosphorus, ribulose bisphosphate regeneration, temperature, tropical forests

Introduction

Tropical moist forests (TMFs) play a significant role in the terrestrial carbon cycle, contributing one-third to global gross primary productivity (Beer *et al.*, 2010; Malhi, 2010). Understanding the factors that regulate leaf photosynthesis (*A*) in TMFs is a prerequisite for modelling carbon storage in tropical ecosystems, with *A* being influenced *inter alia* by nutrient supply [particularly nitrogen (N) and phosphorus (P)], elevation and growth temperature.

Early studies in lowland TMFs implicated low foliar P concentrations as a major influence on light-saturated net photosynthesis (A_{sat}) (Reich & Walters, 1994; Raaimakers *et al.*, 1995), with soil P being a major factor limiting Amazon productivity (Quesada *et al.*, 2012). Foliar P is crucial to the fine-tuning A_{sat} (Fredeen *et al.*, 1989; Jacob & Lawlor, 1993) via regulation of key intermediates in carbon metabolism (e.g. ATP, NADPH and sugar phosphates including ribulose 1,5-bisphosphate - RuBP). While the direct effect of P-limitation is primarily on RuBP regeneration, reductions in Rubisco activity also occur (Brooks, 1986; Jacobs & Lawlor, 1992; Loustau *et al.,* 1999). Although Meir *et al.* (2002; 2007) and Reich *et al.* (2009) showed that A_{sat} at a given leaf N concentration ([N]) was less in lowland tropical trees than their temperate counterparts, the extent to which P limitations *per se* alter $A_{sat}\leftrightarrow$[N] relations within TMFs is uncertain (Bloomfield *et al.*, 2014a; Domingues *et al.*, 2015). A further unknown is the extent to which large elevation gradients affect $A_{sat}\leftrightarrow$[N] relations in the tropics. Upland TMFs are more likely to be limited by N than their lowland counterparts (Tanner *et al.*, 1998). Upland TMFs also experience lower temperatures and atmospheric CO_2 partial pressures, more frequent cloud cover and experience greater leaf wetness (Grubb, 1977; Vitousek, 1984; Girardin *et al.*, 2010; Bruijnzeel *et al.*, 2011). Such factors can limit A_{sat} (Terashima *et al.*, 1995; Bruijnzeel & Veneklaas, 1998; Letts & Mulligan, 2005), leading to declines in productivity (Girardin *et al.*, 2010). A_{sat} in upland TMFs have been documented (e.g. Quilici & Medina, 1998; Cordell *et al.*, 1999; Hikosaka *et al.*, 2002; Letts & Mulligan, 2005; Rada *et al.*, 2009), showing A_{sat}

being constant with increasing elevation (Cordell *et al.*, 1999), or declining with increasing elevation (Hikosaka *et al.*, 2002; Wittich *et al.*, 2012).

Rates of A_{sat} are subject to variations in stomatal conductance (g_s) and the partial pressure of internal leaf CO_2 (C_i) (Santiago & Mulkey, 2003). Since variations in C_i alter both CO_2 uptake and photorespiratory CO_2 release, it could potentially confound our understanding of how environmental gradients alter N investment in *A*. By contrast, variations in g_s have less impact on the fundamental, biochemical parameter of photosynthetic capacity – that being the maximum rate of carboxylation by Rubisco (i.e. V_{cmax}). Positive correlations between V_{cmax} and leaf [N] have been reported for some tropical species (Carswell *et al.*, 2000; Meir *et al.*, 2002; Domingues *et al.*, 2005; Kumagai *et al.*, 2006; Meir *et al.*, 2007; Vårhammar *et al.,* 2015) – whereas in others no strong V_{cmax}↔[N] relationship was observed (Coste *et al.*, 2005; van de Weg *et al.*, 2012; Dusenge *et al.*, 2015). Although reports on V_{cmax} are less widespread in the tropics than A_{sat}, the available data suggest that V_{cmax} values, as well as V_{cmax} per unit N (herein termed '$V_{cmax,N}$'), are lower in lowland TMFs than their non-tropical counterparts (Carswell *et al.*, 2000; Meir *et al.*, 2002; Domingues *et al.*, 2007; Meir *et al.*, 2007; Domingues *et al.*, 2010; Walker *et al.*, 2014; Vårhammar *et al.,* 2015). Kattge *et al.* (2009) re-analysed data to show that V_{cmax} per unit N in TMFs growing on young, relatively high nutrient status soils was higher compared to their older, Ferralsol and Acrisol soil counterparts that are characterised by very low soil P availability (Quesada *et al.*, 2010). These observations are consistent with laboratory studies showing reduced V_{cmax} (Lauer *et al.*, 1989; Loustau *et al.*, 1999) and reduced N allocation to Rubisco (Warren & Adams, 2002) under P-limited conditions. Increased allocation of N to non-photosynthetic components may also play a role (Domingues *et al.*, 2010; Lloyd *et al.*, 2013), as might inactivation of Rubisco (Stitt & Schulze, 1994). Yet, doubt remains regarding the general V_{cmax}↔[N] relationship in TMFs due to the scarcity of data, both in lowland and upland TMFs. Comprehensive surveys of V_{cmax} (and J_{max} - maximum rate of electron transport) across lowland and upland TMFs are required to establish whether there are

144 generalized patterns of photosynthetic capacity in relation to environmental
145 conditions and/or other leaf traits.

146 TMF species with higher leaf nutrient concentrations and lower leaf mass
147 per unit leaf area (M_a) values are often found in more fertile soils (Fyllas *et al.*,
148 2009), and M_a tends to increase with increasing elevation (Hikosaka *et al.*, 2002;
149 van de Weg *et al.*, 2009; Almeida *et al.*, 2012; Asner *et al.*, 2014b); leaf chemistry
150 also systematically shifts along elevation gradients in the tropics (Asner *et al.*,
151 2014b). Large variations in leaf traits also observed among co-occurring species,
152 reflecting the importance of phylogenetic relationships in determining trait values
153 in TMFs (Townsend *et al.*, 2007; Kraft *et al.*, 2008; Fyllas *et al.*, 2009). Whether
154 similar patterns hold for estimates of V_{cmax} in lowland and upland TMFs (and
155 $V_{cmax,N}$), is, however, not known.

156 Variations in $V_{cmax,N}$ underlie variations in photosynthetic N use efficiency.
157 Further insights can be gained by quantifying the proportion of N allocated to
158 the pigment-protein complexes (n_P), electron transport (n_E) and Rubisco (n_R)
159 (Evans & Seemann, 1989; Pons *et al.*, 1994; Hikosaka, 2004). Quantification of
160 V_{cmax}, J_{max}, leaf chlorophyll and [N] can be used to estimate n_P, n_E and n_R (Evans &
161 Seemann, 1989; Niinemets & Tenhunen, 1997). In non-tropical plants, lower A_{sat}
162 at a given N (A_N) are associated with reduced allocation of N to photosynthesis
163 and increased allocation to non-photosynthetic components (Poorter & Evans,
164 1998; Westbeek *et al.*, 1999; Warren & Adams, 2001; Takashima *et al.*, 2004;
165 Hikosaka & Shigeno, 2009). Similarly, variations in A_N were associated with
166 differences in N allocation to and within the photosynthetic apparatus in
167 greenhouse-grown tropical tree seedlings (Coste *et al.*, 2005) and in high
168 elevation TMFs of Rwanda (Dusenge *et al.*, 2015). To our knowledge, no study has
169 quantified N allocation patterns in field-grown tropical trees, and not with respect
170 to field sites in upland and lowland TMFs.

171 We examined variations in photosynthetic capacity and leaf traits across
172 TMF canopies located at 18 sites along a 3,300-m elevation gradient stretching
173 from lowland western Amazonia to the Andean tree line in Peru. The study

174 included 11 lowland sites in northern and southern Peru (elevation 117-223 m
175 a.s.l.), and seven upland sites at elevations of 1527-3379 m a.s.l. in southern Peru.
176 Our site selection enabled an assessment of the potential role of P-availability on
177 photosynthetic performance across Amazonian-Andean TMF sites differing >40-
178 fold in total soil P. The upland sites were characterised by a floristically distinct
179 assemblage of montane forest species, with the transition from lowland moist
180 forests to upland montane forests coinciding with an increase in cloud formation
181 (van de Weg *et al.*, 2009; Bruijnzeel *et al.*, 2011). In conjunction with the recent
182 findings of the key role of P in modulating carbon investment (Quesada *et al.*,
183 2012) and photosynthesis (Bloomfield *et al.*, 2014b) of tropical trees, and that leaf
184 P varies predictably along soil P and elevation gradients (Asner *et al.*, 2014b), we
185 addressed the following questions:

186 (1) Do tropical TMF species growing on low-P soils exhibit lower photosynthetic
187 capacity and photosynthetic N use efficiency than TMF trees growing on
188 sites with higher P availability?

189 (2) Are there marked differences in V_{cmax}, J_{max} and $V_{cmax,N}$ between lowland
190 Amazonian and upland Andean TMFs?

191 (3) Are differences in V_{cmax}, J_{max} and $V_{cmax,N}$ linked to concomitant variations in
192 other leaf traits and/or environmental variables?

193

194 **Materials and Methods**

195

196 *Study sites*

197 Field work was carried out in 18 one-hectare long-term monitoring plots in Peru
198 which contribute to the ABERG and RAINFOR networks of permanent sample
199 plots. The plots are arrayed along gradients of elevation (117 to 3379 m above
200 sea level) and soil nutrient status (Table 1). For each site, climate data were
201 obtained from Asner *et al.* (2014a) and Malhi *et al.* (in prep). Marked changes in
202 species richness, canopy cover and tree height occur along the elevation gradient
203 (Asner *et al.*, 2014a; Girardin *et al.*, 2014b; Silman, 2014), reflecting local geological

substrates, as well as changes in growth temperature, cloud cover and light environment. In addition to marked inter-site differences in total soil [N] (0.6 - 15.5 g N kg^{-1}), substantial variation in total soil [P] occurs across both the lowland (38 - 727 mg P kg^{-1}) and upland sites (496 - 1631 mg P kg^{-1}) (Table 1). Soils at three of the lowland sites in northern Peru (JEN-12, ALP-30 and ALP-40) are notable for being low nutrient status arenosols/podzols ('white sands'). Among the lowland and upland sites, mean annual precipitation (MAP) values range from 1560 to 5300 mm a^{-1}. Mean annual temperature ranged from 8.0 to 18.8 °C across the upland sites, and 24.4 to 26.6 °C among the lowland sites.

At each site, tree climbers collected from dominant tree species upper canopy branches supporting leaves considered to typically be exposed to full sunlight for much of the day, but with little replication of individual species possible at any site. Each tree was initially identified to the genus-level and, whenever possible, to the species-level. A total of 353 individual trees drawn from 210 species were sampled across the 18 sites. See SM1 in Supporting Information for further details.

Leaf gas exchange measurements

Measurements of leaf gas exchange were made during July to September 2011, using portable photosynthesis systems (Licor 6400XT infrared gas analyser, Li-Cor BioSciences, Lincoln, NE, USA). Measurements were made on the most recently fully expanded leaves attached to the cut branches (which had been re-cut under water immediately after harvesting to ensure xylem water continuity).

CO_2 response curves of light-saturated photosynthesis ($A \leftrightarrow C_i$ curves) (at 1800 µmol photons m^{-2} s^{-1}) were performed within 30–60 minutes after branch detachment. CO_2 concentrations inside the reference chamber ranged in a stepped sequence from 35 to 2000 μmol mol^{-1} (see SM2 in Supporting Information for details). Block temperatures within the chamber were set to the prevailing day-time air temperature at each site (from 25-28 °C). The resultant $A \leftrightarrow C_i$ curves (examples shown in Fig. 1) were fitted following the model described by Farquhar *et al.* (1980) in order to calculate V_{cmax} and J_{max} on a leaf area basis –

see SM2 in Supporting Information for details. For every $A \leftrightarrow C_i$ curve, recorded air pressure was used to correct for altitudinal changes in O_2 partial pressure, and to calculate intercellular CO_2 (C_i) values on a partial pressure basis.

Rates of CO_2 exchange were corrected for diffusion through the gasket of the LI-6400 leaf chamber (Bruhn *et al.*, 2002) prior to calculation of V_{cmax} and J_{max}. Assuming infinite internal diffusion conductance (g_m), Michaelis constants of Rubisco for CO_2 (K_c) and O_2 (K_o) at a reference temperature 25°C were assumed to be 40.4 Pa and 24.8 kPa, respectively (von Caemmerer *et al.*, 1994); these values were adjusted to actual leaf temperatures assuming activation energies of 59.4 and 36 kJ mol^{-1} for K_c and K_o, respectively (Farquhar *et al.*, 1980). Fitted parameters were then scaled to a reference temperature of 25°C using activation energies of 64.8 and 37.0 kJ mol^{-1} for V_{cmax} and J_{max}, respectively (Farquhar *et al.*, 1980). Finally, rates of A obtained at ambient CO_2 concentrations of 400 and 2000 μmol mol^{-1} (A_{400} and A_{2000}, respectively) were extracted from the $A \leftrightarrow C_i$ curves and reported separately.

As atmospheric CO_2 was not always saturating for measurements of upland species (due to low atmospheric partial pressure, resulting in insufficient CO_2-saturated rates of A to enable calculate J_{max}), it was likely that J_{max} may have been underestimated in some cases; where this was likely the case (i.e. where there was no clear plateauing of A at high C_i values), we excluded the resultant J_{max} values from the Andean data set. With the exception of a few cases (e.g. *Schefflera* sp.; Fig. 1), $A \leftrightarrow C_i$ curves typically flattened out at high C_i values (> 90% of curves), with A increasing slightly as C_i values increased further (see Fig. 1), suggesting that feedback inhibition of A through limitations in triose-phosphate utilization (TPU) was unlikely.

Leaf structure and chemistry determination

Leaves were collected immediately following the gas exchange measurements. Initially, the leaf mid rib was removed; thereafter, a digital photograph was taken using a high resolution scanner (CanoScan LiDE 210, Vietnam) and later analysed for leaf area (Image J, version 1.38x, NIH, USA). Leaves were then placed in an oven at 70 °C for at least two days, the dry mass measured and leaf mass per unit

leaf area (M_a) calculated for each sample. Total leaf N and P concentrations in dried leaves were extracted using Kjeldahl acid digest method, as detailed in Ayub *et al.* (2011).

Chlorophyll and Rubisco measurements

Leaf discs from the nearest mature leaves adjacent to the gas exchange leaf were collected and transferred to -80 °C cryogenic field container for subsequent chlorophyll and Rubisco assays in the laboratory.

Chlorophyll content of each set of leaf discs was determined using a dual-beam scanning UV-VIS spectrometer (Lambda 25, Perkin-Elmer) after extraction of chlorophyll pigments from two frozen leaf discs (0.77 cm^2 each) with 100% acetone and $MgCO_3$, as outlined in Asner *et al.* (2014b). Chlorophyll a:b ratios varied between 2.45 and 2.75, which is consistent with results of past studies on tropical trees in the Peruvian Amazon (Asner & Martin, 2011).

Protein was extracted from frozen leaf discs following the method outlined in Gaspar *et al.* (1997) with slight modifications (see SM3 in Supporting Information for details on optimization of protein assays). Frozen samples of 0.50 cm^2 were ground in Eppendorf tubes and washed consecutively in 100% methanol, hexane and acetone. Treated leaf powder was then resuspended in protein extraction buffer (140 mM Tris base, 105 mM Tris–HCl, 0.5 mM ethylenediaminetetraacetic acid, 2% lithium dodecyl sulfate (LDS), 10% glycerol) containing 5 mM DTT and protease inhibitor cocktail (Sigma-Aldrich Co, Castle Hill, NSW, Australia), heated for 10 min at 100 °C to completely dissolve extracted protein, then clarified by centrifugation (14,000 x *g*; 10 min; room temperature). The supernatant was used as the source of leaf protein.

Equivalent volumes of supernatant were diluted in 4 × SDS-PAGE sample buffer (Invitrogen - Life Technologies, Carlsbad, CA, USA) then loaded onto gels. Since we extracted protein from a known amount of leaf area, we were able to analyse our samples on an equivalent leaf area basis. Rubisco purified from tobacco with varying concentrations was also loaded onto gels, serving as a

calibration series. Proteins were run on 4-12% NuPAGE Bis-Tris gels (Invitrogen - Life Technologies, Carlsbad, CA, USA) according to the manufacturer's instructions and transferred to Immobilon-P PVDF membranes (Merck Millipore, Kilsyth, Vic., Australia) using an XCell II Blot module (Invitrogen). Membranes were blocked with 5% skim milk powder in Tris-buffered saline containing 0.5% Tween-20 (TBS-T) and an antibody raised in rabbits against tobacco Rubisco (used at 1:5,000) prepared by Spencer Whitney (Research School of Biology, Australian National University, Canberra). Secondary antibody (goat-anti-rabbit-alkaline phosphatase conjugate, Agrisera) was diluted 1:5,000. Blots were visualized using Attophos AP fluorescent substrate system (Promega, Madison, WI, USA) and imaged using a Versa-Doc (Bio-Rad, Hercules, CA, USA) imaging system. Blots were analysed using Quantity One software (Bio-Rad) and relative band densities of each protein determined from duplicate samples, and data averaged. Rubisco concentration was calculated from the large subunit (molecular mass of 55 kD and 16% N by weight).

Estimation of N allocation in photosynthetic metabolism

N allocation in three major components (pigment-protein complexes, electron transport and Rubisco) for all leaves was estimated from chlorophyll concentration, V_{cmax} and J_{max} respectively. N allocation to pigment-protein complexes (n_P) was calculated by assuming 44 mol N per mol of chlorophyll (Evans, 1989). N allocation to Rubisco (n_R) was estimated from values of V_{cmax} according to Harrison *et al.* (2009), with slight modification [2.33 mol CO_2 (mol Rubisco sites)$^{-1}$ s^{-1} for the catalytic turnover number of Rubisco at 25 °C (Harrison *et al.*, 2009)]. We assumed all Rubisco was fully activated and mesophyll conductance was infinite. The allocation of N to electron transport components (n_E) was calculated from J_{max} assuming 160 mol electrons (mol cytochrome *f*)$^{-1}$ s^{-1} and 8.85 mol N (mmol cytochrome *f*)$^{-1}$ (Evans & Seemann, 1989). The proportion of total leaf N allocated to each photosynthetic component was calculated by dividing the N investment in each component by the N content per unit leaf area.

Data analysis

Log_{10} transformations were carried out on leaf traits when necessary to ensure normality and minimize heterogeneity of residuals. Student *T*-tests (two-tailed) were used to compare overall means of lowland and upland species. Standardized major axis (SMA) estimation was used to describe the best-fit relationship between pairs of variables and to assess whether relationships differed between lowland vs upland elevation classes, using SMATR Version 2.0 software (Falster *et al.*, 2006; Warton *et al.*, 2006). The decision to compare upland and lowland trait relationships reflects the strong elevation contrast in environments, phylogeny, floristic composition and forest structure (Gentry, 1988; van de Weg *et al.*, 2009; Asner *et al.*, 2014b). Significance of SMA regression was tested at $\alpha = 0.05$.

In addition to the above bivariate analyses, we also used a mixed-effects linear model combining fixed and random components (Pinheiro & Bates, 2000) to account for variability in area- and N-based rates of V_{cmax}, and area-based rates of J_{max}, where the linear mixed-effects model combined fixed and random components. This approach enabled the structured nature of the data set to be recognized, and for interactions between multiple terms to be considered. The fixed effect included continuous variables only: leaf traits (M_a, area-based leaf N and P), and environment variables (soil P and N concentration, mean annual temperature (MAT) and effective cation exchange capacity of soil (ECEC)). Model specification and validation was based on the protocols outlined in Zuur *et al.* (2009) and fitted using the *nlme* package (R package ver. 3.1–105, R Foundation for Statistical Computing, Vienna, Austria, R Development Core Team 2011). Details on the model selection process are provided in Table S6. Briefly, phylogeny (family/genus/species) were treated as random effects, placing focus on the variation contained within these terms, rather than mean values for each level. For the mixed-effects linear model, site variation was captured by soil and environmental factors considered in the fixed component; because of this, no site term was included in the random component. Model comparisons and the

significance of fixed-effects terms were assessed using Akaike's information criterion (AIC). Unless otherwise stated, statistical analysis was performed using SPSS version 20 (IBM Corporation, NY, USA).

Results

Variations in leaf chemistry and structure

Among lowland sites, there was a six-fold variation in leaf N:P ratios (7.6 - 45.9) (Table S1, Supporting Information), but for upland sites, when ranked according to increasing elevation, mean values of leaf N:P were largely consistent across sites of similar elevation (Table 1). Across all sites (lowland and upland combined), variations in leaf N:P ratios were predominantly driven by variations in leaf [P] (r^2=0.59, p<0.01; Table S2) rather than leaf [N]. Variations in area-based leaf [P] (P_a) were positively correlated with soil [P] (r^2=0.37, p<0.01) and elevation (r^2=0.48, p<0.01). Weaker positive associations were observed for area-based leaf [N] (N_a) with total soil [N] (r^2=0.10, p<0.01) and elevation (r^2=0.14, p<0.01).

Leaf mass per unit leaf area (M_a) varied widely, both among and within lowland (54-230 g m^{-2}) and upland (60-249 g m^{-2}) sites (Table 1 and Table S1). Although variations in M_a were not correlated with variations in soil [P], there were significant (but weak) correlations between M_a and total soil [N] (r^2=0.04, p<0.01) and elevation (r^2=0.03, p<0.01) (Table S2). Overall means of M_a for the sampled upland species (143±39 g m^{-2}) were significantly higher than that of the lowland species (132±35 g m^{-2}; Table 2, p<0.05).

Across all 18 sites, leaf N_a was positively correlated with M_a (p<0.01, r^2=0.12; Table S2), with the $N_a \leftrightarrow M_a$ relationship being stronger among upland than lowland sites (r^2=0.07 for lowland sites and r^2=0.20 for upland; see Table S3 for p-values, slopes and intercepts of each SMA relationship). The slope and intercept of the relationship differed between the two elevation classes (Fig. 2A) - upland species exhibited higher N_a for a given M_a than lowland species, particularly in low M_a species. Across all sites, leaf P_a exhibited a weak, positive

correlation with M_a (p<0.01, r^2=0.04; Table S2). Similarly, a weak positive $P_a \leftrightarrow M_a$ relationship (p=0.003, r^2=0.04; Table S3) was found among upland species (Fig 2B). Although no significant $P_a \leftrightarrow M_a$ relationship was found among lowland species (with leaf P_a varying 20-fold; Table S1), mean values of P_a at a given M_a were lower than their upland counterparts.

Variations in photosynthetic metabolism

Light-saturated rates of photosynthesis per unit leaf area, measured at the prevailing day-time air temperature (T) at each site and at an atmospheric CO_2 concentration of 400 μmol mol^{-1} ($A_{400,a}$), differed among co-occurring species (Table S1). However, there was no significant difference between mean values of $A_{400,a}$ from lowland and upland classes (Table 2). This uniformity of $A_{400,a}$ occurred despite significantly lower measuring Ts at the high elevation sites [overall means: lowland 29.4 ± 0.9°C; upland 25.7 ± 2.1°C, p<0.05] and lower intercellular CO_2 partial pressure (C_i) (overall means: lowland 28.4 ± 3.7 Pa; upland 18.8 ± 3.0 Pa, p<0.05) (Table S4). Assessed on a per unit leaf N basis ($A_{400,N}$), average rates were lower at the upland sites compared to their lowland counterparts (Tables 2 and S4), reflecting higher leaf N_a for trees at high elevation (Table 1). Across sites, mean $A_{400,N}$ decreased with decreasing mean annual temperature (MAT) (Figure S1D). Area-based rates of photosynthesis at elevated CO_2 ($A_{2000,a}$) were higher in upland (17.1-26.5 μmol m^{-2} s^{-1}; Table S4) than lowland (16.1-22.6 μmol m^{-2} s^{-1}) species (p<0.05). The higher values of $A_{2000,a}$ at the upland sites were achieved despite the colder temperatures. On a per unit leaf N basis ($A_{2000,N}$), average rates were similar for both elevation classifications (Table S4; Fig. S1E).

To explore differences in rates of the underlying components of net photosynthesis, we compared maximal area-based rates of CO_2 fixation by Rubisco ($V_{cmax,a}$) and photosynthetic electron transport ($J_{max,a}$), using values normalized to a measuring temperature of 25 °C (i.e. $V_{cmax,a}^{25}$ and $J_{max,a}^{25}$). Site mean values of $V_{cmax,a}^{25}$ and $J_{max,a}^{25}$ were significantly higher in the upland class ($V_{cmax,a}^{25}$ and $J_{max,a}^{25}$ were 36 and 45% higher, respectively, in the upland class;

Table 2; $p<0.05$), reflecting the parameters' negative relationships with MAT (Fig. S1A, B). Similarly, the mean $V_{cmax,N}$ at 25 °C ($V_{cmax,N}^{25}$) of the upland group was greater than that of lowland counterparts (Table 2; $p<0.05$). Thus, when assessed at a common T and when controlling for elevation differences in C_i (by adopting V_{cmax}), photosynthetic N use efficiency was, on average, greater at high elevations. Importantly, considerable within-site variability was observed for all three parameters ($V_{cmax,a}^{25}$, $J_{max,a}^{25}$, and $V_{cmax,N}^{25}$) (Fig. 3; Table S1), highlighting the heterogeneity of these key photosynthetic traits among trees within each site. Within-site variability was particularly pronounced at the upland sites (Fig. 3; Table S1).

Variations in $J_{max,a}^{25}$ were strongly correlated with $V_{cmax,a}^{25}$, both for lowland ($r^2=0.59$) and upland classifications ($r^2=0.75$) (Fig. 4). Overall, the $J_{max,a}^{25} \leftrightarrow V_{cmax,a}^{25}$relationship was similar in the two elevation groups, with mean $J_{max,a}^{25}$:$V_{cmax,a}^{25}$ ratios being statistically equivalent in lowland and upland classes (Table 2). Importantly, marked differences in $J_{max,a}^{25}$:$V_{cmax,a}^{25}$ ratios were observed among individuals (Figs 3 and 4), underpinned by fundamental differences in the CO_2 response of net photosynthesis (e.g. Fig. 1B). In most leaves, $J_{max,a}^{25}$ and $V_{cmax,a}^{25}$ co-varied, resulting in relatively constant $J_{max,a}^{25}$:$V_{cmax,25}$ ratios, as illustrated by data from individual plants of *Cecropia angustifolia* and *Glycydendron amazonicum* where the $J_{max,a}^{25}$:$V_{cmax,a}^{25}$ ratio was 1.8 (Fig. 1A and Fig. 4). However, some leaves exhibited high $V_{cmax,a}^{25}$ but low $J_{max,a}^{25}$ (Fig. 1B; individual of *Schefflera* sp., where $J_{max,a}^{25}$: $V_{cmax,a}^{25}$ = 1.1) while other leaves with a similar $V_{cmax,a}^{25}$ had markedly higher $J_{max,a}^{25}$ (e.g. the *Citronella incarum* individual in Fig. 1B) leading to a higher $J_{max,a}^{25}$:$V_{cmax,a}^{25}$value (2.4). Such variations in $J_{max,a}^{25}$ and $V_{cmax,a}^{25}$ likely reflect intra- and/or inter-specific variations in relative allocation of N allocation to Rubisco versus electron transport/bioenergetics.

Bivariate relationships

Across all 18 sites, $V_{cmax,a}^{25}$ and $J_{max,a}^{25}$ exhibited positive correlations with soil P, soil N and elevation, and negative correlations with MAT (Table S2); the strength

447 of these relationships was greater for $J_{max,a}^{25}$ than $V_{cmax,a}^{25}$. Relationships with
448 MAP were either weak ($J_{max,a}^{25}$) and not significant ($V_{cmax,a}^{25}$) (Table S2). Across all
449 sites, variations in $V_{cmax,a}^{25}$ and $J_{max,a}^{25}$ were also correlated with leaf chemical
450 composition traits (Table S2), with bivariate relationships being stronger against
451 P_a ($p<0.01$, $r^2= 0.11$ for $V_{cmax,a}^{25}$, $r^2= 0.13$ for $J_{max,a}^{25}$) than N_a ($p<0.01$, $r^2= 0.05$ for
452 both $V_{cmax,a}^{25}$ and $J_{max,a}^{25}$). Leaf N:P ratios exhibited weak, negative correlations
453 with $V_{cmax,a}^{25}$ and $J_{max,a}^{25}$ ($p<0.01$, $r^2= 0.08$ for $V_{cmax,a}^{25}$, $r^2= 0.06$ for $J_{max,a}^{25}$; Table
454 S2). No significant relationship was found between $V_{cmax,a}^{25}$ and M_a, whereas the
455 $J_{max,a}^{25} \leftrightarrow M_a$ relationship was significant ($p<0.05$, $r^2= 0.04$; Table S2).
456 When assessed among upland sites, no significant relationships were
457 found between $V_{cmax,a}^{25}$, M_a, N_a, P_a or N:P ratio (Fig. 5A-D). For lowland sites,
458 $V_{cmax,a}^{25}$ was positively related with P_a ($p=0.013$, $r^2= 0.04$; Table S3) and N_a
459 ($p=0.050$, $r^2=0.02$; Table S3), but not leaf N:P ratio or M_a (Fig 5A-D). The absence
460 of a N:P effect for upland or lowland classes was consistent with SMA analyses
461 comparing the slopes of $V_{cmax,a}^{25} \leftrightarrow N_a$, $V_{cmax,a}^{25} \leftrightarrow P_a$ and $V_{cmax,a}^{25} \leftrightarrow M_a$ for the
462 lowland class, split according to leaf N:P ratios below and above 20 - this ratio
463 generally being thought to be roughly indicative of the N:P above which
464 physiological processes are more likely to be limited by P as opposed to N (and
465 vice versa) (Güsewell, 2004). No significant difference in slopes of the relationships
466 were found ($p>0.05$, data not shown). Similar patterns were observed for $J_{max,a}^{25}$
467 (Fig. 5E-H), which was positively related with N_a ($p=0.012$, $r^2=0.05$; Table S3) and
468 P_a ($p=0.002$, $r^2= 0.08$; Table S3) for the lowland class only.
469 Investigating whether variations in photosynthetic N use efficiency were
470 related to M_a, both across all sites (Table S2) and within each elevation class (Fig.
471 6A), there was no significant $V_{cmax,N}^{25} \leftrightarrow M_a$ relationship across all 18 sites (Table
472 S2) or within the upland elevation class (Table S3). Nevertheless, for the lowland
473 class, a weak negative $V_{cmax,N}^{25} \leftrightarrow M_a$ relationship was observed ($p=0.01$; Table S3).
474 On average, $V_{cmax,N}^{25}$ at a given M_a was higher in upland species than their lowland
475 counterparts. With respect to foliar phosphorus, there was no significant
476 relationship between $V_{cmax,N}^{25}$ and leaf P_a or with leaf N:P when considering the

elevation classes separately. This conclusion was held for $V_{cmax,N}^{25} \leftrightarrow P_a$ when combining upland and lowland data (Table S2). For $V_{cmax,N}^{25} \leftrightarrow$N:P, combining upland and lowland data resulted in a weak significant relationship ($p<0.05$, r^2 = 0.02; Table S2); similarly, relationships between $V_{cmax,N}^{25}$ and soil P, soil N and elevation were relatively weak (Table S2). Collectively, these results show that the proportion of the variance in $V_{cmax,N}^{25}$ accounted for by the above soil and leaf level parameters was negligible.

Variation in N-allocation patterns

To further explore what factors might contribute to variations in $V_{cmax,N}^{25}$, we calculated the fraction of leaf N allocated to photosynthesis (n_A); n_A is dependent on the allocation of leaf N to Rubisco (n_R), electron transport (n_E) and pigment-protein complexes (n_P). Figure 7 shows that mean values of n_A and its underlying components exhibited relatively little variation across sites. Nevertheless, inter-specific variations were evident at each site, with n_R varying up to seven-fold at some sites (e.g. CUZ-03; 0.03-0.20; Table S1). A large proportion of N was inferred to be allocated in pigment-protein complexes, with n_P being greater than n_R and n_E combined. The overall mean of n_R for the upland class (0.105) was significantly higher than that for the lowland class (0.090; Table 2, $p<0.05$). Similarly, n_E was higher for upland (0.034) than for lowland groups (0.028; Table 2, $p<0.05$). There was no difference between the elevation classes in n_P. Overall, n_A was similar in the lowland and upland groupings (37-38%; Table 2).

There was considerable variability in n_A among lowland and upland species (0.1 to 0.6), with significant negative correlations being found with M_a, N_a and P_a for the lowland group (Fig. 8, Table S5). Similar significant correlations existed for the upland class but with the important caveat that upland species consistently exhibited higher n_A at a given N_a and P_a (Figs. 8 and S2; Table S5). Thus, while mean values of n_A were similar in upland and lowland species, the fraction of leaf N allocated to photosynthesis was greater in upland plants when comparisons were made at common leaf N_a and P_a values.

Validation of Rubisco estimates by in vitro *assays*

We used *in vitro* Rubisco assays on 16 lowland species (Fig. 9A) to quantify n_R, thus allowing direct comparison of n_R obtained for these *in vitro* assays with that of the *in vivo* estimates derived from $V_{cmax,a}^{25}$. Figure 9B shows that there was considerable discrepancy between *in vitro* and *in vivo* predicted n_R. If one assumes that the *in vitro* values provide an estimate of potential Rubisco capacity, and that the *in vivo* values are indicative of the realized maximum rate in intact tissues, then it is possible that the *in vivo* approach underestimates the proportion of N allocated in Rubisco. Reliance on the *in vitro* values resulted in marked increases in n_R at a given M_a, albeit with the overall pattern of increasing n_R with decreasing M_a still held (Fig. S3A). Considering the overall N investment pattern in photosynthetic metabolism, adopting *in vitro* estimates of n_R resulted in marked increases in the total fraction of N allocated to photosynthesis compared to *in vivo* (Fig. S4). Indeed, in some cases *in vitro* estimates of N allocation to Rubisco was similar to, or even higher than, N allocation to pigment protein complexes (Fig. S4). Collectively, these results suggest that the answer to the question '*how much leaf N is allocated to photosynthesis'* will depend on whether *in vivo* or *in vitro* estimates of n_R are used in the underlying calculations.

Modelling variations in $V_{cmax,a}^{25}$, $J_{max,a}^{25}$ *and* $V_{cmax,N}^{25}$

We used linear mixed-effects to model variations in $V_{cmax,a}^{25}$, $J_{max,a}^{25}$ and $V_{cmax,N}^{25}$; the starting model included only continuous terms for leaf traits and environmental variables. Additional details of the model selection procedure are provided in Table S6. When presented with information on soil and leaf P and N as key nutrients driving maximum carboxylation capacity of Rubisco, the final preferred model for $V_{cmax,a}^{25}$ (model 6, Table S6) retained P only, suggesting an increase of $V_{cmax,a}^{25}$ as soil and foliar P increase (Table 3). A combination of site-level soil P and individual-level foliar P as fixed effects, and family as a random effect, explained 39% of the variation in $V_{cmax,a}^{25}$ (Fig. S5). Inclusion of MAT, soil

N, leaf N_a, M_a and effective cation exchange capacity of soils as fixed effects did not improve the criteria score (Table S6). The model's variance components, as defined by the random term, indicated that family accounted for only 2.5% of the unexplained variance (i.e. the response variance not accounted for by the fixed terms) (Table 3). Finer phylogenetic detail (genera and species) did not improve the model. A review of diagnostic plots from the final preferred model showed that inclusion of elevation class did not improve model performance, when a range of environmental variables that describe the elevation gradient (e.g. soil P, soil N and MAT) were included. Hence, it was not necessary to include elevation class in the fixed components of the mixed-effects model.

Similar to $V_{cmax,a}^{25}$, variations in $J_{max,a}^{25}$ were largely accounted for by a combination of site-level soil P and individual-level foliar P, with $J_{max,a}^{25}$ increasing with increasing soil and foliar P (Table 3); the final model explained 44% of the variation in $J_{max,a}^{25}$ (Fig. S5). The preferred model (determined by assessing the effect of dropping sequentially explanatory variables; Table S6) did not retain soil N, leaf N_a, M_a or MAT (Table S6). For the random effects, family contributed 2.8% to the unexplained variance (Table 3).

For $V_{cmax,N}^{25}$ (i.e. photosynthetic N use efficiency), we attempted to construct a model using combinations of soil and leaf P, soil and leaf N, soil ECEC, and climate (MAT). However, in contrast to $V_{cmax,a}^{25}$ and $J_{max,a}^{25}$, $V_{cmax,N}^{25}$ model performance was not improved via sequential deletion of explanatory terms; thus, the inputted soil, climate and leaf variables did not permit identification of the key factors influencing variation in $V_{cmax,N}^{25}$. This suggests that other factors, such as how leaf N is allocated and/or whether Rubisco is fully active may have played a role.

Discussion

Regional and inter-biome context

Past studies on tropical and non-tropical forests revealed variability in the slope

of $V_{cmax,a}^{25} \leftrightarrow N_a$ relationships, with lower rates of V_{cmax} per unit N in nutrient-poor, lowland tropical forests compared to lowland forests on more fertile soils, upland tropical forests and temperate broadleaf forests (Carswell *et al.*, 2000; Domingues *et al.*, 2007; Meir *et al.*, 2007; Kattge *et al.*, 2009; Domingues *et al.*, 2010; Mercado *et al.*, 2011; van de Weg *et al.*, 2012). Moreover, Reich *et al.* (2009) concluded that the slope of mass-based $A \leftrightarrow N$ relationships is lower in the tropics than in colder arctic and temperate biomes. Our study supports such studies, with $V_{cmax,N}^{25}$ values for our upland and lowland TMFs (22.5 and 18.9 μmol CO_2 g N^{-1} s^{-1}, respectively) being markedly lower than reported for temperate broadleaved trees [34 μmol CO_2 g N^{-1} s^{-1} (Kattge *et al.*, 2009)].

How do our results compare with other analyses of photosynthetic capacity in tropical ecosystems? The range of $V_{cmax,a}^{25}$ (6–96 μmol m^{-2} s^{-1}; Table S1) and $J_{max,a}^{25}$ (21 –176 μmol m^{-2} s^{-1}; Table S1) values from our study were wider than those reported for drier tropical sites in West Africa (Domingues *et al.*, 2010), perhaps reflecting environmental differences, or differences in the number of species sampled (210 here versus 39 in the West African study). For our lowland TMFs (which included three low nutrient status white sand sites in Northern Peru), the overall mean $V_{cmax,a}^{25}$ (36±15 μmol m^{-2} s^{-1}) was lower than previously reported tropical values: Carswell *et al.* (2000): 43 μmol m^{-2} s^{-1}; Domingues *et al.* (2007): 53 μmol m^{-2} s^{-1}; Meir *et al.* (2007): 49-68 μmol m^{-2} s^{-1}; Kattge *et al.* (2009): 41 μmol m^{-2} s^{-1} (non-oxisol); Bloomfield *et al.* (2014a): 63 μmol m^{-2} s^{-1}; Domingues *et al.* (2015): 39-46 μmol m^{-2} s^{-1}. By contrast, our mean $V_{cmax,a}^{25}$ values were higher than the values for lowland TMFs only growing on nutrient-poor, oxisol [29 μmol m^{-2} s^{-1} (Kattge *et al.*, 2009)]. Since $J_{max,a}^{25}$ was tightly correlated with $V_{cmax,a}^{25}$ (Fig. 4), our estimates of $J_{max,a}^{25}$ for lowland TMFs were also lower than those reported in above-mentioned studies. Rates of $V_{cmax,a}^{25}$ at our upland sites (49±20 μmol m^{-2} s^{-1}) were similar to those reported by van de Weg *et al.* (2012): 56 μmol m^{-2} s^{-1} for the same Andean region, and fell mid-range of values reported in Dusenge *et al.* (2015) and Vårhammar *et al.* (2015) for high elevation tropical trees of Rwanda.

Taken together, our results support the hypothesis that both $V_{cmax,a}^{25}$ and photosynthetic N efficiency are lower in lowland TMFs than in temperate broadleaved forests. In addition, each parameter is highly variable, both among co-existing tropical species growing at individual sites and between environmentally-contrasting sites.

Phosphorus –does it modulate photosynthetic capacity and/or N-use efficiency?

Our site selection aimed to assess the potential role of phosphorus-limitation on photosynthetic performance across TMFs in western Amazonia and the Andes where substantial variations in soil P occur (lowland sites: 38-727 mg P kg^{-1}; upland sites: 496-1631 mg P kg^{-1}). Low P availability can limit rates of photosynthesis via reduced maximal rates of RuBP regeneration (i.e. J_{max}), with maximal Rubisco activity (i.e. V_{cmax}) also often being reduced (Brooks, 1986; Jacobs & Lawlor, 1992; Loustau *et al.,* 1999). While the mechanisms responsible for reduced V_{cmax} remain uncertain, possible factors include the need to maintain co-limitation by RuBP regeneration and carboxylation, as well as feedback inhibition on Rubisco resulting from inability to export triose phosphates to the cytosol (Wullschleger, 1993; Walker *et al.,* 2014).

The hypothesis that photosynthetic capacity would be positively correlated with soil [P] and leaf P_a was supported by our results – a finding consistent with earlier studies on tropical species in South America, West Africa and Australia (Domingues *et al.*, 2007; Meir *et al.*, 2007; Kattge *et al.*, 2009; Domingues *et al.*, 2010; Bloomfield *et al.*, 2014b). Among lowland sites alone, and the combination of lowland and upland sites together, significant positive relationships were observed between photosynthetic capacity (expressed either as $V_{cmax,a}^{25}$ or $J_{max,a}^{25}$) and foliar P_a, and against soil [P] (Tables S2, S3). Across all 18 TMF sites, $V_{cmax,a}^{25}$ and $J_{max,a}^{25}$ also exhibited significant negative relationships with leaf N:P (Table S2). Moreover, foliar P_a and soil [P] emerged as significant explanatory variables in linear mixed-effect models of variations in photosynthetic capacity (Table 3), accounting for ~40% of the observed variations in $V_{cmax,a}^{25}$ and $J_{max,a}^{25}$. The

absence of mean annual temperature (MAT) in the preferred models suggest that, while growth temperature can affect photosynthetic capacity (Hikosaka *et al.*, 2006; Sage & Kubien, 2007) and patterns of N investment, knowledge of growth temperature along the western Amazon-Andes elevation gradient is not required when data on leaf and soil P is available.

Past studies reported that P-deficiencies also reduce photosynthetic N use efficiency (Reich *et al.*, 2009) and the fraction of leaf N allocated to photosynthesis (Warren & Adams, 2002). While average values $V_{cmax,N}$ and foliar [P] were highest in our upland trees, no significant $V_{cmax,N} \leftrightarrow P_a$ relationships were observed, either across all sites or within each elevation class. Furthermore, we could not identify key factors explaining variation in $V_{cmax,N}$ using linear mixed-effects models; this included models that contained data on soil and foliar [P]. While this does not preclude a role for deficiencies in cytosolic [P] in regulating *in vivo* values of $V_{cmax,N}$, it seems unlikely that either soil or total leaf [P] can be used a predictor of variations in *in vivo* Rubisco capacity per unit leaf N.

Activation state of Rubisco

In vitro quantification in several lowland TMF species revealed that Rubisco content inferred from CO_2 response curves may have substantially underestimated absolute levels of this key protein (Fig. 9). When estimating Rubisco abundance from $A \leftrightarrow C_i$ curves, Rubisco is assumed to be fully activated – however, there is growing evidence that Rubisco often operates at less than maximum activity or is in excess of CO_2 fixation requirements (Stitt & Schulze, 1994; Warren *et al.*, 2000). Partial activation could be linked to limitations in sink demand for carbohydrates and/or co-limitation by other rock-derived nutrients such as calcium [e.g. Asner *et al.* (2014b)]. Inactive Rubisco might serve as a temporary N store - as such, Rubisco can act as both a metabolic and non-metabolic protein (Stitt & Schulze, 1994; Warren *et al.*, 2000). Viewed from this perspective, *in vivo* estimates of V_{cmax} provide insights into N investment into the *metabolically active* Rubisco, relevant when modelling gross primary productivity

of TMF ecosystems. However, if the objective is to assess how plants differ in N investment in both active and inactive forms of Rubisco, then n_R estimated from other approaches, such as Western blots (or similar quantitative techniques) might be required.

As noted earlier, the observed values of $V_{cmax,N}^{25}$ were lower than that of trees growing in temperate environments (Kattge *et al.*, 2009). Similarly, when compared at any given M_a, *in vivo* estimates of n_R (i.e. fraction of leaf N allocated to Rubisco estimated from gas exchange) were, on average, lower in our TMF trees compared to the global average (Hikosaka, 2004; Wright *et al.*, 2004) (Fig. S3). By contrast, *in vitro* estimates of n_R (i.e. n_R estimated from Western blots) were often higher than the global average (Fig. S3). This finding raises the possibility that the efficiency of N investment in Rubisco may not necessarily be lower in TMFs; rather, it may be that the activation state is lower in tropical forests compared with their temperate counterparts. Further work is needed to explore this question; additional work is also needed to determine what role, if any, limitations in mesophyll conductance (g_m) have on estimates of V_{cmax} and the associated values of n_R.

Additional factors influencing V_{cmax} estimates

In our study, we have so far estimated *in vivo* rates of $V_{cmax,a}^{25}$ assuming a common, single set of kinetic constants (K_c and K_o) for Rubisco (von Caemmerer *et al.*, 1994) and associated activation energies (E_a) (Farquhar *et al.*, 1980), as well as infinite g_m. Such assumptions were made necessary in the absence of K_c, K_o, E_a and g_m values for tropical species. Application of different K_c and K_o values, such as those reported by Bernacchi *et al.* (2002), would alter estimates of $V_{cmax,a}^{25}$ for all trees but would not alter relative differences among sites or elevational classes. By contrast, application of Bernacchi *et al.* (2002) E_a values for K_c and K_o (80.99 and 23.72 kJ mol^{-1}, respectively), and V_{cmax} (65.3 kJ mol^{-1}) could potentially relative differences in $V_{cmax,a}^{25}$ between upland and lowland trees, depending on the extent to which leaf temperatures differed among the sites. Similarly, replacement

687 of the Farquhar *et al.* (1980) E_a values of V_{cmax} and J_{max} (of 64.8 and 37.0 kJ mol^{-1},
688 respectively) with those of Bernacchi *et al.* (2002) (65.3 and 43.9 kJ mol^{-1},
689 respectively) could alter the relative differences in $V_{cmax,a}^{25}$ and $J_{max,a}^{25}$ between
690 upland and lowland sites. To check whether application of alternative E_a values
691 change our conclusions regarding site-to-site differences, we calculated $V_{cmax,a}^{25}$
692 and $J_{max,a}^{25}$ using the respective activation energies of Farquhar *et al.* (1980) and
693 Bernacchi *et al.* (2002). Use of the Bernacchi *et al.* (2002) E_a values resulted in an
694 average 10.6% increase in estimates of V_{cmax25} for lowland trees (Table S7),
695 reflecting the fact that lowland leaf temperatures were near 30°C (Table S4).
696 Upland estimates were less affected (3.5% increase; Table S7) as the average leaf
697 temperature of upland group was 25.7˚C (Table S4). Despite the increased
698 estimates of V_{cmax25} for lowland trees when using E_a values from Bernacchi *et al.*
699 (2002), there remained a significant difference between lowland and upland mean
700 V_{cmax25} values (Table S7); the same was true for $J_{max,a}^{25}$ (Table S7). As a result,
701 relationships between photosynthetic properties and site MAT and soil P were
702 similar when using Farquhar *et al.* (1980) and Bernacchi *et al.* (2002) E_a values (Fig.
703 S1). Thus, irrespective of which E_a values are used [see Medlyn *et al.* (2002) for
704 further discussion the temperature dependence of these constants], we are
705 confident that that mean values of V_{cmax25} and $J_{max,a}^{25}$ are indeed higher in the
706 upland plants growing in the Peruvian Andes.
707 What impact might systematic differences in g_m between upland and
708 lowland TMFs have on our results? If g_m was finite, but similar in upland and
709 lowland TMF environments, then our conclusion that $V_{cmax,a}^{25}$ is higher in upland
710 species would hold (albeit with modified values). However, if g_m was more limiting
711 in lowland TMF trees than their upland counterparts, then calculation of V_{cmax}
712 using A-C_c curves might fail to differentiate between the upland and lowland
713 groups. A definitive assessment of this issue will require further work assessing
714 g_m in tropical trees (e.g. using concurrent measurements of leaf as exchange and
715 carbon isotope discrimination or chlorophyll fluorescence). Although g_m tends to
716 decrease with increasing M_a (Flexas *et al.*, 2008), the M_a difference between

717 lowland and upland groups was small (Table 1). Given the potential for large
718 variations in g_m among species (at a given M_a), it is unlikely that g_m would have
719 been higher in the selected lowland TMF trees. Irrespective of the effect of
720 elevation on g_m, rates of $A_{40,a}$ and $A_{200,a}$ (measured at prevailing leaf *T*s) were
721 surprisingly high in plants at the cooler, high elevation sites (Table S4). Given this
722 and our extensive sample size, we feel confident that photosynthetic capacity at
723 a standardised *T* is likely larger in trees growing at high elevations in the Andes
724 compared to those in the lowland regions of Amazonia, as proposed by van de
725 Weg *et al.* (2012; 2014). Enhanced photosynthetic capacity at high altitude could
726 help negate the inhibitory effects of low *T* on leaf-level CO_2 uptake, with the result
727 that gross primary productivity (GPP) would not decline with increasing elevation
728 as much as expected.

729 Recent modelling of C-exchange processes at a high elevation TMF site
730 (3025 m a.s.l.) in Peru suggested that gross primary productivity (GPP) may be 20-
731 40% lower compared to lowland TMFs (Girardin *et al.*, 2014a; van de Weg *et al.*,
732 2014); low *T* appeared to be most important factor limiting GPP at high elevations
733 (van de Weg *et al.*, 2014). Our results suggest that the inhibitory effect of low *T*
734 on GPP of upland TMFs would be greater if photosynthetic capacity remained
735 constant across the elevation gradient. Thus, the greater photosynthetic capacity
736 of upland TMFs might contribute to GPP being relatively homeostatic across the
737 Peruvian Amazon-Andes elevation gradient. Further work is needed to explore
738 how elevation-dependent variations in photosynthetic capacity impact on current
739 and future net primary productivity (NPP) of TMFs, when taking into account
740 other NPP components (e.g. leaf area index, biomass allocation, litter fall,
741 autotrophic respiration).

742

743 *Concluding statements*

744 Our findings reveal greater photosynthetic capacity in Andean forest leaves
745 compared to lowland western Amazonian leaves, underpinned by greater
746 concentrations of leaf N and N-use efficiency per unit leaf area (Table 2, Fig. 8).

Our data also support the hypothesis that variations in leaf and soil P play key role in modulating photosynthetic capacity of TMFs (Fig. 5, Table 3 and S2), with the mixed-effects models (Table 3) providing the modelling community with predictive equations that will enable model parameterization based arguably the largest single tropical V_{cmax} datasets available. Finally, our analyses indicate that a substantial fraction of Rubisco is inactive in trees growing in the Peruvian Amazon and suggest that a greater fraction of leaf N may well be invested in photosynthetic machinery than indicated by leaf gas exchange measurements.

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Author Contributions

O.K.A., J.L., P.M., Y.M., O.L.P., G.P.A., R.E.M., F.Y.I., L.K.W., R.G., O.S.O., N.H.A.B., J.R.E. and B.M.L. planned and designed the research. N.H.A.B., F.Y.I., L.K.W., R.G., O.S.O., K.J.B., G.P.A., R.E.M., J.L., Y.M., N.S., E.G.C., T.D., C.A.Q., F.S., A.E.V., P.P.Z.C., J. dA.-P., K.Q.H., I.C.T., R.B.L., Y.P.T., J.H.O. and O.K.A conducted fieldwork and/or analysed field-based data. N.H.A.B., F.Y.I., G.P.A., R.E.M., B.M.L. and J.R.E. performed laboratory experiments and analysed chemical/biochemical data. N.H.A.B., O.K.A., K.J.B., J.L., O.L.P., P.M., G.P.A., J.M., O.S.O., R.G., L.K.W., J.R.E. and B.M.L. wrote the manuscript.

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Supporting Information

Additional supporting information may be found in the online version of this article.

SM1: Additional study site details

SM2: Identification of outliers and $A \leftrightarrow C_i$ curve methodological details

SM3: Optimization of protocols for protein extraction from the leaves of recalcitrant tree species

Table S1. Summary of species sampled at each site and their parameters

Table S2. Pearson correlations for bivariate relationships among leaf traits and environmental parameters

Table S3. Standardized major axis regression slopes for relationships in Figs 2, 4, 5 & 6

Table S4. Means ± standard deviation of leaf physiology and chemistry, expressed on area basis for each site

Table S5. Standardized major axis regression slopes for relationships in Figs 8 & S2

Table S6: Stepwise selection process for the fixed component of the linear mixed effect model to determine the best predictive model given in Table 3

Figure S1. Plots of photosynthetic parameters against mean annual temperature and soil [P] for each site

Figure S2. Plots of % n_P, % n_R, and % n_E, in relation to M_a, N_a, and P_a

Figure S3. Plots of fraction of leaf N allocated in Rubisco, n_R in relation to leaf mass per unit leaf area, M_a

Figure S4. Stacked graph show n_E, n_P and n_R (*in vivo* and *in vitro*) for individual leaves

Figure S5. Plots for linear mixed-effects model goodness of fits, including fixed and random terms for $V_{cmax,a}^{25}$ and $J_{max,a}^{25}$

Figure S6: Comparison of $V_{cmax,a}^{25}$ in upland and lowland plants calculated using different activation energies

Table 1: Description of the sampled Peruvian field sites.

Category	Site Code	Latitude	Longitude	Elevation (m a.s.l.)	No. of species	MAT (°C)	MAP (m)	Atm. Pressure (kPa)	Soil classification	Total soil		Leaf chemistry			
										[N] ($g\ kg^{-1}$)	[P] ($mg\ kg^{-1}$)	Leaf N_a ($g\ m^{-2}$)	Leaf P_a ($g\ m^{-2}$)	Leaf N:P	M_a ($g\ m^{-2}$)
Lowland	SUC-05	-3.2558	-72.8942	132	20	26.2	2.75	100	Alisols	1.9	276	1.94 ± 0.61	0.06 ± 0.04	30.1 ± 7.03	129 ± 31
	TAM-05	-12.8309	-69.2705	223	8	24.4	1.90	99	Cambisols	1.6	256	2.14 ± 0.27	0.08 ± 0.02	28.6 ± 9.49	119 ± 27
	JEN-11	-4.8781	-73.6295	131	18	26.6	2.70	100	Acrisols	1.8	141	2.12 ± 0.52	0.06 ± 0.02	27.9 ± 10.4	144 ± 37
	ALP-01	-3.9500	-73.4333	120	18	25.2	2.69	100	Gleysols	0.6	110	1.90 ± 0.40	0.08 ± 0.03	26.2 ± 8.62	119 ± 24
	SUC-01	-3.2519	-72.9078	117	17	26.2	2.75	100	Plinthosols	1.7	305	1.81 ± 0.63	0.09 ± 0.03	22.1 ± 4.99	123 ± 27
	JEN-12	-4.8990	-73.6276	135	19	26.6	2.70	100	Podzols	6.9	133	1.97 ± 0.52	0.09 ± 0.05	21.9 ± 10.42	156 ± 31
	ALP-30	-3.9543	-73.4267	150	21	25.2	2.69	100	Arenosols	0.8	38	1.67 ± 0.47	0.09 ± 0.04	20.8 ± 6.85	145 ± 46
	CUZ-03	-12.5344	-69.0539	205	12	24.4	1.90	99	Cambisols	2.4	727	1.88 ± 0.47	0.10 ± 0.04	17.2 ± 5.97	109 ± 18
	ALP-40	-3.9410	-73.4400	142	12	26.3	2.76	100	Podzols	2.1	59	1.84 ± 0.36	0.10 ± 0.02	16.8 ± 5.00	171 ± 50
	TAM-09	-12.8309	-69.2843	219	13	24.4	1.90	99	Alisols	1.1	326	2.19 ± 0.45	0.14 ± 0.03	16.4 ± 3.77	105 ± 21
	TAM-06	-12.8385	-69.2960	215	13	24.4	1.90	99	Alisols	1.7	529	2.56 ± 0.34	0.17 ± 0.04	15.3 ± 2.84	126 ± 26
Upland	SPD-02	-13.0491	-71.5365	1527	19	18.8	5.30	83	Cambisols	8.8	1631	2.23 ± 0.45	0.16 ± 0.05	15.4 ± 4.05	126 ± 36
	SPD-01	-13.0475	-71.5423	1776	21	17.4	5.30	85	Cambisols	11.9	1071	2.25 ± 0.35	0.16 ± 0.04	14.3 ± 3.34	124 ± 29
	TRU-08	-13.0702	-71.5559	1885	20	18.0	2.47	82	Cambisols	8.1	496	1.99 ± 0.36	0.12 ± 0.05	16.9 ± 3.54	165 ± 38
	ESP-01	-13.1751	-71.5948	2863	17	13.1	1.56	72	Umbrisols	14.8	981	2.39 ± 0.50	0.19 ± 0.05	12.7 ± 1.78	140 ± 32
	TRU-03	-13.1097	-71.5995	3044	13	11.8	1.78	71	Umbrisols	15.5	787	2.24 ± 0.44	0.21 ± 0.04	10.5 ± 2.35	164 ± 40
	WAQ-01	-13.1908	-71.5874	3045	13	11.8	1.56	72	Umbrisols	8.8	1414	2.68 ± 0.42	0.24 ± 0.05	11.5 ± 2.16	149 ± 46
	TRU-01	-13.1136	-71.6069	3379	16	8.0	1.98	67	Umbrisols	15.0	856	2.53 ± 0.31	0.21 ± 0.04	11.2 ± 3.10	151 ± 49

Lowland sites are listed in order of decreasing leaf N:P ratios, while upland sites are listed in order of increasing elevation. Extremely low soil P did not necessarily produce low leaf P as in the case of ALP-03 and ALP-04, therefore lowland sites were ranked according to leaf N to P ratio which provides better indication of nutrient limitation (Aerts & Chapin, 2000). Atmospheric pressure was obtained from a Licor 6400 gas exchange system. For each site name, a site code is shown as designated by the JACARE (the Joint Amazon Carnegie RAINFOR Expedition); values of total soil nitrogen and phosphorus are shown (expressed per unit soil dry mass). Also shown are average leaf area-based concentrations of total nitrogen (N_a) and phosphorus (P_a), as well as the ratio of leaf N:P and leaf mass per unit area, M_a, all shown with SD. Soil classification follows World Reference Base (WRB). Abbreviations: MAP = mean annual precipitation, MAT = mean annual temperature. Source Asner *et al.* (2014a), Quesada (*et al.* 2010; pers. comm. 2014) and Malhi *et al.* (in preparation)

Table 2: Mean values and standard deviation of leaf traits for upland and lowland species.

Leaf Traits	Leaf N_a (g m^{-2})	Leaf P_a (g m^{-2})	Leaf N:P	M_a (g m^{-2})	$A_{400,a}$ (µmol m^{-2} s^{-1})	$A_{400,N}$ (µmol gN^{-1} s^{-1})	$V_{cmax,a}^{25}$ (µmol m^{-2} s^{-1})	$J_{max,a}^{25}$ (µmol m^{-2} s^{-1})	$J_{max,a}^{25}$:$V_{cmax,a}^{25}$	$V_{cmax,N}^{25}$ (µmol gN^{-1} s^{-1})	n_A	n_P	n_R	n_E
Lowland species	1.96 ± 0.52[a]	0.09 ± 0.05[a]	22.2 ± 8.6[a]	132 ± 35[a]	8.2 ± 3.9[a]	4.3 ± 2.2[a]	35.9 ± 14.6[a]	66.7 ± 18.6[a]	1.86 ± 0.40[a]	18.9 ± 8.1[a]	37 ± 1[a]	24 ± 1[a]	9.0 ± 4.0[a]	2.8 ± 1.0[a]
Upland species	2.31 ± 0.44[b]	0.18 ± 0.06[b]	13.5 ± 3.6[b]	143 ± 39[b]	7.6 ± 3.6[a]	3.4 ± 1.7[b]	48.8 ± 20.0[b]	96.9 ± 36.9[b]	1.92 ± 0.36[a]	22.5 ± 9.4[b]	38 ± 1[a]	22 ±1[a]	10.5 ± 4.3[b]	3.4± 1.4[b]

Values expressed on area basis. Abbreviation: leaf N_a = leaf nitrogen, leaf P_a = leaf phosphorus, leaf N:P = leaf nitrogen to phosphorus ratio, M_a = leaf mass per unit leaf area, $A_{400,a}$ = area-based light-saturated net photosynthesis measured at 400 µmol mol^{-1} atmospheric [CO_2], $A_{400,N}$ = area-based light-saturated net photosynthesis measured at 400 µmol mol^{-1} atmospheric [CO_2] per unit leaf nitrogen, $V_{cmax,a}^{25}$ = maximum carboxylation velocity of Rubisco normalised to 25°C, $J_{max,a}^{25}$ = maximum rate of electron transport normalised to 25°C, $J_{max,a}^{25}$:$V_{cmax,a}^{25}$ = ratio of maximum Rubisco carboxylation velocity over maximum rate of electron transport, both normalised to 25°C, $V_{cmax,N}^{25}$ = ratio of maximum carboxylation velocity of Rubisco normalised to 25°C per unit leaf nitrogen, n_A = total fraction of leaf N allocated in photosynthetic metabolism, n_P = fraction of leaf N in pigment-protein complexes, n_R = fraction of leaf N in Rubisco, and n_E = fraction of leaf N in electron transport.
Values are overall mean ± SD of leaf traits for lowland and upland sites. Significantly different means are indicated by different letters (p<0.05).

Table 3: Output from linear mixed-effects models, with $V_{cmax,a}^{25}$ and $J_{max,a}^{25}$ as the response variables, each showing fixed and random effects.

Final model ($V_{cmax,a}^{25}$)			
Fixed effect	Estimate	S.E	t value
Intercept	41.470	1.578	26.288
log10 (Soil P)	7.909	2.466	3.207
P_a	68.148	22.558	3.021
Random effect		**Variance**	**% of total**
Intercept variance: family		45.568	2.49%
Residual error (within family)		1783.626	97.51%
			100.00%
AIC	1645.6		
BIC	1662.0		
-2LL	-817.8		

Final model ($J_{max,a}^{25}$)			
Fixed effect	Estimate	S.E	t value
Intercept	77.217	2.712	28.477
log10 (Soil P)	16.866	4.327	3.898
P_a	94.483	40.245	2.348
Random effect		**Variance**	**% of total**
Intercept variance: family		121.3	2.79%
Residual error (within family)		4232.9	97.21%
			100.00%
AIC	1342.4		
BIC	1357.3		
-2LL	-666.2		

$V_{cmax,a}^{25}$= 41.47 + (7.91*log10[SoilP]) + (68.15*P_a)

$J_{max,a}^{25}$ = 77.22 + (16.87*log10[SoilP]) + (94.48*P_a)

Predictive equations for $V_{cmax,a}^{25}$ and $J_{max,a}^{25}$ based on final preferred models are shown at the bottom. For the $V_{cmax,a}^{25}$ and $J_{max,a}^{25}$ model, the fixed component explanatory variables were soil P and leaf P. Parameter estimate, standard error (S.E.) and t-values are given for the explanatory variables. The best predictive models were selected based on a stepwise selection process outlined in Table S6. Prior to inclusion in the models, continuous explanatory variables were centred on the population mean.

Figure Legends

Figure 1: Fitted curves of the response of CO_2 assimilation rate, A (area-based) to intercellular CO_2 (C_i) at saturating light for (A) a lowland species *Glycydendron amazonicum* (TAM-09) and an upland species *Cecropia angustifolia* (SPD-01) and (B) two upland species *Citronella incarum* (TRU-03) and *Schefflera* sp. (WAQ-01). Closed circles are the measured rates of assimilation, A. Solid lines correspond to fitted response and dashed lines correspond to estimated response at high C_i. V_{cmax} (maximum Rubisco carboxylation capacity) was calculated from the curvature of dashed line and J_{max} (maximum electron transport rate) were calculated from the points where A saturated. Individual leaf was measured at varying temperature close to growth temperature, therefore V_{cmax} and J_{max} were then normalised to 25°C. CO_2 was not always saturating for most upland measurement due to low partial pressure and/or phosphate limitation.

Figure 2: Log-log plots of (A) leaf N-area, N_a and (B) leaf P-area, P_a in relation to leaf mass per unit leaf area, M_a. Data points represent individual leaf values (149 lowland species and 97 upland species). Standardized major axis (SMA) tests for common slopes revealed significant differences when comparing $N_a \leftrightarrow M_a$ and $P_a \leftrightarrow M_a$ relationship between lowland and upland species. Symbols: closed symbols, lowland species; open symbols, upland species. SMA regressions: solid line, lowland species; dashed line, upland species. SMA regressions are given only when the relationships are significant ($p < 0.05$), refer to Table S3.

Figure 3: Box and whisker plots of (A) maximum carboxylation velocity of Rubisco normalised to 25°C, $V_{cmax,a}^{25}$, (B) maximum rate of electron transport normalised to 25°C, $J_{max,a}^{25}$, (C) $J_{max,25}$:$V_{cmax,25}$ ratio, and (D) ratio of $V_{cmax,a}^{25}$ over leaf N, $V_{cmax,N}^{25}$ for each site. Values expressed on area basis. Sites are arranged according to decreasing leaf N:P for lowland and increasing elevation for upland sites. The upper and the lower edges of each box indicate the 75th and 25th percentiles, respectively. The horizontal line within each box is the median and the vertical bars indicate the 10th to the 90th percentile ranges.

Figure 4: Plot of maximum carboxylation velocity of Rubisco normalised to 25°C ($V_{cmax,a}^{25}$) against maximum rate of electron transport normalised to 25°C ($J_{max,a}^{25}$). Data points represent individual leaf values (138 lowland species and 69 upland species). Arrows correspond to the four species depicted in the $A \leftrightarrow C_i$ curves. Symbols: closed symbols, lowland species; open symbols, upland species.

Figure 5: Top panel shows log-log plots of maximum carboxylation velocity of Rubisco normalised to 25°C ($V_{cmax,a}^{25}$) in relation to (A) leaf mass per unit leaf area, M_a, (B) leaf N-area, N_a, (C) leaf P-area, P_a and (D) leaf N:P. Data points represent individual leaf values (150 lowland species and 95 upland species). SMA tests for common slopes revealed significant difference when comparing $V_{cmax,a}^{25} \leftrightarrow N_a$,

$V_{cmax,a}^{25}$↔P_a and $V_{cmax,a}^{25}$↔leaf N:P relationships between lowland and upland species, but no significant difference when comparing slopes of $V_{cmax,a}^{25}$↔M_a relationships between lowland and upland species. Bottom panel shows log-log plots of maximum rate of electron transport normalised to 25°C ($J_{max,a}^{25}$) in relation to (E) leaf mass per unit leaf area, M_a, (F) leaf N-area, N_a, (G) leaf P-area, P_a and (H) leaf N:P. Data points represent individual leaf values (127 lowland species and 58 upland species). SMA tests for common slopes revealed significant difference when comparing $J_{max,a}^{25}$ and leaf traits relationships between lowland and upland species. Symbols: closed symbols, lowland species; open symbols, upland species. SMA regressions are given only when the relationships are significant (p<0.05), refer to Table S3.

Figure 6: Log-log plots of ratio of $V_{cmax,a}^{25}$ to leaf N ($V_{cmax,N}^{25}$) in relation to (A) leaf mass per unit leaf area, M_a, (B) leaf P-area, P_a and (C) leaf N:P. Data points represent individual leaf values (150 lowland species and 95 upland species). SMA tests for common slopes revealed significant difference only when comparing $V_{cmax,N}^{25}$↔P_a between lowland and upland species. Symbols: closed symbols, lowland species; open symbols, upland species. SMA regressions are given only when the relationships are significant (p<0.05), refer to Table S3.

Figure 7: Stacked graph show fraction of leaf N in pigment-protein complexes, n_P; fraction of leaf N in electron transport, n_E; fraction of leaf N in Rubisco; n_R, for each sites. n_R was estimated from maximum carboxylation velocity of Rubisco (normalised to 25°C), $V_{cmax,a}^{25}$, n_E estimated from maximum electron transport rate (normalised to 25°C), $J_{max,a}^{25}$, and n_P estimated from chlorophyll concentration. n_P were unavailable for five sites due to thawing of leaf samples. Sites are arranged according to decreasing leaf N:P for lowland and increasing elevation for upland sites. Error bar represent standard error of mean.

Figure 8: Log-log plots of the total fraction of leaf N allocated in photosynthetic metabolism, n_A in relation to (A) leaf mass per unit leaf area, M_a, (B) leaf N-area, N_a, and (C) leaf P-area, P_a. Data points represent individual leaf values (126 lowland species and 40 upland species). SMA tests for common slopes revealed no significant difference when comparing relationships between lowland and upland species, but with the elevation (i.e. y-axis intercept) of the bivariate relationship being higher in upland species than in lowland species. Symbols: closed symbols, lowland species; open symbols, upland species. SMA regressions: solid line, lowland species; dashed line, upland species. SMA regressions are given only when the relationships are significant (p<0.05), refer to Table S5.

Figure 9 (A): SDS-PAGE profile of native Rubisco extracted from frozen fresh leaf discs. Individual bands show large subunits of Rubisco. The last five bands on the right side (A-E) correspond to 0.47, 0.54, 0.57, 0.78 and 1.21 g m^{-2} of Rubisco of lowland species (*Licania unguiculata* from *Chrysobalanaceae* family), which then translate to n_R

of 0.03, 0.04, 0.04, 0.06, 0.09. In this case, the final value of *in vitro* n_R for *L. unguiculata* was 0.04, as calculated from A - C, since these values fall within the tobacco standard curve. Standard curve was made of a dilution series of tobacco Rubisco. Figure 8 (B): *in vitro* n_R estimated from Rubisco western blot assay plotted against *in vivo* n_R derived from maximum carboxylation velocity of Rubisco (normalised to 25°C), $V_{cmax,a}^{25}$. n=16

Figure 1:

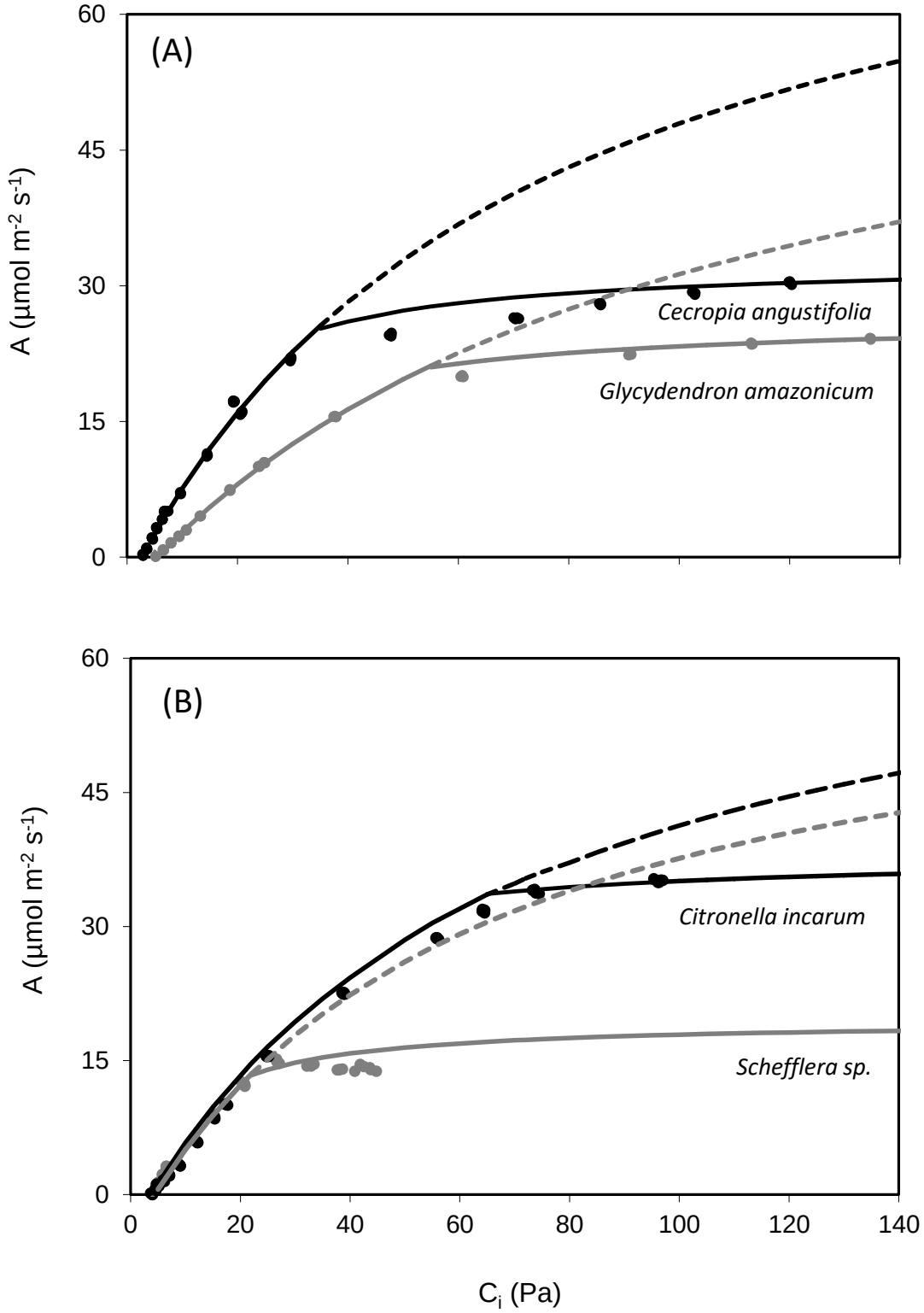

(A)
(B)
A (µmol m-2 s-1)
Ci (Pa)
Cecropia angustifolia
Glycydendron amazonicum
Citronella incarum
Schefflera sp.
0
15
30
45
60
0
20
40
60
80
100
120
140

Figure 2:

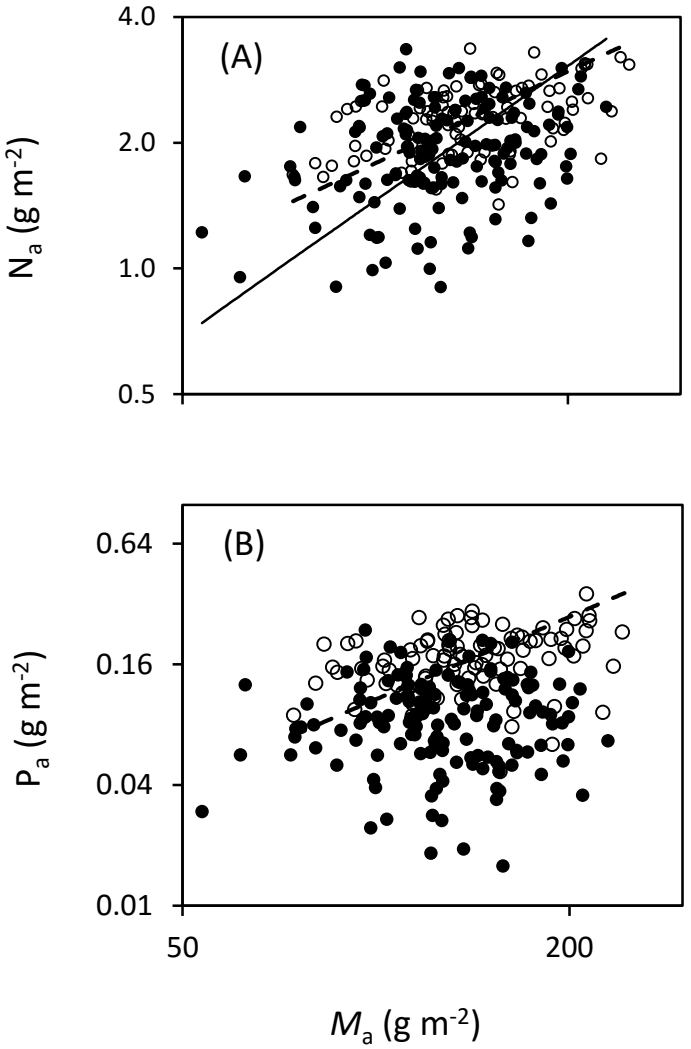


Figure 3:

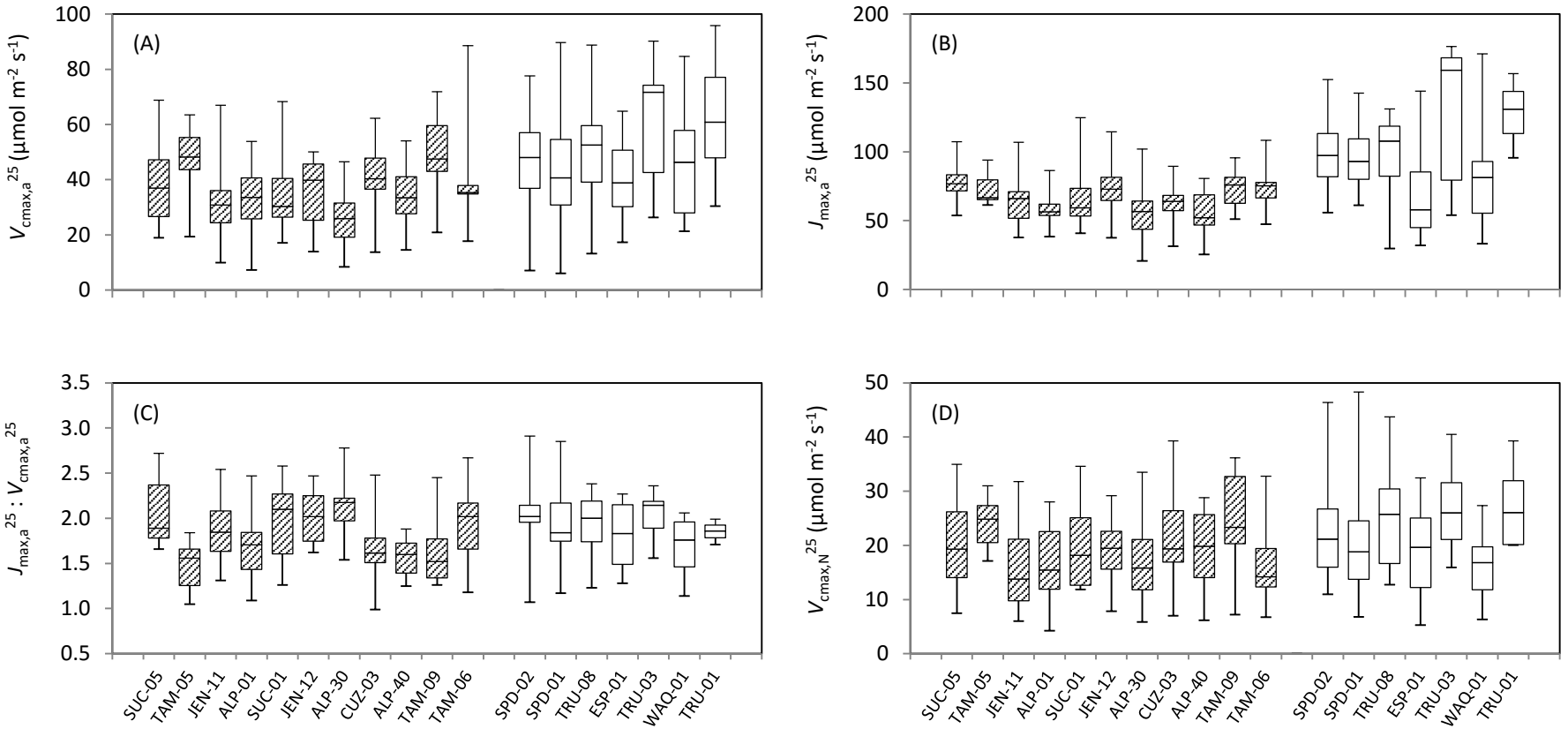

(A)
(B)
(C)
(D)
$V_{cmax,a}^{25}$ (µmol m^{-2} s^{-1})
$J_{max,a}^{25}$ (µmol m^{-2} s^{-1})
$J_{max,a}^{25}$: $V_{cmax,a}^{25}$
$V_{cmax,N}^{25}$ (µmol m^{-2} s^{-1})
SUC-05
TAM-05
JEN-11
ALP-01
SUC-01
JEN-12
ALP-30
CUZ-03
ALP-40
TAM-09
TAM-06
SPD-02
SPD-01
TRU-08
ESP-01
TRU-03
WAQ-01
TRU-01

Figure 4:

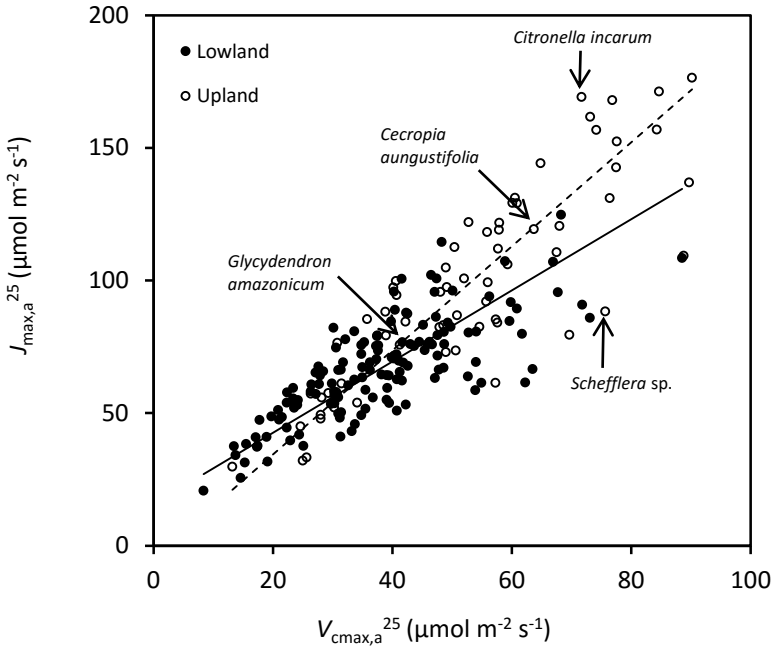

Lowland
Upland
Citronella incarum
Cecropia aungustifolia
Glycydendron amazonicum
Schefflera sp.
$J_{max,a}^{25}$ (µmol m^{-2} s^{-1})
$V_{cmax,a}^{25}$ (µmol m^{-2} s^{-1})
0
50
100
150
200
0
20
40
60
80
100

Figure 5:

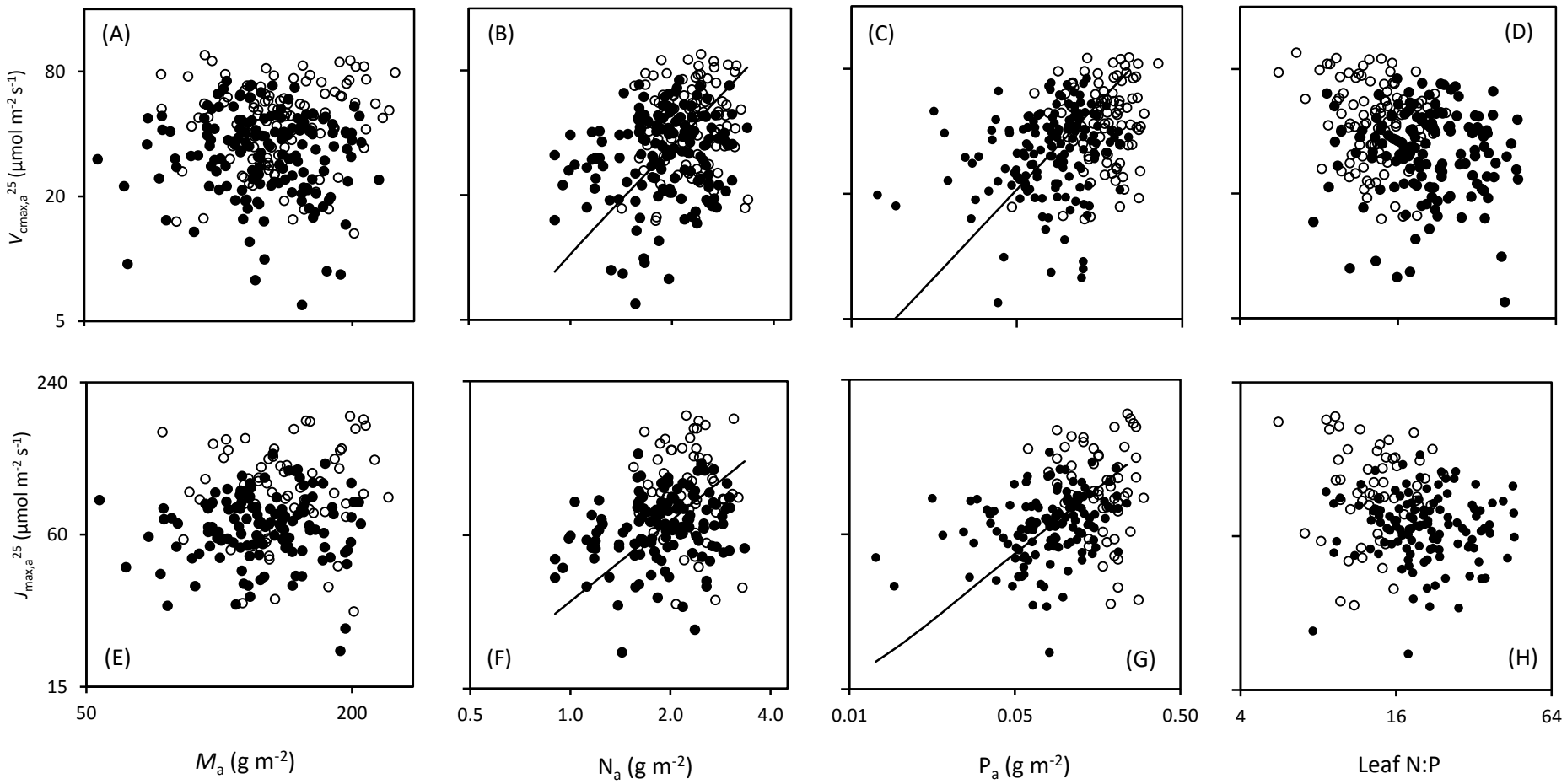

(A)
(B)
(C)
(D)
(E)
(F)
(G)
(H)
$V_{cmax,a}^{25}$ (µmol m^{-2} s^{-1})
$J_{max,a}^{25}$ (µmol m^{-2} s^{-1})
80
20
5
240
60
15
50
200
0.5
1.0
2.0
4.0
0.01
0.05
0.50
4
16
64
M_a (g m^{-2})
N_a (g m^{-2})
P_a (g m^{-2})
Leaf N:P

Figure 6:

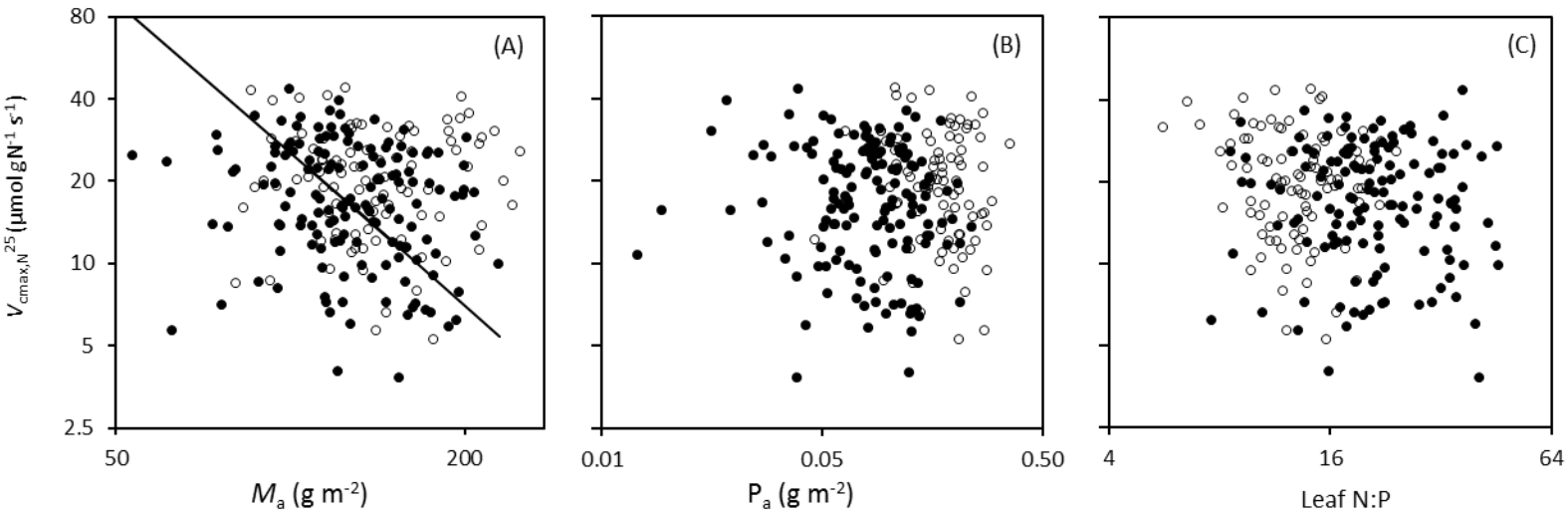

(A)
(B)
(C)
80
40
20
10
5
2.5
50
200
0.01
0.05
0.50
4
16
64
$V_{cmax,N}^{25}$ (μmol g N^{-1} s^{-1})
M_a (g m^{-2})
P_a (g m^{-2})
Leaf N:P

Figure 7:

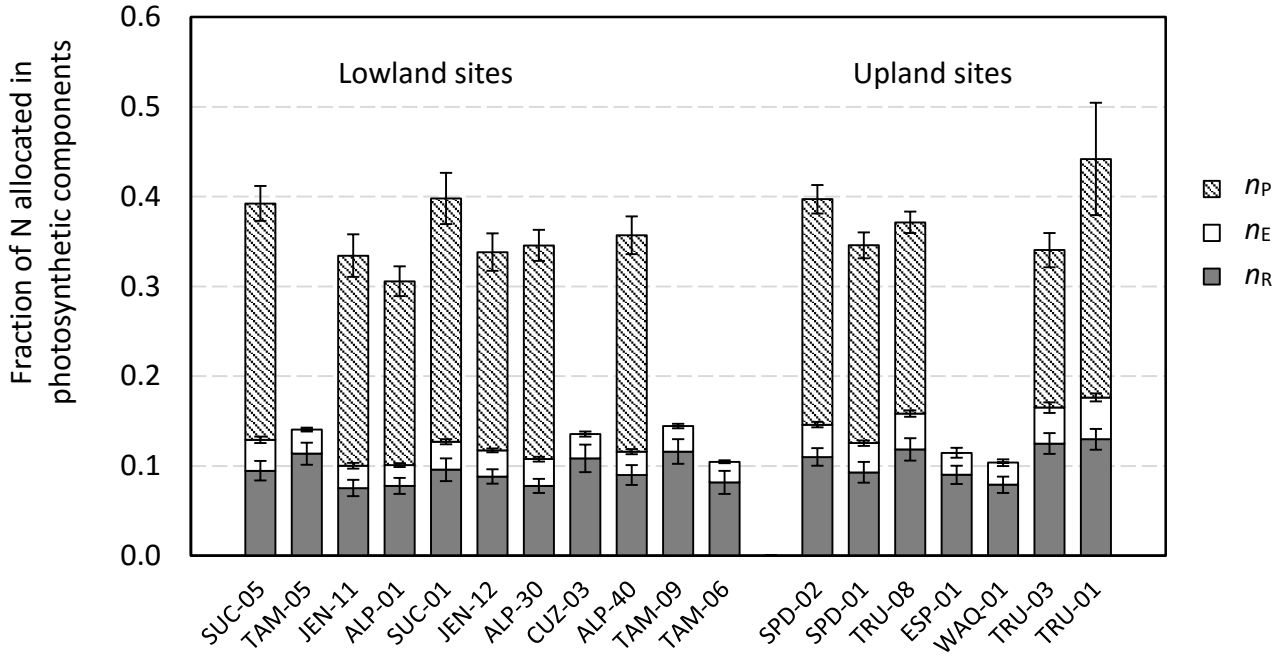

Fraction of N allocated in photosynthetic components
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Lowland sites
Upland sites
n_P
n_E
n_R
SUC-05
TAM-05
JEN-11
ALP-01
SUC-01
JEN-12
ALP-30
CUZ-03
ALP-40
TAM-09
TAM-06
SPD-02
SPD-01
TRU-08
ESP-01
WAQ-01
TRU-03
TRU-01

Figure 8:

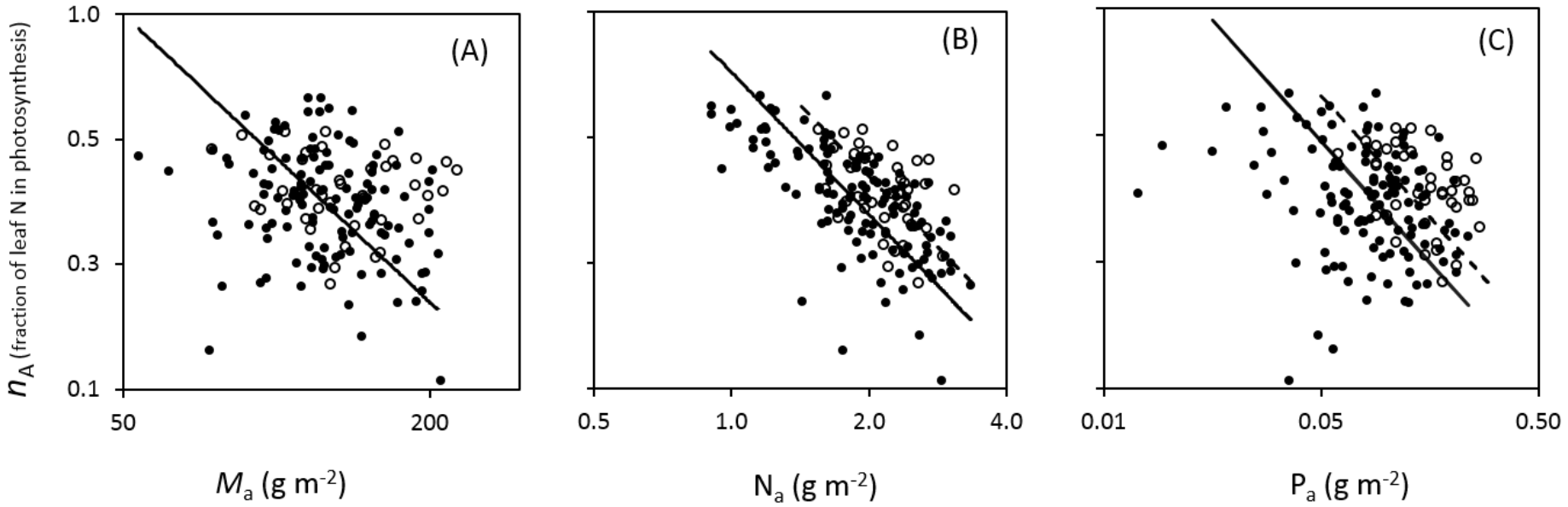
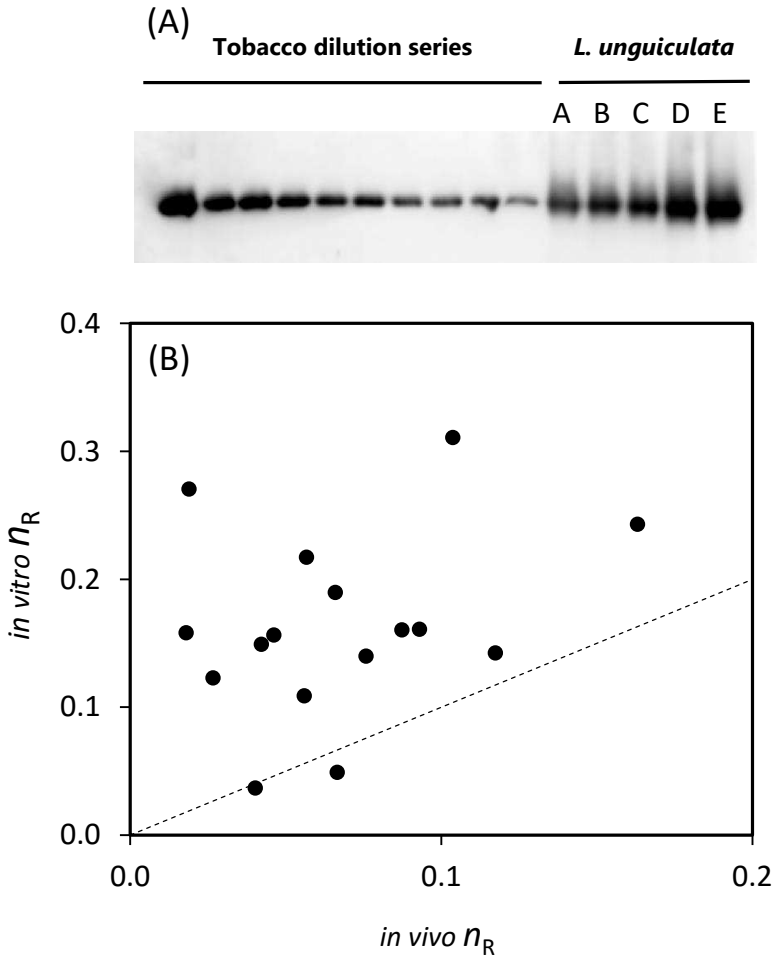

n_A (fraction of leaf N in photosynthesis)
1.0
0.5
0.3
0.1
(A)
50
200
M_a (g m^{-2})
(B)
0.5
1.0
2.0
4.0
N_a (g m^{-2})
(C)
0.01
0.05
0.50
P_a (g m^{-2})

Figure 9:


(A)
Tobacco dilution series
L. unguiculata
A B C D E
(B)
0.4
0.3
0.2
0.1
0.0
0.0
0.1
0.2
in vitro n_R
in vivo n_R

Supporting Information

Authors: Bahar, Ishida, Weerasinghe *et al.*

Title: Leaf-level photosynthetic capacity in lowland Amazonian and high-elevation, Andean tropical moist forests of Peru

SM1: Additional study site details

Four of the lowland sites (TAM-09, TAM-06, TAM-05 and CUZ-03) were located in the Tambopata watersheds of SE Peru, while seven additional lowland sites (ALP-01, ALP-30, ALP-40, JEN-11, JEN-12, SUC-01, and SUC-05) were located in the Ucayali watershed in NE Peru. Seven upland sites (SPD-01, SPD-02, ESP-01, WAQ-01, TRU-01, TRU-03, and TRU-08) were distributed along SE slopes of the Andes in the Kosñipata valley. The 18 plots used in this study are part of the ABERG Kosñipata study transect (www.andesconservation.org/), Amazon Forest Inventory Network (RAINFOR; http://www.rainfor.org/) and the Carnegie Spectranomics Project (http://spectranomics.ciw.edu/). The lowland sites lie on a mosaic of young to old soil substrates, whereas upland forests exist primarily on young geologic substrates (van de Weg *et al.*, 2009; Quesada *et al.*, 2010; Fisher *et al.*, 2013). Data on soil type, as well as total N and P concentrations in soils, were obtained from Dr Carlos Alberto Quesada (Instituto Nacional de Pesquisas da Amazônia), using a combination of unpublished and published (Quesada *et al.*, 2010) data. For each tree, voucher specimens were collected and matched to herbarium collections at the National Agrarian University La Molina Herbarium in Peru and the Missouri Botanical Garden for full taxonomic verification by Carnegie Institution taxonomists.

SM2: Identification of outliers and $A \leftrightarrow C_i$ curve methodological details

CO_2 response curves of light-saturated photosynthesis (i.e. $A \leftrightarrow C_i$ curves) were quantified within 30–60 minutes after branch detachment, with CO_2 concentrations inside the reference chamber ranging from 3.5 to 2000 μmol mol^{-1}; initial measurements were made at 400 μmol mol^{-1}, followed by decreases in CO_2 to 300, 200, 150, 125, 100, 75, 50 and 35 μmol mol^{-1}; thereafter, CO_2 concentrations were increased back to 400 μmol mol^{-1}, and then to 600, 900, 1250, 1500, 1750 and finally 2000 μmol mol^{-1}. Block temperatures within the chamber were set to that of the prevailing day-time air temperature at each site (ranging from 25-28 °C depending on the site). A photosynthetic active radiation (PAR) flux density of 1800 µmol m^{-2} s^{-1}, generated from an artificial light source (6400-02B Red/Blue LED Light Source, Li-Cor, Inc.), was used for all measurements. The resultant $A \leftrightarrow C_i$ curves (examples shown in Figure 1 – main text) were fitted following the model described by the Farquhar, von Caemmerer and Berry (1980) in order to calculate V_{cmax} and maximum rate of electron transport (J_{max}) on a leaf area basis. V_{cmax} and J_{max} values at the prevailing leaf temperature were determined via minimizing the sum of squares of modelled vs observed estimates of net CO_2 exchange at given C_i values. This was done for both the CO_2-limited and CO_2-saturated regions of $A \leftrightarrow C_i$ curves (using C_i values expressed on a partial pressure basis, corrected for altitudinal changes in air pressure), with these regions being defined individually for each replicate. V_{cmax} at the prevailing leaf temperature was calculated under the assumption that at C_i values below 15-20 Pa (depending on site altitude) photosynthesis was limited by Rubisco only. Rates of A at these low CO_2 values were fitted to the Rubisco-limited equation of photosynthesis:

$$A = \left[\frac{V_{cmax}(C_i - \Gamma_*)}{\left(C_i + K_c\left(1 + {}^{O}/_{K_o}\right)\right)}\right] - R_{light} \qquad \text{(Eqn 1)}$$

where R_{light} is respiration in the light, $\Gamma*$ is the CO_2 compensation point in the absence of photorespiration (3.69 Pa at 25ºC; von Caemmerer *et al.* (1994)), K_c and K_o are the effective Michaelis-Menten constants for CO_2 and O_2 at 25˚C [40.4 Pa and 24.8 kPa,

respectively, von Caemmerer *et al.* (1994)] and O is partial pressure of O_2, corrected for atmospheric pressure at each altitude, according to:

$$O_2\ partial\ pressure\ at\ site\ =\ O_2\ partial\ pressure\ at\ sea\ level \times \frac{air\ pressure\ at\ site}{air\ pressure\ at\ sea\ level}$$

The resultant O_2 partial pressures at each site were then used to modify estimates of Γ^* and K'. C_i values were corrected for air pressure in the same manner. We assumed that K_c and K_o at the measurement temperature could be calculated assuming activation energies (E_a) of K_c and K_o of 59.4 and 36 kJ mol^{-1}, respectively (Farquhar *et al.*, 1980). These enzymatic kinetic constants were taken from von Caemmerer *et al.* (1994), assuming an infinite internal conductance. $\Gamma*$ at each leaf temperature was assumed to follow the temperature dependency reported by Brooks and Farquhar (1985). Rates of J_{max} were calculated using the electron-transport-limited equation of CO_2 assimilation:

$$A = \left[\frac{J_{max}(C_i - \Gamma_*)}{(4C_i + 8\Gamma_*)}\right] - R_{light} \qquad \text{(Eqn 2)}$$

assuming that A is limited by RuBP regeneration at higher concentrations of atmospheric CO_2 (Fig. 1). As atmospheric CO_2 was not always saturating for measurements of upland species (due to low atmospheric partial pressure), J_{max} may have been underestimated in some cases and we excluded these J_{max} values from the Andean data set. Rates of CO_2 exchange were corrected for diffusion through the gasket of the LI-6400 leaf chamber (Bruhn *et al.*, 2002) prior to calculation of V_{cmax} and J_{max}. Fitted parameters were scaled to a reference temperature of 25°C using activation energies of 64.8 and 37.0 kJ mol^{-1} for V_{cmax} and J_{max}, respectively (Farquhar *et al.*, 1980).

Alterations in stomatal conductance (g_s) resulting from branch cutting were assumed to not affect the maximum carboxylation velocity of Rubisco (V_{cmax}) (Miyazawa *et al.*, 2011), except where g_s declined to very low levels (Santiago & Mulkey, 2003); in instances where g_s values fell below 0.04 mol m^{-2} s^{-1}, data were discarded from the analyses. We also applied a further check on data quality as used elsewhere (Kattge *et al.*, 2009; Domingues *et al.*, 2010; van de Weg *et al.*, 2012) where rates of A_N less than 2 μmol CO_2 g N^{-1} s^{-1} were excluded from analysis (52 out of a total of 353 measurements).

SM3: Optimization of protocols for protein extraction from the leaves of recalcitrant tree species

Trouble-shooting using temperate and tropical evergreen species

The analysis of protein recalcitrant to extraction from some tree species is complicated by the abundance of lipids, tannins, phenols, waxes, oils and other secondary compounds (Ekramoddoullah, 1993; Gaspar *et al.*, 1997). The leaves of many of the species analysed in this study are characteristically aromatic and tough in nature and initial attempts to extract protein resulted in smeared bands on SDS-PAGE gels and highly oxidized extracts in most cases. Invariably, the extraction of proteins in their native confirmation (for example for the analysis of Rubisco active site concentration) was impossible. Moreover, previous attempts to isolate protein and Rubisco from hard-leaved species had been unsuccessful (Harrison *et al.*, 2009, Bloomfield, Long, Evans, unpublished). Using a combination of protein extraction from recalcitrant species (Gaspar *et al.*, 1997) and detergent based-extraction buffer (Brown *et al.*, 2008), we successfully extracted protein from Peruvian tropical leaves and Australian tropical and temperate leaves (Long, Atkin, Xiang, Bahar, unpublished).

The process of extracting protein from the leaves was modified from that described by Gaspar *et al.* (1997) in order to allow the extraction and measurement of chlorophyll prior to protein analysis. Leaves were initially pulverised using a Tissue-Lyser (Qiagen) and were treated with one of the following extraction solvents:

1) Acetic acid, methanol and water (1:10:9) (as per Gaspar *et al.* (1997))
2) 80% (v/v) acetone
3) 100% (v/v) methanol

After initial extraction in these solvents, precipitated protein was further washed in hexane and acetone as described by Gaspar *et al.* (1997) to remove lipids and remaining pigments, leaving a protein pellet. Proteins were dissolved in protein extraction buffer [PEB, (Brown *et al.*, 2008)] containing 140 mM Tris base, 105 mM Tris–HCl, 0.5 mM

ethylenediaminetetraacetic acid (EDTA), 2% lithium dodecyl sulfate (LDS), 10% glycerol, 0.1 mg/mL PefaBloc SC (AEBSF) protease inhibitor (Roche) and 5 mM dithiothreitol (DTT) for analysis by SDS-PAGE and Western blotting for Rubisco proteins.

Analysis by SDS-PAGE and Western blotting was performed according to protocols described in *Materials and Methods: Chlorophyll and Rubisco measurements* in the main text. Based on this analysis, extraction with 100% methanol consistently provided the cleanest protein extracts as assessed by SDS-PAGE (lanes 11-15; Fig. SM3.1). The smearing of protein on SDS-PAGE gels may reflect either interference by unwanted compounds in the extract (e.g. lipids) or the degradation of Rubisco. Thus, the clean-up and extraction of protein in a way which prevents this interference/degradation is vital for accurate Rubisco estimation. When applied to protein extraction from the leaves of different tree species, each solvent provided similar estimations of leaf Rubisco content (Fig. SM3.2).

We estimated Rubisco content using an antibody raised against tobacco Rubisco. An alternative approach using Coomassie staining is a common practice, where the relatively high concentration of Rubisco large and small subunits in the total protein extract makes estimation of their concentration possible. Rubisco concentrations determined from Western blotting were compared with those estimated from Coomassie staining (Fig. SM3.3); the Rubisco estimates suggest that estimation of Rubisco from the Western blot were in a similar range to the estimates made by Coomassie staining of gels. Despite the samples being treated differently, both approaches yielded similar estimations of leaf Rubisco content, consistent with the result obtained in Fig SM3.2. Additional tests to check that the primary antibody recognized Rubisco of the study species were performed by spiking temperate evergreen species with Rubisco from tobacco prior to SDS-PAGE analysis. Figure SM3.4 shows a comparison of Rubisco concentration of tree species alone versus that spiked with known concentration of tobacco Rubisco (0.5 µg μL^{-1}). The western blot assay estimated 0.31 µg µL-1 Rubisco in the sample and 0.78 µg µL-1 in the spiked

sample; a difference closely equivalent to the spike. This suggests that the Western blot antibody assay, typically designed for crop species, is compatible with temperate and tropical evergreen species and that the antibody used can successfully be applied to a variety of land plants (Kellogg & Juliano, 1997). Moreover, this result suggests that possible interference by compounds found in tropical leaves did not affect Rubisco quantification after sample clean-up.

Trouble-shooting using Peruvian tropical species

Leaf protein of lowland Peruvian tree species was extracted using a modified protocol as described above. After initial extraction of chlorophyll using 100% methanol, precipitated protein was further washed in hexane and acetone as described by Gaspar *et al.* (1997) and dissolved in PEB containing 5 mM DTT (Brown *et al.*, 2008). This method was compatible with Peruvian tropical species, as protein bands were observed on Western blot (Fig. SM3.5). However, some of the leaf discs were degraded due to thawing during shipment from Peru, which resulted in no visible bands on the gel. Approximately less than 1.6 µg sample was required per lane to yield clear, unsaturated band with low background intensity (Fig. SM3.5).

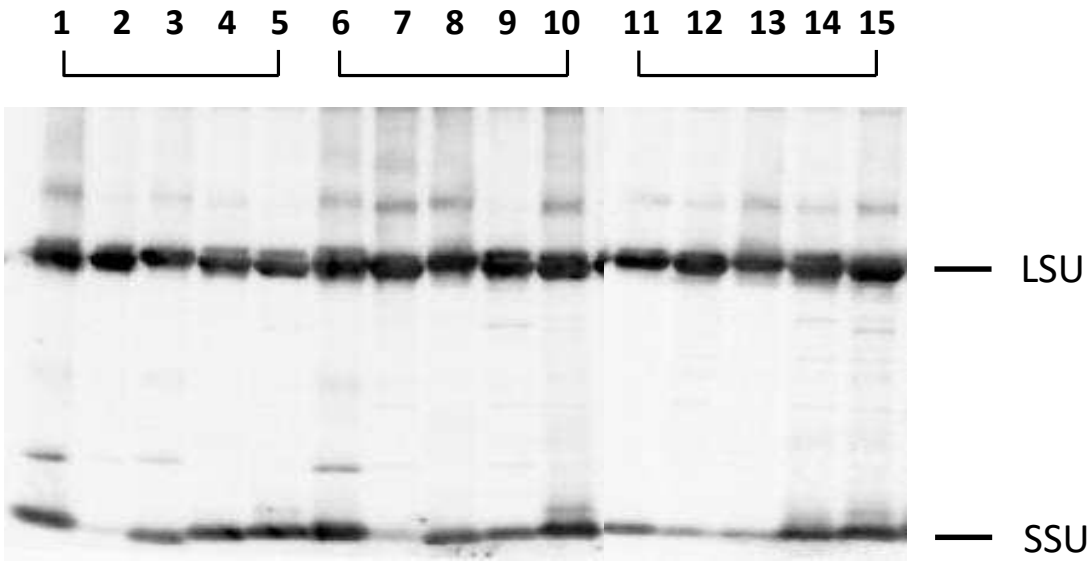


Figure SM3.1: **The effect of leaf extraction solvents on Rubisco western blot quality.** Typical western blot profile of Rubisco extracted from five temperate evergreen species after acetic acid, methanol and water (1:10:9) (1-5), 80% (v/v) acetone (6-10) and 100% methanol (11-15) clean-up, prior to washing with hexane and acetone (Gaspar *et al.*, 1997) and dissolution in PEB containing 5 mM DTT (Brown *et al.*, 2008). Individual bands represent Rubisco large subunits (LSU, ~55 kDa) and small subunits (SSU, 15 kDa). Greatest quality blots were consistently observed from 100% methanol-treated leaf samples.

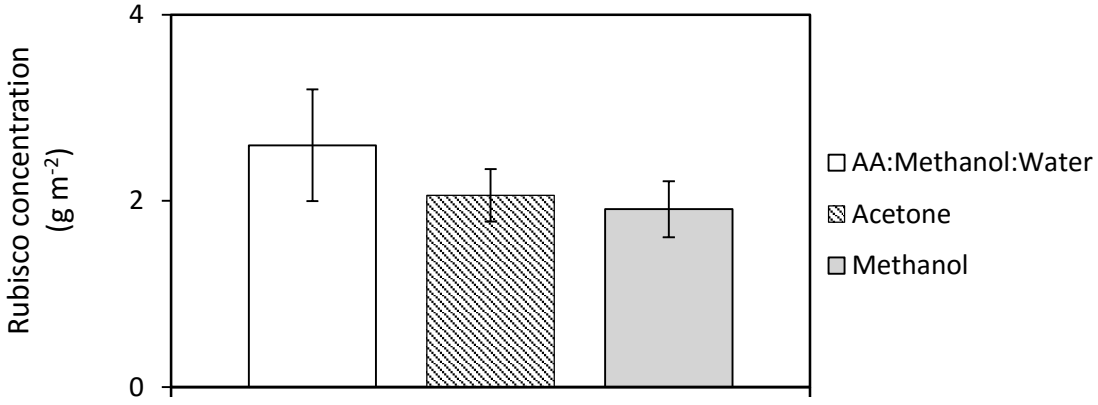


Figure SM3.2: **The effect of leaf extraction solvents on estimated Rubisco in protein extracts.** The graph shows estimated Rubisco concentration in leaves of five temperate evergreen species (± S.E.) after acetic acid (AA), methanol and water (1:10:9), 80% acetone and 100% methanol clean-up, prior to washing with hexane and acetone (Gaspar *et al.*, 1997) and dissolution in PEB containing 5 mM DTT (Brown *et al.*, 2008).

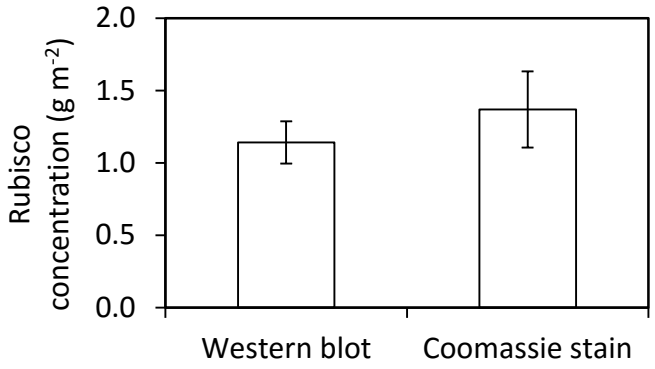


Figure SM3.3: **Comparison of western blotting and Coomassie staining for estimation of Rubisco quantities in leaf extracts.** Shown are estimated Rubisco concentrations (± S.E.) of *Atherosperma moschatum* leaves (n=3), determined from Western blot antibody and Coomassie staining. Rubisco estimated from Western blotting was washed with 100% methanol, hexane and acetone, while Rubisco estimated from Coomassie staining was washed with acetic acid, methanol and water (1:10:9), prior to washing with hexane and acetone according to Gaspar *et. al* (1997). Protein was dissolved in PEB containing 5 mM DTT (Brown *et al.*, 2008).

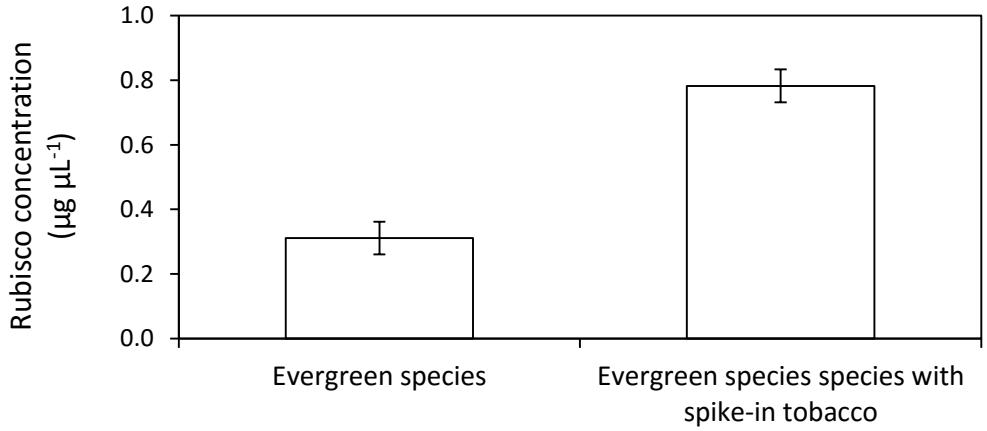


Figure SM3.4: **Measurement of Rubisco by western blotting with and without additional Rubisco spike.** Estimated Rubisco concentration of *Atherosperma moschatum* (temperate evergreen) and *Micrandra spruceana* (tropical evergreen) determined from protein extract alone and extract with Rubisco from tobacco spiked into the samples (0.5 µg μL^{-1}). Rubisco from evergreen species was prepared from 100% methanol clean-up, prior to washing with hexane and acetone (Gaspar *et al.*, 1997) and dissolution in PEB containing 5 mM DTT (Brown *et al.*, 2008). Rubisco from tobacco was extracted using extraction buffer (50mM EPPS [4-(2-hydroxyethyl)-1-piperazinepropanesulfonic acid]-NaOH, 1mM EDTA, 1% Polyvinylpolypyrrolidone (PVPP), 10mM DTT, 0.01% Triton, pH 7.8).

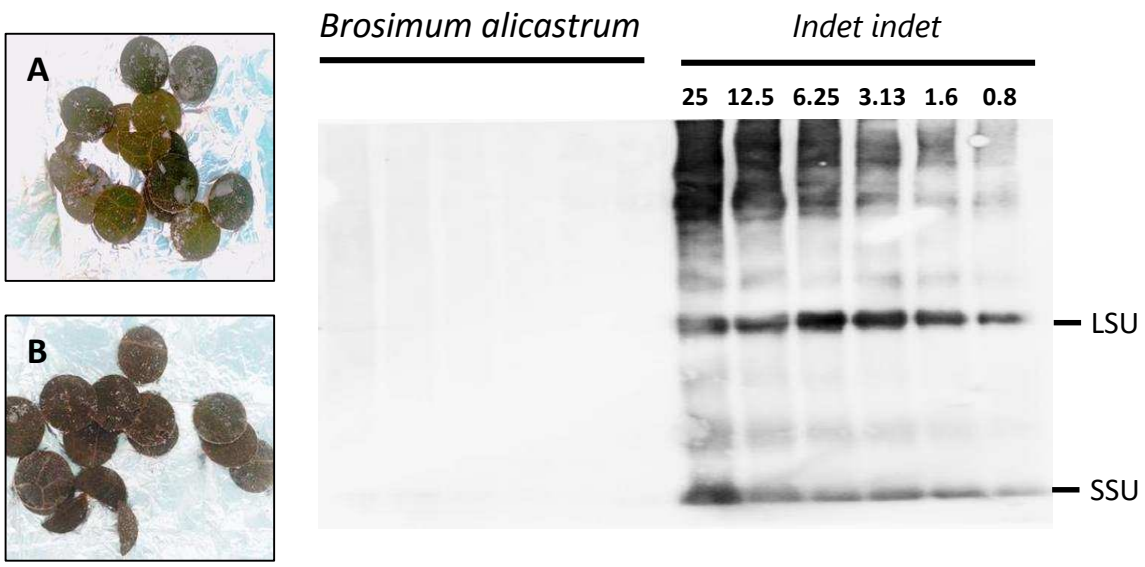


Figure SM3.5: **Isolation of Rubisco from tropical leaf samples.** Western blot profile of Rubisco extracted from two lowland species (A) *Indet indet* and (B) *Brosimum alicastrum*. Samples were loaded in a dilution series (25 to 0.8 µg) to estimate the amount of protein to load per lane that yields clear and unsaturated band. No visible bands were seen for *B. alicastrum*, which were consistent with brownish appearance of the leaf discs (A) resulting from thawing during transport. Individual bands represent Rubisco large subunits (LSU, ~55 kDa) and small subunits (SSU, 15 kDa).

Table S1: Summary of species sampled at each site and their parameters. Sites are sorted according to decreasing leaf N:P for lowland sites and increasing elevation for upland sites. * marked species site average where n=2.

Abbreviations: M_a= leaf mass per unit leaf area, leaf N_a = leaf nitrogen, leaf P_a = leaf phosphorus, $A_{400,a}$ = light-saturated net photosynthesis measured under 400 µmol mol^{-1} atmospheric [CO_2], $A_{2000,a}$ = light-saturated net photosynthesis measured under 2000 µmol mol^{-1} atmospheric [CO_2], $V_{cmax,a}^{25}$ = maximum carboxylation velocity of Rubisco normalised to 25°C, $J_{max,a}^{25}$ = maximum rate of electron transport normalised to 25°C, R_{light} = leaf respiration measured in the light at 400 µmol mol^{-1} atmospheric [CO_2], Leaf T= leaf temperature inside gas exchange cuvette, Chl = chlorophyll a and b content, n_E = fraction of leaf N in electron transport, n_R = fraction of leaf N in Rubisco, n_P = fraction of leaf N in pigment-protein complexes.

Site	Family	Genus	Species	M_a (g m^{-2})	Leaf N_a (g m^{-2})	Leaf P_a (g m^{-2})	$A_{400,a}$ (µmol m^{-2} s^{-1})	$A_{2000,a}$ (µmol m^{-2} s^{-1})	$V_{cmax,a}^{25}$ (µmol m^{-2} s^{-1})	$J_{max,a}^{25}$ (µmol m^{-2} s^{-1})	R_{light} (µmol m^{-2} s^{-1})	Leaf T (°C)	Chl (g m^{-2})	n_E	n_R	n_P
SUC-05	*Urticaceae*	*Pourouma*	*bicolor*	144	2.54	0.09	15.8	30.8	58.9	107.3	1.3	28.8	0.74	0.03	0.11	0.20
SUC-05	*Chrysobalanaceae*	*Couepia*	*bracteosa*	172	1.88	0.06	13.7	26.2	47.1	95.7	0.9	28.0	0.76	0.04	0.12	0.28
SUC-05	*Burseraceae*	*Protium*	*paniculatum*	123	1.56	0.03	2.7	15.3	23.4	55.5	1.3	29.2	0.63	0.03	0.07	0.28
SUC-05	*Sapotaceae*	*Micropholis*	*guyanensis*	163	2.29	0.13	3.5	14.8	19.8	.	1.2	29.2	0.40	.	0.04	0.12
SUC-05	*Myristicaceae*	*Osteophloeum*	*platyspermum*	122	1.87	0.06	13.8	24.6	41.7	76.7	-0.4	29.5	0.78	0.03	0.11	0.29
SUC-05	*Sapotaceae*	*Pouteria*	*caimito*	158	1.62	0.02	13.9	23.8	49.8	82.5	0.7	28.5	0.65	0.04	0.15	0.27
SUC-05	*Apocynaceae*	*Rhigospira*	*quadrangularis*	54	1.22	0.03	6.2	22.5	30.2	82.1	1.4	28.5	0.51	0.05	0.12	0.29
SUC-05	*Rubiaceae*	*Chimarrhis*	*gentryana*	96	2.52	0.09	5.4	18.4	27.9	64.2	1.5	29.4	1.17	0.02	0.05	0.32
SUC-05	*Sapotaceae*	*Pouteria*	*filipes*	95	2.75	0.09	5.8	15.6	22.3	53.9	1.2	29.4	0.71	0.02	0.04	0.18
SUC-05	*Chrysobalanaceae*	*Licania*	*latifolia*	104	1.03	0.03	6.8	22.4	33.6	80.8	1.3	28.1	0.49	0.06	0.15	0.32
SUC-05	*Moraceae*	*Naucleopsis*	*mello-barretoi*	115	2.53	0.07	4.1	14.5	19.0	.	1.2	29.6	1.09		0.04	0.30
SUC-05	*Rubiaceae*	*Ladenbergia*	*magnifolia*	127	1.59	0.06	10.0	29.1	47.4	100.7	2.3	29.4	0.57	0.05	0.14	0.24
SUC-05	*Myristicaceae*	*Virola*	*calophylla*	.	.	.	7.2	12.0	27.7	.	1.4	28.5	.	.	.	0.11
SUC-05	unidentified	unidentified	unidentified	119	.	.	14.3	35.7	68.8	.	0.7	28.8	.	.	.	.
SUC-05	*Anacardiaceae*	*Tapirira*	*obtusa*	.	.	.	10.9	20.7	40.4	71.5	1.4	29.2	.	.	.	0.22
SUC-05	*Moraceae*	*Pseudolmedia*	*rigida*	122	1.16	0.04	7.8	18.6	40.4	71.7	1.9	28.5	0.70	0.05	0.17	0.42
SUC-05	*Apocynaceae*	*Parahancornia*	*peruviana*	137	1.47	0.02	5.4	16.7	23.2	.	1.2	28.4	0.87		0.07	0.41
SUC-05	*Humiriaceae*	*Humiriastrum*	*excelsum*	154	1.97	0.03	2.3	20.0	30.6	74.6	1.9	28.7	0.90	0.03	0.07	0.31
SUC-05	*Moraceae*	*Helicostylis*	*scabra*	135	3.01	0.13	15.1	16.7	49.3	84.0	1.0	28.0	0.84	0.02	0.08	0.19
SUC-05	*Lauraceae*	*Licaria*	*cannella*	181	.	0.06	11.7	20.6	44.5	76.8	1.2	28.0	.	0.02	.	.
TAM-05	*Ulmaceae*	*Ampelocera*	*edentula*	.	.	.	6.0	17.2	19.4	.	0.5	30.0	.	.	.	.
TAM-05	*Bixaceae*	*Bixa*	*arborea*	75	1.65	0.07	13.0	22.6	48.7	76.0	0.1	28.8	.	0.04	0.14	.
TAM-05	*Lauraceae*	*Ocotea*	*bofo*	127	2.28	0.06	9.5	20.6	39.0	64.3	0.3	29.8	.	0.02	0.08	.
TAM-05	unidentified	unidentified	unidentified	138	2.52	0.07	6.6	21.2	47.8	66.4	0.5	30.3	.	0.02	0.09	.
TAM-05	*Sapotaceae*	*Pouteria*	*torta subsp. tuberculata*	117	2.05	0.10	6.8	25.9	45.2	83.3	1.3	30.4	.	0.03	0.10	.

TAM-05	*Malvaceae*	*Huberodendron*	*switenioides*	95	2.17	0.12	10.6	20.5	54.9	61.4	0.4	30.4	.	0.02	0.12	.
TAM-05	*Melastomataceae*	*Miconia*	*pyrifolia*	155	2.27	0.05	11.9	28.7	56.3	94.0	1.6	30.6	.	0.03	0.12	.
TAM-05	*Elaeocarpaceae*	*Sloanea*	*brevipes*	125	2.05	0.08	11.5	20.7	63.5	66.6	1.3	31.0	.	0.03	0.15	.
JEN-11	*Sapotaceae*	*Micropholis*	*guyanensis*	156	.	0.05	2.5	22.1	32.1	77.8	2.2	29.5	.	0.02	.	.
JEN-11	*Olacaceae*	*Aptandra*	*liriosmoides*	165	2.35	0.11	5.3	15.7	18.2	.	1.0	29.5	0.98	.	0.04	0.29
JEN-11	*Lauraceae*	*Mezilaurus*	*synandra*	230	2.43	0.07	3.9	21.0	29.2	.	1.6	29.5	.	.	0.06	0.43
JEN-11	*Lecythidaceae*	*Eschweilera*	*coriacea*	124	1.74	0.06	5.3	18.8	27.7	67.6	1.3	28.8	0.35	0.03	0.08	0.14
JEN-11	*Vochysiaceae*	*Qualea*	*paraensis*	154	1.79	.	11.2	14.6	35.5	51.7	0.4	28.4	0.83	0.02	0.09	0.32
JEN-11	*Melastomataceae*	*Mouriri*	*nigra*	124	2.57	0.04	4.5	10.3	22.9	39.6	1.1	28.7	0.73	0.01	0.04	0.19
JEN-11	*Sapotaceae*	*Pouteria*	*guianensis*	163	1.78	0.05	4.9	16.1	24.2	.	1.1	28.9	0.71	.	0.06	0.27
JEN-11	*Goupiaceae*	*Goupia*	*glabra*	103	2.07	0.08	15.5	37.4	65.8	.	1.6	28.9	0.52	0.05	0.15	0.17
JEN-11	*Myristicaceae*	*Osteophloeum*	*platyspermum*	141	2.86	0.11	11.6	17.5	39.9	70.9	1.0	28.5	0.88	0.02	0.07	0.21
JEN-11	*Sapotaceae*	*Pouteria*	*platyphylla*	149	1.98	0.06	9.5	10.8	31.4	41.1	0.2	28.6	0.77	0.02	0.08	0.27
JEN-11	unidentified	unidentified	unidentified	.	.	.	7.7	20.2	37.6	73.5	2.3	29.2	.	.	.	.
JEN-11	*Myrtaceae*	*Myrciaria*	*floribunda*	127	1.65	0.04	3.2	5.5	9.9	.	0.5	28.4	0.62		0.03	0.26
JEN-11	*Urticaceae*	*Pourouma*	*bicolor*	149	2.42	0.10	.	31.1	66.9	107.0	0.6	28.7	0.69	0.03	0.13	0.20
JEN-11	*Chrysobalanaceae*	*Licania*	*indet*	147	2.57	0.05	9.0	10.5	25.1	37.7	0.6	28.4	0.41	0.01	0.05	0.11
JEN-11	*Lecythidaceae*	*Eschweilera*	*tessmannii*	134	2.39	0.05	7.5	16.0	23.4	59.4	1.3	28.5	0.69	0.02	0.05	0.20
JEN-11	*Apocynaceae*	*Couma*	*macrocarpa*	81	1.25	0.06	2.8	12.7	31.4	66.3	1.5	29.0	0.51	0.04	0.12	0.28
JEN-11	*Sapotaceae*	*Micropholis*	*guyanensis*	210	2.88	0.04	10.3	18.2	36.3	66.2	1.0	29.0	0.23	0.02	0.06	0.05
JEN-11	*Elaeocarpaceae*	*Sloanea*	*brevipes*	101	1.19	0.08	9.4	15.1	30.3	56.8	1.2	28.2	0.64	0.04	0.12	0.37
ALP-01	*Fabaceae*	*Dipteryx*	*micrantha*	143	1.96	0.09	11.4	16.6	39.5	53.7	0.0	29.1	0.70	0.02	0.10	0.24
ALP-01	*Sapotaceae*	*Pouteria*	*subrotata*	.	.	.	11.6	26.7	47.3	86.3	0.9	29.4	.	.	.	.
ALP-01	*Chrysobalanaceae*	*Licania*	*arachnoidea*	98	1.20	0.02	6.9	7.5	29.9	61.2	0.8	30.1	0.47	0.04	0.12	0.27
ALP-01	*Annonaceae*	*Guatteria*	*schomburgkiana*	125	2.20	0.07	2.9	22.1	32.4	.	2.0	29.7	0.47	.	0.07	0.15
ALP-01	*Olacaceae*	*Minquartia*	*guianensis*	126	1.40	0.05	9.7	19.3	39.1	55.0	0.4	30.6	0.61	0.03	0.13	0.30
ALP-01	*Myristicaceae*	*Iryanthera*	*lancifolia*	154	1.81	0.08	12.7	21.9	43.7	75.2	0.3	28.8	0.45	0.03	0.11	0.17
ALP-01	*Euphorbiaceae*	*Hevea*	*pauciflora*	121	1.96	0.12	0.9	4.5	8.3	.	1.2	30.5	0.52	.	0.02	0.18
ALP-01	*Olacaceae*	*Chaunochiton*	*kappleri*	124	2.43	0.15	7.5	17.7	30.8	57.0	1.3	30.2	0.70	0.02	0.06	0.20
ALP-01	*Ochnaceae*	*Cespedesia*	*spathulata*	119	1.86	0.10	4.2	22.5	30.0	.	1.2	30.0	0.58	.	0.08	0.21
ALP-01	*Fabaceae*	*Taralea*	*oppositifolia*	154	1.56	0.04	1.9	7.0	7.2	.	0.5	30.6	0.78	.	0.02	0.34
ALP-01	*Moraceae*	*Brosimum*	*rubescens*	114	1.61	0.07	2.9	12.0	15.5	38.3	0.9	30.2	.	0.02	0.05	.
ALP-01	*Fabaceae*	*Swartzia*	*polyphylla*	117	2.49	0.06	7.4	17.9	34.8	49.2	0.9	30.4	0.60	0.02	0.07	0.16
ALP-01	*Lepidobotryaceae*	*Ruptiliocarpon*	*caracolito*	74	1.75	0.06	5.5	15.6	24.4	41.8	0.6	30.3	0.18	0.02	0.07	0.07

ALP-01	*Clusiaceae*	*Caraipa*	*punctulata*	161	1.94	0.06	9.5	23.1	41.6	62.3	0.9	30.6	0.49	0.03	0.10	0.17
ALP-01	*Euphorbiaceae*	*Senefeldera*	*inclinata*	116	2.67	0.09	2.3	18.6	23.3	54.2	1.2	29.3	0.86	0.02	0.04	0.22
ALP-01	*Urticaceae*	*Pourouma*	*guianensis subsp. guianensi*	100	1.95	0.09	15.9	19.3	53.9	58.6	-0.3	29.6	0.59	0.02	0.13	0.21
ALP-01	*Euphorbiaceae*	*Hevea*	*pauciflora*	108	1.67	0.11	10.2	19.0	36.8	55.8	0.3	29.2	0.57	0.03	0.10	0.24
ALP-01	*Fabaceae*	*Inga*	*striata*	78	.	0.10	11.9	21.6	41.1	69.7	0.1	29.0	0.62	0.02	0.06	0.14
SUC-01	*Myristicaceae*	*Virola*	*sebifera*	124	2.57	0.11	1.4	25.2	32.2	.	3.2	30.6	0.63	.	0.06	0.17
SUC-01	*Myristicaceae*	*Otoba*	*glycycarpa*	132	.	.	6.0	16.2	27.1	.	1.3	29.8	0.34	.	.	.
SUC-01	*Elaeocarpaceae*	*Sloanea*	*gladysiae*	127	0.90	0.03	1.7	12.2	17.1	40.8	0.8	29.6	0.62	0.04	0.09	0.47
SUC-01	*Sapotaceae*	*Pouteria*	*filipes*	113	1.89	0.09	3.3	18.0	26.5	.	1.7	27.8	0.46	.	0.07	0.16
SUC-01	*Urticaceae*	*Pourouma*	*bicolor*	118	1.91	0.09	16.9	24.7	59.8	91.8	1.2	27.9	0.75	0.04	0.15	0.27
SUC-01	*Lepidobotryaceae*	*Ruptiliocarpon*	*caracolito*	101	1.18	0.06	5.9	13.9	21.5	48.5	0.8	28.6	0.71	0.03	0.09	0.41
SUC-01	*Myristicaceae*	*Iryanthera*	*lancifolia*	131	1.82	0.09	11.3	24.3	48.6	67.1	-0.5	31.0	0.54	0.03	0.13	0.20
SUC-01	*Lecythidaceae*	*Gustavia*	*hexapetala*	112	3.35	0.15	9.2	20.8	42.3	53.2	0.5	31.1	0.73	0.01	0.06	0.15
SUC-01	*Chrysobalanaceae*	*Licania*	*heteromorpha*	.	.	.	3.6	17.7	27.8	60.9	1.6	29.7	.	.	.	0.42
SUC-01	*Humiriaceae*	*Schistostemon*	*reticulatum subsp. reticula*	187	2.20	0.09	4.9	14.0	.	.	.	31.3	0.80	.	.	0.25
SUC-01	*Moraceae*	*Helicostylis*	*scabra*	80	1.40	0.08	8.3	15.7	30.3	53.6	1.7	29.9	0.65	0.03	0.10	0.32
SUC-01	*Sapindaceae*	*Talisia*	*sylvatica*	173	2.18	0.12	7.0	17.7	26.4	60.8	0.8	29.1	0.39	0.02	0.06	0.12
SUC-01	*Fabaceae*	*Inga*	*capitata*	139	.	0.13	10.2	21.7	37.7	75.5	1.0	28.8	0.91	0.01	0.04	0.14
SUC-01	*Lecythidaceae*	*Eschweilera*	*itayensis*	87	0.90	0.05	10.2	14.2	31.2	48.3	0.5	29.0	0.48	0.04	0.16	0.37
SUC-01	*Hypericaceae*	*Vismia*	*amazonica*	132	1.61	0.08	18.8	37.5	68.3	124.8	0.6	29.2	0.59	0.06	0.20	0.25
SUC-01	*Euphorbiaceae*	*Nealchornea*	*yapurensis*	115	1.61	0.09	10.0	25.7	40.5	88.9	1.3	29.1	1.10	0.04	0.12	0.47
SUC-01	*Olacaceae*	*Minquartia*	*guianensis*	105	1.63	0.09	4.6	16.5	22.4	57.8	1.1	29.1	0.58	0.03	0.07	0.24
SUC-01	*Combretaceae*	*Buchenavia*	*tomentosa*	120	2.04	0.10	7.2	16.3	24.2	54.8	0.8	29.4	0.55	0.02	0.06	0.19
JEN-12	*Apocynaceae*	*Macoubea*	*sprucei*	116	1.24	0.08	9.4	18.7	36.3	69.1	0.8	28.0	0.73	0.04	0.14	0.40
JEN-12	*Sapotaceae*	*Pouteria*	*lucumifolia*	175	1.32	0.13	1.0	9.1	13.9	.	1.5	28.8	0.61	.	0.05	0.32
JEN-12	*Clusiaceae*	*Caraipa*	*tereticaulis*	181	1.60	0.05	9.5	16.3	40.3	.	1.5	28.8	0.44	.	0.12	0.19
JEN-12	*Icacinaceae*	*Emmotum*	*floribundum*	.	.	.	9.2	26.6	45.8	75.9	-1.7	29.0	.	.	.	.
JEN-12	*Linaceae*	*Roucheria*	*columbiana*	.	.	.	5.2	13.2	17.1	.	0.7	28.8	.	.	.	0.36
JEN-12	*Euphorbiaceae*	*Micrandra*	*spruceana*	123	1.93	0.10	6.6	16.8	31.0	66.2	1.8	28.4	0.44	0.03	0.08	0.15
JEN-12	*Melastomataceae*	*Mouriri*	*nigra*	196	3.01	0.05	7.8	14.1	23.6	52.0	0.7	28.3	0.83	0.01	0.04	0.19
JEN-12	*Moraceae*	*Brosimum*	*utile subsp. ovatifolium*	134	1.80	0.13	12.3	20.4	40.7	72.2	0.9	28.5	0.43	0.03	0.11	0.16
JEN-12	*Clusiaceae*	*Tovomita*	*calophyllophylla*	179	1.83	0.01	4.6	13.5	19.7	48.7	0.8	28.5	0.78	0.02	0.05	0.29
JEN-12	*Apocynaceae*	*Aspidosperma*	*desmanthum*	163	2.02	0.21	5.0	23.6	39.8	84.5	1.8	29.1	0.50	0.03	0.09	0.17

JEN-12	*Lauraceae*	*Licaria*	*cannella*	166	2.04	0.06	7.3	18.1	33.6	62.6	1.3	29.1	0.62	0.02	0.08	0.21
JEN-12	*Malvaceae*	*Lueheopsis*	*althaeiflora*	208	2.69	0.12	15.4	23.6	48.6	80.6	0.6	28.9	0.61	0.02	0.09	0.16
JEN-12	*Burseraceae*	*Protium*	*polybotryum*	152	1.97	0.08	8.3	29.2	41.6	100.6	1.9	29.4	0.50	0.04	0.10	0.17
JEN-12	*Moraceae*	*Brosimum*	*rubescens*	156	1.70	0.04	13.6	21.6	45.4	73.7	1.0	29.0	0.42	0.03	0.13	0.17
JEN-12	*Moraceae*	*Pseudolmedia*	*rigida*	160	2.71	0.14	1.5	17.8	27.1	65.2	1.7	29.1	0.68	0.02	0.05	0.17
JEN-12	*Sapotaceae*	*Chrysophyllum*	*sanguinolentum*	163	1.97	0.11	14.6	23.7	50.1	96.1	1.0	28.3	0.63	0.04	0.12	0.22
JEN-12	*Euphorbiaceae*	*Alchornea*	*triplinervia*	93	2.12	0.07	13.7	23.5	47.6	79.4	0.8	29.1	0.28	0.03	0.11	0.09
JEN-12	*Apocynaceae*	*Parahancornia*	*peruviana*	117	1.11	0.01	4.1	10.6	17.4	37.6	1.3	29.1	0.61	0.03	0.07	0.37
JEN-12	*Sapotaceae*	*Micropholis*	*guyanensis subsp. guyanensi*	174	2.48	0.15	13.4	37.2	48.3	114.4	1.3	28.9	0.65	0.04	0.09	0.18
ALP-30	*Fabaceae*	*Tachigali*	*bracteosa*	151	2.48	0.15	4.4	22.9	31.5	.	1.9	29.6	0.84	.	0.06	0.23
ALP-30	*Moraceae*	*Brosimum*	*potabile*	158	2.57	0.14	5.6	16.5	21.9	.	1.5	29.4	0.44	.	0.04	0.12
ALP-30	*Elaeocarpaceae*	*Sloanea*	*floribunda*	.	.	0.06	5.6	13.6	21.0	47.5	1.1	29.2		0.02	0.05	0.24
ALP-30	*Euphorbiaceae*	*Micrandra*	*spruceana*	63	1.66	0.13	2.0	7.1	10.3	.	0.5	29.3	0.29	.	0.03	0.12
ALP-30	*Simaroubaceae*	*Simarouba*	*amara*	182	1.88	0.09	8.4	20.5	34.8	72.3	1.5	29.5	0.45	0.03	0.09	0.16
ALP-30	*Humiriaceae*	*Humiria*	*balsamifera*	140	1.12	0.12	7.6	15.7	27.2	57.2	0.8	28.5	0.56	0.04	0.12	0.34
ALP-30	*Lauraceae*	*Ocotea*	*aciphylla*	199	1.75	0.06	8.2	16.2	31.0	56.0	0.6	28.8	0.59	0.03	0.08	0.23
ALP-30	*Apocynaceae*	*Aspidosperma*	*desmanthum*	199	2.18	0.19	10.0	27.4	40.3	95.8	1.4	28.8	0.56	0.03	0.09	0.18
ALP-30	*Fabaceae*	*Diplotropis*	*sp*	113	1.63	0.08	13.6	31.0	46.5	102.1	0.6	29.2	0.44	0.05	0.14	0.18
ALP-30	*Annonaceae*	*Guatteria*	*decurrens*	142	1.19	0.05	5.7	14.7	24.1	53.1	1.0	28.5	0.62	0.04	0.10	0.36
ALP-30	*Euphorbiaceae*	*Micrandra*	*elata*	88	1.57	0.07	2.5	11.0	13.5	37.5	0.8	29.4	0.58	0.02	0.04	0.25
ALP-30	*Lauraceae*	*Ocotea*	*myriantha*	166	2.00	0.06	4.6	14.3	18.0	.	0.5	30.5	0.46	.	0.04	0.16
ALP-30	*Apocynaceae*	*Aspidosperma*	*excelsum*	159	1.88	0.12	3.9	21.4	25.9	.	1.4	29.5	0.69	.	0.07	0.25
ALP-30	*Myrtaceae*	*Calyptranthes*	*bipennis*	154	1.31	0.05	3.9	12.8	18.9	41.0	0.8	30.1	0.55	0.02	0.07	0.29
ALP-30	*Lauraceae*	*Aniba*	*perutilis*	144	1.75	0.06	8.2	15.3	30.3	58.1	1.2	28.1	0.61	0.03	0.08	0.24
ALP-30	*Fabaceae*	*Macrolobium*	*microcalyx*	109	1.39	0.06	7.7	8.5	19.1	31.7	0.6	28.7	0.58	0.02	0.07	0.28
ALP-30	*Myristicaceae*	*Virola*	*pavonis*	141	1.22	0.05	12.7	16.6	40.8	62.7	0.9	29.0	0.69	0.04	0.16	0.39
ALP-30	*Chrysobalanaceae*	*Licania*	*unguiculata*	140	2.25	0.18	11.1	18.5	31.8	69.1	1.4	28.2	0.59	0.02	0.07	0.18
ALP-30	*Anacardiaceae*	*Tapirira*	*guianensis*	62	0.95	0.06	6.5	12.2	22.3	44.6	0.8	28.3	0.38	0.04	0.11	0.27
ALP-30	*Linaceae*	*Roucheria*	*schomburgkii*	99	0.99	0.04	6.1	15.6	26.3	58.1	1.3	28.8	0.52	0.05	0.13	0.36
ALP-30	*Icacinaceae*	*Emmotum*	*floribundum*	188	1.43	0.08	2.9	5.6	8.4	20.8	0.8	29.3	0.34	0.01	0.03	0.16
CUZ-03	*Moraceae*	*Pseudolmedia*	*laevis*	95	1.48	0.08	10.0	19.9	39.4	64.2	0.6	29.9	.	0.03	0.13	.
CUZ-03	*Sapotaceae*	*Pouteria*	*torta subsp. glabra*	138	2.01	0.11	10.0	19.8	52.7	63.8	1.2	30.4	.	0.03	0.12	.
CUZ-03	*Moraceae*	*Poulsenia*	*armata*	119	1.59	0.12	6.8	23.5	46.3	76.8	1.4	29.9	.	0.04	0.14	.
CUZ-03	*Combretaceae*	*Terminalia*	*oblonga*	130	2.26	0.14	5.5	20.0	41.3	65.5	1.4	30.0	.	0.02	0.09	.

CUZ-03	*Malvaceae*	*Guazuma*	*crinita*	112	2.37	.	16.2	28.0	60.9	89.5	-0.1	29.2	.	0.03	0.12	.
CUZ-03	*Sapotaceae*	*Pouteria*	*franciscana*	111	2.16	0.15	8.2	19.5	38.2	64.5	1.0	30.0	.	0.02	0.08	.
CUZ-03	*Phytolaccaceae*	*Gallesia*	*integrifolia*	98	2.62	0.10	8.2	27.0	42.3	87.8	1.0	29.8	.	0.03	0.08	.
CUZ-03	*Dichapetalaceae*	*Tapura*	*sp.*	122	1.00	0.02	8.3	17.8	39.2	59.5	1.2	29.9	.	0.05	0.19	.
CUZ-03	*Meliaceae*	*Trichilia*	*sp.*	90	1.63	0.15	7.7	14.5	31.5	50.3	0.8	30.0	.	0.02	0.09	.
CUZ-03	*Meliaceae*	*Trichilia*	*sp.*	118	1.83	0.10	3.3	10.4	13.7	34.1	1.0	30.4	.	0.01	0.04	.
CUZ-03	*Malvaceae*	*Apeiba*	*aspera*	100	1.44	0.04	11.0	20.7	62.3	61.5	1.1	30.8	.	0.03	0.20	.
CUZ-03	*Fabaceae*	*Swartzia*	*sp.*	76	2.18	0.08	4.3	9.2	15.3	31.3	0.3	28.9	.	0.01	0.03	.
ALP-40	*Fabaceae*	*Dicymbe*	*uaiparuensis*	113	1.93	0.10	5.8	15.8	33.2	43.2	2.3	31.7	0.81	0.02	0.08	0.29
ALP-40	*Sapotaceae*	*Chrysophyllum*	*sanguinolentum*	202	1.88	0.10	15.9	25.1	54.0	80.7	-0.3	29.5	0.70	0.03	0.14	0.25
ALP-40	*Myristicaceae*	*Virola*	*pavonis*	193	2.33	0.13	8.3	18.7	40.8	51.0	1.8	31.4	0.47	0.02	0.08	0.14
ALP-40	unidentified	unidentified	unidentified	195	.	0.08	8.4	15.7	33.8	45.8	1.1	30.6	.	0.02	.	.
ALP-40	*Icacinaceae*	*Emmotum*	*floribundum*	.	1.97	.	4.8	18.4	21.4	.	2.0	31.3	.	.	0.05	0.25
ALP-40	*Fabaceae*	*Jacqueshuberia*	*loretensis*	75	1.63	0.08	10.5	21.8	41.8	69.0	0.8	29.5	0.38	0.03	0.12	0.16
ALP-40	*Elaeocarpaceae*	*Sloanea*	*robusta*	174	1.16	0.09	6.7	19.5	29.7	53.4	1.1	30.8	0.62	0.04	0.12	0.37
ALP-40	*Myrsinaceae*	*Cybianthus*	*nestorii*	200	1.64	0.09	9.4	21.7	37.3	70.3	0.3	30.4	0.61	0.03	0.11	0.25
ALP-40	*Icacinaceae*	*Emmotum*	*floribundum*	123	1.56	0.07	2.6	15.8	30.9	49.8	1.4	31.1	0.59	0.03	0.09	0.26
ALP-40	unidentified	unidentified	unidentified	193	2.37	.	3.5	8.9	14.6	25.5	0.9	32.4	0.62	0.01	0.03	0.18
ALP-40	*Apocynaceae*	*Indet*	*indet*	147	1.61	0.12	6.5	23.8	42.6	67.7	2.6	31.2	.	0.03	0.13	.
ALP-40	*Araliaceae*	*Dendropanax*	*resinosus*	177	2.13	0.10	3.6	14.3	19.2	.	1.0	31.1	0.82	.	0.04	0.26
TAM-09	*Lauraceae*	*Ocotea*	*sp*	112	2.09	0.11	11.3	25.2	46.7	75.9	0.8	30.7	.	0.03	0.11	.
TAM-09	*Urticaceae*	*Pourouma*	*minor*	108	2.28	0.14	14.2	17.5	54.0	69.2	0.9	30.7	.	0.02	0.11	.
TAM-09	*Annonaceae*	.	.	69	.	.	11.2	19.0	35.5	58.8	0.3	30.2	.	.	.	.
TAM-09	*Urticaceae*	*Pourouma*	*sp.*	.	.	.	10.7	9.8	47.2	63.2	0.7	30.1	.	.	.	.
TAM-09	*Burseraceae*	*Trattinnickia*	*glaziovii*	97	1.60	0.17	12.3	19.8	52.8	80.4	0.6	29.5	.	0.04	0.16	.
TAM-09	*Euphorbiaceae*	*Glycydendron*	*amazonicum*	94	2.19	0.11	10.0	24.4	43.0	76.0	0.6	30.1	.	0.03	0.09	.
TAM-09	*Boraginaceae*	*Cordia*	.	118	2.95	0.13	11.1	29.6	67.8	95.5	0.4	29.9	.	0.03	0.11	.
TAM-09	*Fabaceae*	*Hymenaea*	*longifolia*	112	1.96	0.11	14.5	21.6	61.7	79.8	0.6	27.7	.	0.03	0.15	.
TAM-09	*Anacardiaceae*	*Thyrsodium*	*sp*	118	1.65	0.12	11.2	22.7	59.6	84.6	0.8	28.0	.	0.04	0.17	.
TAM-09	*Moraceae*	*Pseudolmedia*	*macrophylla*	112	2.14	0.13	6.2	16.5	32.6	60.4	0.5	28.1	.	0.02	0.07	.
TAM-09	*Meliaceae*	*Cabralea*	*canjerana*	70	.	.	9.3	26.2	47.5	.	1.2	28.5	.	0.03	.	.
TAM-09	*Lauraceae*	*Nectandra*	*purpurea*	105	2.10	0.13	14.1	24.1	71.8	90.9	0.5	27.5	.	0.03	0.16	.
TAM-09	*Moraceae*	*Castilla*	*sp.*	147	2.89	0.21	8.9	14.7	20.9	51.2	-0.5	27.8	.	0.01	0.03	.
TAM-06	*Euphorbiaceae*	*Sapium*	*marmieri*	.	.	.	7.6	28.0	37.9	.	1.3	30.6	.	.	.	.

TAM-06	*Fabaceae*	*Inga*	*alba*	.	.	.	7.3	22.0	35.0	67.3	0.7	30.3	.	.	.	.
TAM-06	*Moraceae*	*Ficus*	*schultesii*	151	2.30	0.15	13.2	23.0	47.6	71.6	0.9	30.8	.	0.02	0.10	.
TAM-06	*Fabaceae*	*Pterocarpus*	*rohrii*	.	.	.	7.1	24.8	28.7	.	1.0	30.2	.	.	.	.
TAM-06	*Moraceae*	*Pseudolmedia*	*laevis*	137	1.83	0.10	7.4	19.7	28.4	65.8	0.4	29.2	.	0.03	0.07	.
TAM-06	unidentified	unidentified	unidentified	96	2.74	0.24	7.2	24.4	37.5	79.0	1.4	30.2	.	0.02	0.07	.
TAM-06	*Moraceae*	*Sorocea*	*pileata*	109	3.02	0.18	9.1	22.7	35.3	76.7	0.6	29.3	.	0.02	0.06	.
TAM-06	*Fabaceae*	*Dipteryx*	*alata*	112	2.34	0.14	16.4	26.4	73.1	86.0	1.2	29.9	.	0.03	0.15	.
TAM-06	*Moraceae*	*Sorocea*	*trophoides*	96	2.52	0.15	9.9	20.4	35.0	63.5	0.2	29.9	.	0.02	0.07	.
TAM-06	*Lecythidaceae*	*Bertolletia*	*excelsa*	151	2.70	0.20	14.8	.	88.6	108.4	-2.7	28.8	.	0.03	0.16	.
TAM-06	*Moraceae*	*Brosimum*	*sp.*	172	2.63	0.13	4.0	14.0	17.8	47.5	1.0	29.4	.	0.01	0.03	.
TAM-06	*Cannabaceae*	*Celtis*	*schippii*	131	2.93	0.21	9.8	23.0	34.8	75.6	0.8	29.5	.	0.02	0.06	.
TAM-06	*Moraceae*	*Clarisia*	*racemosa*	105	2.56	0.20	8.2	22.4	37.3	75.2	1.7	30.0	.	0.02	0.07	.
SPD-02	*Burseraceae*	*Protium*	*sagotianum*	170	2.70	0.19	8.7	25.6	40.2	97.3	0.4	27.3	1.36	0.03	0.07	0.35
SPD-02	*Phyllanthaceae*	*Hieronyma*	*macrocarpa*	105	2.02	0.15	7.7	31.2	60.2	129.2	1.5	26.7	0.48	0.05	0.14	0.16
SPD-02	*Sapotaceae*	*Chrysophyllum*	*sp.*	182	2.91	0.24	4.8	25.1	43.0	.	1.9	27.3	1.19	.	0.07	0.28
SPD-02	*Sapindaceae*	*Matayba*	*guianensis*	210	3.01	0.20	.	.	7.1	.	1.1	25.9	1.17	.	.	0.27
SPD-02	*Fabaceae*	*Inga*	*killipiana*	95	2.51	0.15	8.0	8.2	48.1	.	0.4	27.1	0.71		0.09	0.19
SPD-02	*Melastomataceae*	*Miconia*	*coelestis*	74	1.67	0.09	11.8	39.5	77.6	152.4	0.1	26.9	0.45	0.07	0.22	0.18
SPD-02	*Ebenaceae*	*sp1(1046WFR)*	*sp.*	108	1.69	0.13	5.8	19.9	34.9	.	0.6	27.8	0.86	.	0.10	0.35
SPD-02	*Burseraceae*	*Protium*	*nodulosum*	60	.	.	7.1	23.4	32.7	.	0.0	27.7	0.21	.	.	.
SPD-02	*Burseraceae*	*Protium*	*spruceanum cf*	113	1.95	0.12	5.2	21.1	42.2	84.4	0.6	27.5	0.89	0.03	0.10	0.31
SPD-02	*Lauraceae*	*Beilschmiedia*	*latifolia*	123	2.25	0.11	12.7	27.7	52.0	100.7	-0.7	27.6	1.11	0.04	0.11	0.34
SPD-02	*Caryocaraceae*	*Caryocar*	*sp.*	120	1.85	0.14	5.3	16.0	22.6	.	0.2	26.9	0.56	.	0.06	0.21
SPD-02	*Araliaceae*	*Dendropanax*	*cuneatus*	128	2.57	0.18	6.4	11.8	28.2	55.8	1.0	27.4	0.58	0.02	0.05	0.16
SPD-02	*Aquifoliaceae*	*Ilex*	*sp.*	163	1.91	0.08	9.4	26.9	49.0	104.8	0.5	27.2	0.90	0.04	0.12	0.32
SPD-02	*Moraceae*	*Pseudolmedia*	*laevigata*	103	2.82	0.17	8.6	33.4	56.8	.	2.0	27.1	0.65	.	0.10	0.16
SPD-02	*Moraceae*	**Ficus*	*americana subsp. guianensis*	140	2.04	0.22	11.7	17.5	56.5	76.7	1.7	27.4	0.69	0.03	0.13	0.23
SPD-02	*Sapotaceae*	*Pouteria*	*torta*	121	2.38	0.11	9.7	21.4	38.9	79.3	-0.2	27.3	0.83	0.03	0.08	0.24
SPD-02	*Rubiaceae*	*Elaeagia*	*mariae*	.	.	.	11.4	31.9	58.0	121.7	0.3	27.3	.	.	.	0.27
SPD-02	*Cunoniaceae*	*Weinmannia*	*lechleriana*	116	1.67	0.11	5.6	36.5	68.4	.	6.1	26.7	0.81	.	0.19	0.33
SPD-02	*Lauraceae*	*Nectandra*	*sp.*	134	2.10	0.20	7.9	45.2	.	.		27.0	0.64	.	.	0.21
SPD-01	*Euphorbiaceae*	*Alchornea*	*anamariae*	123	2.32	0.18	10.6	27.1	49.1	97.5	-0.3	27.8	0.79	0.03	0.10	0.23
SPD-01	*Lauraceae*	*Ocotea*	*cernua*	114	1.98	0.10	6.4	21.8	37.5	79.3	0.3	27.9	1.00	0.03	0.09	0.34
SPD-01	*Lauraceae*	*Endlicheria*	*chalisea*	156	2.90	0.15	11.5	24.3	54.6	82.5	-0.2	28.6	0.63	0.02	0.09	0.15

SPD-01	*Brunelliaceae*	*Brunellia*	*stenoptera*	97	1.86	0.13	19.0	38.8	89.7	137.0	-1.0	28.0	0.47	0.06	.	0.17
SPD-01	*Lauraceae*	*Endlicheria*	*macrophylla*	90	2.40	0.20	5.6	22.3	47.9	82.4	0.1	28.4	0.79	0.03	0.09	0.23
SPD-01	*Lauraceae*	*Licaria*	*cannella*	81	1.79	0.13	3.1	10.7	17.1	.	1.0	26.0	0.39		0.05	0.15
SPD-01	*Urticaceae*	*Cecropia*	*angustifolia*	103	2.44	0.16	15.9	30.3	68.0	120.6	-1.5	25.6	0.73	0.04	0.13	0.21
SPD-01	*Euphorbiaceae*	*Hyeronima*	*moritziana*	117	2.42	0.20	10.2	21.7	33.4	.	1.4	25.9	1.07	.	0.07	0.30
SPD-01	*Meliaceae*	*Cabralea*	*canjerana*	117	2.67	0.27	9.5	24.4	40.6	99.8	0.1	25.9	0.79	0.03	0.07	0.20
SPD-01	*Urticaceae*	*Pourouma*	*bicolor subsp. scobina*	93	1.96	0.21	10.4	25.5	56.0	99.3	-0.6	26.2	0.47	0.04	0.14	0.16
SPD-01	*Flacourtiaceae*	*sp5(1101KGC)*	*sp.*	93	1.80	0.10	4.5	10.1	15.6	.	0.1	27.5	0.34	.	0.04	0.13
SPD-01	*Chrysobalanaceae*	*Licania*	*sp.*	143	2.48	0.15	5.9	29.9	50.4	112.6	0.6	27.5	0.65	0.04	0.10	0.18
SPD-01	*Lauraceae*	*Endlicheria*	*sp.*	168	.	0.15	1.8	.	9.5	.	0.6	27.7	.	0.01	.	.
SPD-01	*Lauraceae*	*Nectandra*	*amazonum*	147	2.34	0.14	3.4	8.5	15.9	.	0.7	27.9	1.07	.	0.03	0.31
SPD-01	*Sapotaceae*	*Pouteria*	*sagotiana*	137	2.38	0.17	5.3	15.9	31.5	61.2	-0.1	27.1	0.67	0.02	0.06	0.19
SPD-01	*Phyllanthaceae*	*Hieronyma*	*asperifolia*	166	2.66	0.22	3.5	26.1	36.3	.	2.2	28.2	0.70	.	0.06	0.18
SPD-01	*Hypericaceae*	**Vismia*	*glaziovii*	95	1.85	0.14	15.6	29.7	76.6	115.5	-0.9	27.8	0.74	0.05	0.20	0.27
SPD-01	*Anacardiaceae*	**Tapirira*	*obtusa*	154	2.09	0.17	7.4	20.1	36.0	76.1	0.4	27.5	0.61	0.03	0.08	0.21
SPD-01	*Sapindaceae*	*Matayba*	*guianensis*	154	2.64	0.13	.	.	6.1	.	0.3	27.2	1.18	.	.	0.31
TRU-08	*Aquifoliaceae*	*Ilex*	*rimbachii*	194	.	.	7.7	12.2	40.3	70.6	1.2	24.2	0.56	.	.	.
TRU-08	*Anacardiaceae*	*Tapirira*	*obtusa*	140	.	.	11.9	22.3	59.3	106.1	1.0	24.0	0.48	.	.	.
TRU-08	*Myrtaceae*	*Siphoneugena*	*densiflora*	202	.	.	4.9	5.9	13.2	29.8	0.2	23.3	0.71	.	.	.
TRU-08	*Rubiaceae*	*Elaeagia*	*mariae*	138	.	.	10.6	24.1	57.7	112.0	0.7	24.3	0.44	.	.	.
TRU-08	*Lauraceae*	*Nectandra*	*laurel*	183	.	.	12.7	26.0	63.7	119.3	0.3	24.0	0.75	.	.	.
TRU-08	*Proteaceae*	*Panopsis*	*rubescens var. sprucei*	182	.	.	9.3	18.9	42.6	87.5	0.5	24.0	0.50	.	.	.
TRU-08	*Alzateaceae*	*Alzatea*	*verticillata subsp. vertici*	120	.	.	6.8	22.0	55.9	.	2.8	24.4	0.33	.	.	.
TRU-08	*Clethraceae*	*Clethra*	*fagifolia*	190	2.17	0.10	10.9	28.7	60.6	131.2	0.9	24.4	0.45	0.05	0.13	0.14
TRU-08	*Myrtaceae*	*Myrcia*	*fallax*	156	1.42	0.05	2.9	12.7	22.0	.	1.3	25.1	0.39	.	0.07	0.19
TRU-08	*Araliaceae*	*Schefflera*	*patula*	130	2.20	0.21	4.0	8.5	28.0	47.8	1.5	24.5	0.54	0.02	0.06	0.17
TRU-08	*Proteaceae*	*Roupala*	*monosperma*	225	1.83	0.09	10.4	25.9	55.9	118.3	1.2	24.7	0.61	0.05	0.14	0.23
TRU-08	*Moraceae*	*Ficus*	*americana*	187	2.66	0.21	13.8	21.7	88.8	109.4	1.9	24.9	0.77	0.03	0.16	0.20
TRU-08	*Lauraceae*	*Nectandra*	*cuspidata*	188	2.01	0.06	12.6	29.8	60.9	129.1	0.3	25.0	0.76	0.05	0.14	0.26
TRU-08	*Annonaceae*	*Guatteria*	*terminalis*	114	1.71	0.09	5.8	20.8	40.7	94.4	1.2	25.1	0.42	0.04	0.11	0.17
TRU-08	*Melastomataceae*	*Miconia*	*sp.*	136	2.03	0.11	7.6	25.1	52.4	.	1.6	24.9	0.80	.	0.12	0.27
TRU-08	*Myrtaceae*	*Myrcia*	*mollis*	.	2.15	0.11	7.4	18.3	35.8	85.4	1.2	24.6	.	0.03	0.08	0.17
TRU-08	*Rosaceae*	*Prunus*	*pleiantha*	164	1.61	0.09	9.8	15.2	49.0	73.0	0.4	25.3	0.59	0.04	0.14	0.25
TRU-08	*Hypericaceae*	*Vismia*	*schultesii*	125	1.55	0.11	16.5	25.5	67.5	110.6	-0.5	24.3	0.59	0.06	0.21	0.26

TRU-08	*Euphorbiaceae*	*Alchornea*	*anamariae*	133	2.35	0.16	11.4	24.9	52.8	121.9	1.9	24.4	0.86	0.04	0.11	0.25
TRU-08	*Sapindaceae*	*Cupania*	*rubiginosa*	134	2.24	0.13	3.5	10.4	29.0	.	2.0	24.3	0.70		0.06	0.21
ESP-01	*Clethraceae*	*Clethra*	*scabra*	143	2.35	0.16	6.2	13.3	57.3	85.3	1.0	25.5	.	0.03	0.12	.
ESP-01	*Primulaceae*	**Myrsine*	*coriacea*	125	2.29	0.20	6.7	20.7	47.7	.	1.2	26.5	.	.	0.11	.
ESP-01	*Rosaceae*	*Prunus*	*integrifolia*	141	2.86	0.25	6.9	12.7	34.4	.	0.8	26.7	.	.	0.06	.
ESP-01	*Myricaceae*	*Morella*	*pavonis*	115	2.29	0.11	8.5	34.9	64.8	144.1	1.8	27.0		0.05	0.13	.
ESP-01	*Brunelliaceae*	*Brunellia*	*cuzcoensis*	129	.	.	5.7	13.2	30.6	57.8	1.3	26.4	.	.	.	.
ESP-01	*Melastomataceae*	*Miconia*	*livida*	106	.	.	2.7	10.8	30.2	52.1	1.1	25.9	.	.	.	.
ESP-01	*Cunoniaceae*	*Weinmannia*	*pubescens*	132	1.87	0.15	2.8	20.9	38.8	88.1	1.6	26.6	.	0.04	0.10	.
ESP-01	*Primulaceae*	**Myrsine*	*youngii*	120	2.27	0.18	6.4	15.4	43.6	32.1	1.5	26.8	.	0.01	0.09	.
ESP-01	*Lauraceae*	*Persea*	*buchtienii*	174	2.74	0.21	6.6	10.5	50.6	73.6	2.3	29.9		0.02	0.09	.
ESP-01	*Melastomataceae*	*Miconia*	*sp*	114	1.80	0.17	6.0	26.7	43.4	.	1.2	27.8	.	.	0.11	
ESP-01	*Lauraceae*	*Cinnamomum*	*floccosum*	215	3.08	0.28	1.9	23.9	44.0	.	2.9	29.7	.	.	0.07	.
ESP-01	*Clethraceae*	*Clethra*	*sp.*	186	2.43	0.17	2.2	11.3	24.6	45.0	1.2	29.0	.	0.01	0.05	.
ESP-01	*Icacinaceae*	*Citronella*	*sp.*	177	3.29	0.21	2.8	8.4	17.3	37.2	0.9	26.6	.	0.01	0.03	.
ESP-01	*Melastomataceae*	*Miconia*	*theizans*	.	.	.	3.0	12.9	22.3	.	0.8	25.6	.	.	.	.
ESP-01	*Lauraceae*	*Ocotea*	*cernua*	110	1.69	0.12	2.6	19.2	46.3	.	2.1	24.5	.	.	0.13	.
WAQ-01	*Lauraceae*	*Ocotea*	*sp6(1674KGC)*	134	2.73	0.28	6.1	6.2	25.6	33.3	1.3	29.1	.	0.01	0.04	.
WAQ-01	*Araliaceae*	*Schefflera*	*sp.*	194	2.70	0.22	11.3	14.2	69.7	79.5	1.1	25.6	.	0.02	0.12	.
WAQ-01	*Myrsinaceae*	*Myrsine*	*coriaceae*	141	3.36	0.27	4.0	17.9	21.3	.	0.3	28.5	.	.	0.03	.
WAQ-01	*Chloranthaceae*	*Hedyosmum*	*maximum*	130	2.37	0.20	5.4	12.1	28.0	49.3	1.2	28.3	.	0.02	0.06	.
WAQ-01	*Melastomataceae*	*Axinaea*	*sp.*	77	.	.	5.4	24.1	62.0	.	2.6	25.4	.	0.03	.	.
WAQ-01	*Escalloniaceae*	*Escallonia*	*paniculata*	130	2.58	0.27	10.4	25.9	57.9	119.1	1.4	24.7	.	0.04	0.11	.
WAQ-01	*Chletraceae*	*Chletra*	*cuneata*	213	3.10	.	6.8	42.8	84.7	171.2	2.7	27.0	.	0.04	0.13	.
WAQ-01	*Lauraceae*	*Cinnamomum*	*floccosum*	141	2.88	0.30	6.8	17.6	48.6	83.1	1.9	27.3	.	0.02	0.08	.
WAQ-01	*Podocarpaceae*	*Podocarpus*	*oleifolius*	169	2.29	0.22	3.4	13.9	27.0	.	1.1	24.3	.	.	0.06	.
WAQ-01	*Melastomataceae*	*Miconia*	*coelestis*	139	1.90	0.14	3.1	15.1	29.3	57.5	0.4	27.4	.	0.02	0.07	.
WAQ-01	*Rubiaceae*	*Cinchona*	*officinalis*	87	2.30	0.15	5.3	25.2	43.4	.	-0.1	26.9	.	.	0.09	.
WAQ-01	*Styracaceae*	*Styrax*	*foveolaria*	242	3.20	0.23	5.3	17.1	57.6	84.1	1.1	24.8	.	0.02	0.09	.
WAQ-01	*Lauraceae*	*Persea*	*sp.*	147	2.76	0.27	6.0	18.3	46.3	.	1.3	27.0	.	.	0.08	.
TRU-03	*Cunoniaceae*	*Weinmannia*	*auriculata*	119	1.60	0.14	2.5	10.6	34.1	53.9	0.9	23.8	0.59	0.03	0.10	0.25
TRU-03	*Cardiopteridacea*	*Citronella*	*incarum*	157	.	0.25	8.7	35.2	71.7	169.2	1.8	24.0	.	0.03	.	.
TRU-03	*Lauraceae*	*Persea*	*corymbosa*	213	3.07	0.24	6.2	17.8	50.9	86.9	2.6	25.2	1.24	0.02	0.08	0.28
TRU-03	*Primulaceae*	*Myrsine*	*sp.*	128	2.67	0.23	6.4	28.3	84.0	.	1.3	22.3	0.79	.	0.15	0.20

TRU-03	*Araliaceae*	*Schefflera*	*allocotantha*	162	1.87	0.22	13.1	17.8	42.6	.	-0.5	22.7	0.48	.	0.11	0.17
TRU-03	unidentified	unidentified	unidentified	83	1.65	0.20	4.0	10.1	26.3	57.3	1.6	22.5	.	0.03	0.08	.
TRU-03	*Aquifoliaceae*	*Ilex*	*biserrulata*	203	2.51	0.18	4.3	23.9	58.4	.	1.7	23.0	0.35	.	0.11	0.10
TRU-03	*Clethraceae*	*Clethra*	*cuneata*	215	2.55	0.26	8.8	31.8	73.1	161.7	1.3	22.6	0.95	0.05	0.14	0.26
TRU-03	*Aquifoliaceae*	*Ilex*	*sessiliflora*	197	2.15	0.19	9.1	35.6	72.5	.	1.4	22.7	0.36	.	0.16	0.12
TRU-03	*Primulaceae*	*Myrsine*	*coriacea*	148	2.35	0.20	8.1	31.3	74.2	156.7	1.2	23.5	0.57	0.05	0.15	0.17
TRU-03	*Clethraceae*	*Clethra*	*sp.*	198	2.23	0.24	8.8	34.5	90.2	176.4	1.5	22.8	0.37	0.06	0.19	0.11
TRU-03	*Pentaphylacaceae*	*Freziera*	*karsteniana*	161	2.43	.	13.5	33.2	76.9	167.9	0.7	22.4	0.42	0.05	0.15	0.12
TRU-03	*Lauraceae*	*Persea*	*buchtienii*	146	1.82	0.16	9.1	17.4	37.4	.	0.0	22.4	0.43	.	0.10	0.16
TRU-01	*Melastomataceae*	*Miconia*	*cf. denticulata*	135	2.18	0.18	7.2	23.6	43.8	.	0.7	24.8	1.25	.	0.10	0.39
TRU-01	*Primulaceae*	*Myrsine*	*andina*	120	2.27	0.21	.	.	59.1	.	1.4	24.2	.	.	0.12	.
TRU-01	*Melastomataceae*	*Miconia*	*setulosa*	133	2.39	0.23	9.2	24.0	76.4	131.0	1.2	25.4	0.69	0.04	0.15	0.20
TRU-01	*Melastomataceae*	*Miconia*	*media*	145	2.75	0.20	5.9	26.7	55.4	.	1.8	22.8	.	.	0.10	.
TRU-01	*Asteraceae*	*Senecio*	*sp*	93	2.44	.	10.1	40.6	95.8	.	1.9	22.8	.	.	0.19	.
TRU-01	*Symplocaceae*	*Symplocos*	*psiloclada*	234	2.37	0.16	5.9	20.2	47.6	.	0.8	21.8	0.72	.	0.10	0.21
TRU-01	*Melastomataceae*	*Miconia*	*atrofusca*	155	2.93	0.19	10.9	39.9	85.3	.	1.0	22.6	.	.	0.14	.
TRU-01	*Clethraceae*	**Clethra*	*cuneata*	227	2.74	0.27	10.9	31.0	81.6	156.9	1.1	22.4	.	0.05	0.14	.
TRU-01	*Cunoniaceae*	*Weinmannia*	*microphylla*	75	.	.	4.3	32.0	64.8	.	3.3	23.4	.	.	.	.
TRU-01	*Aquifoliaceae*	*Ilex*	*sessiliflora*	171	.	.	9.5	30.4	71.1	.	1.1	23.5	0.74	.	.	.
TRU-01	*Symplocaceae*	*Symplocos*	*quitensis*	174	.	.	11.6	33.2	62.5	.	0.5	22.5	0.78	.	.	.
TRU-01	*Lauraceae*	*Persea*	*ferruginea*	.	.	.	7.9	22.0	51.7	.	0.7	23.3	.	.	.	.
TRU-01	*Melastomataceae*	*Miconia*	*sp.*	128	.	.	3.9	15.0	48.0	95.6	0.9	22.0	.	.	.	.
TRU-01	*Brunelliaceae*	**Brunellia*	*inermis*	122	.	.	4.3	14.1	26.8	.	1.1	21.8	0.68	.	.	.

Table S2. Pearson correlations for bivariate relationships among leaf traits and environmental parameters. Number of replicates is given in bracket. Abbreviations: N_a = leaf nitrogen, P_a = leaf phosphorus, leaf N:P = leaf nitrogen to phosphorus ratio, M_a = leaf mass per unit leaf area, Chl = chlorophyll a and b content, $V_{cmax,a}^{25}$ = maximum carboxylation velocity of Rubisco normalised to 25°C, $J_{max,a}^{25}$ = maximum rate of electron transport normalised to 25°C, $V_{N,25}$ = ratio of maximum carboxylation velocity of Rubisco normalised to 25°C over leaf nitrogen, Soil P=soil phosphorus, Soil N=soil nitrogen, MAT = mean annual temperature, MAP = mean annual precipitation. Environmental parameters at each site were obtained using site information from Quesada (*et al.* 2010; pers. comm. 2014) and Asner *et al.* (2014a). Note that the coefficient of determination, r^2, equals the square of the Pearson correlation coefficient.

	N_a	P_a	Leaf N:P	M_a	Chl	$V_{cmax,a}^{25}$	$J_{max,a}^{25}$	$V_{cmax,N}^{25}$	Soil P	Soil N	Elevation	MAT	MAP
N_a ($g\ m^{-2}$)	1 (248)	0.613** (240)	-0.208** (232)	0.353** (246)	0.370** (171)	0.226** (246)	0.227** (184)	-0.297** (242)	0.356** (248)	0.319** (248)	0.368** (248)	-0.375** (248)	-0.041 (248)
P_a ($g\ m^{-2}$)		1 (248)	-0.769** (227)	0.188** (246)	0.229** (170)	0.331** (241)	0.366** (186)	-0.013 (234)	0.611** (248)	0.623** (248)	0.694** (248)	-0.711** (248)	-0.004 (248)
Leaf N:P			1 (245)	-0.085 (232)	-0.047 (159)	-0.280** (243)	-0.244** (177)	-0.157* (227)	-0.476** (245)	-0.512** (245)	-0.539** (245)	0.551** (245)	-0.020 (245)
M_a ($g\ m^{-2}$)				1 (274)	0.157* (185)	0.077 (272)	0.196** (199)	-0.095 (240)	-0.029 (274)	0.195** (274)	0.194** (274)	-0.162** (274)	-0.111 (274)
Chl ($g\ m^{-2}$)					1 (185)	-0.001 (183)	0.085 (133)	-0.109 (166)	0.285** (185)	0.153* (185)	0.145* (185)	-0.151* (185)	0.239** (185)
$V_{cmax,a}^{25}$ ($\mu mol\ m^{-2}\ s^{-1}$)						1 (283)	0.840** (209)	0.810** (242)	0.287** (290)	0.354** (290)	0.384** (283)	-0.399** (283)	-0.070 (283)
$J_{max,a}^{25}$ ($\mu mol\ m^{-2}\ s^{-1}$)							1 (209)	0.629** (182)	0.373** (209)	0.475** (209)	0.461** (209)	-0.462** (209)	0.152* (209)
$V_{cmax,N}^{25}$ ($\mu mol\ gN^{-1}\ s^{-1}$)								1 (242)	0.143* (242)	0.201** (242)	0.186** (242)	-0.198** (242)	0.028 (242)
Soil P ($mg\ kg^{-1}$)									1 (292)	0.681** (292)	0.716** (292)	-0.720** (292)	0.380** (292)
Soil N ($g\ kg^{-1}$)										1 (292)	0.921** (292)	-0.902** (292)	0.104 (292)
Elevation (m a.s.l.)											1 (292)	-0.992** (292)	-0.068 (292)
MAT (°C)												1 (292)	0.070 (292)
MAP (mm)													1 (292)

** Correlation is significant at p<0.01

* Correlation is significant at p<0.05

Table S3: Standardized major axis regression slopes and their confidence intervals for log-log transformed relationships comparing leaf traits of lowland (~173 species) and upland (~120 species) species, depicted in Figures 2, 4 and 5 in the main text. Analysis undertaken using individual replicates. Coefficients of determination (r^2) and significance values (p) of each bivariate relationship are shown. Significantly different p values are shown in bold. 95% confidence intervals (CI) of SMA slopes and y-axis intercepts are shown in parentheses. Where SMA tests for common slopes revealed no significant differences between the two groups (i.e. p > 0·05), common slopes were used (with CI of the common slopes provided). Where there was a significant difference in the elevation (i.e. y-axis intercept) of the common-slope SMA regressions, values for the y-axis intercept are provided. Where appropriate, significant shifts along a common slope are indicated.

Bivariate relationship (y- vs. x-axis)	Group	r^2	p	Slope	Slope CI	Intercept	p	Common slope	Common slope CI	p	Common slope y-axis intercept	Shift along a common slope?
N_a vs. M_a	Lowland	0.069	**0.001**	1.027	(0.879, 1.199)	-1.889	0.003					
	Upland	0.198	**<0.001**	0.709	(0.593, 0.848)	-1.165						
P_a vs. M_a	Lowland	<0.001	0.985	-2.096	(-2.463, -1.784)	3.323	0.002					
	Upland	0.038	**0.034**	1.345	(1.104 , 1.639)	-3.661						
$V_{cmax,a}^{25}$ vs. M_a	Lowland	0.003	0.468	-1.753	(-2.054, -1.495)	5.183	0.595	1.705	(1.511, 1.925)	0.010	-2.089	Yes, p < 0.001
	Upland	0.014	0.212	1.642	(1.362, 1.981)	-1.863					-1.999	
$V_{cmax,a}^{25}$ vs. N_a	Lowland	0.024	**0.050**	1.707	(1.454, 2.005)	1.022	0.014					
	Upland	0.003	0.613	2.384	(1.950, 2.914)	0.801						
$V_{cmax,a}^{25}$ vs. P_a	Lowland	0.041	**0.013**	0.841	(0.717, 0.986)	2.417	0.003					
	Upland	0.005	0.502	1.231	(1.003, 1.511)	2.602						
$V_{cmax,a}^{25}$ vs. leaf N:P	Lowland	0.002	0.563	-1.246	(-1.468, -1.057)	3.136	0.028					
	Upland	0.027	0.113	-1.657	(-2.030, -1.353)	3.494						
$J_{max,a}^{25}$ vs. M_a	Lowland	0.004	0.473	1.136	(0.956, 1.349)	-0.577	0.022					
	Upland	0.005	0.552	1.620	(1.268, 2.069)	-1.533						
$J_{max,a}^{25}$ vs. N_a	Lowland	0.050	**0.012**	1.046	(0.881, 1.242)	1.518	0.001					
	Upland	0.001	0.794	-2.224	(-2.897, -1.707)	2.736						
$J_{max,a}^{25}$ vs. P_a	Lowland	0.077	**0.002**	0.5113	(0.432, 0.605)	2.368	0.001					
	Upland	0.029	0.205	-1.101	(-1.432, -0.846)	1.086						
$J_{max,a}^{25}$ vs. leaf N:P	Lowland	<0.001	0.888	-0.813	(-0.974, -0.679)	2.876	0.003					
	Upland	<0.001	0.930	-1.378	(-1.800, -1.055)	3.493						
$V_{cmax,N}^{25}$ vs. M_a	Lowland	0.044	**0.010**	-1.841	(-2.157, -1.570)	5.092	0.789	-1.866	(-1.647, -2.114)	<0.001	5.146	No, P= 0.809
	Upland	0.010	0.327	-1.908	(-2.336, -1.559)	5.385					5.295	
$V_{cmax,N}^{25}$ vs. P_a	Lowland	0.012	0.195	-0.890	(-1.048, -0.756)	0.239	0.004					
	Upland	0.030	0.101	-1.301	(-1.599, -1.059)	0.275						
$V_{cmax,N}^{25}$ vs. leaf N:P	Lowland	0.003	0.536	-1.307	(-1.548, -1.103)	2.945	0.057	-1.455	(-1.455, -1.274)	<0.001	3.141	Yes, p < 0.001
	Upland	0.020	0.185	-1.709	(-2.105, -1.388)	3.185					2.903	
$J_{max,a}^{25}$ vs. $V_{cmax,a}^{25}$	Lowland	0.590	**<0.001**	1.341	(1.204, 1.439)	15.81	0.001					
(not log-transformed)	Upland	0.748	**<0.001**	1.962	(1.736, 2.217)	-4.803						

Table S4: Means ± standard deviation of leaf physiology and chemistry, expressed on area basis for each site. Leaf traits are sorted according to decreasing leaf N:P for lowland sites and increasing elevation for upland sites.

Abbreviations: $A_{400,a}$ light-saturated net photosynthesis measured under 400 µmol mol $^{-1}$ atmospheric [CO_2]; C_{i400}, intercellular CO_2 partial pressure at 400 µmol mol $^{-1}$ atmospheric [CO_2]; C_{a400}, atmospheric CO_2 partial pressure at 400 µmol mol $^{-1}$ atmospheric [CO_2]; C_{i400}: C_{a400}, ratio of intercellular to atmospheric CO_2 at 400 µmol mol $^{-1}$ [CO_2]; A_{400}:N, ratio of light-saturated net photosynthesis measured under 400 µmol mol $^{-1}$ atmospheric [CO_2] over leaf N; $A_{2000,a}$, light-saturated net photosynthesis measured under 2000 µmol mol $^{-1}$ atmospheric [CO_2]; C_{i2000}, intercellular CO_2 at 2000 µmol mol $^{-1}$ atmospheric [CO_2]; A_{2000}:N, ratio of light-saturated net photosynthesis measured under 2000 µmol mol $^{-1}$ atmospheric [CO_2] over leaf N; R_d, leaf dark respiration measured at 400 µmol mol $^{-1}$ atmospheric [CO_2]; Leaf *T*, leaf temperature inside gas exchange cuvette; Chl, chlorophyll a and b content.

	Sites	$A_{400,a}$ (µmol m^{-2} s^{-1})	C_{i400} (Pa)	C_{a400} (Pa)	C_{i400}: C_{a400}	$A_{400,N}$ (µmol gN^{-1} s^{-1})	$A_{2000,a}$ (µmol m^{-2} s^{-1})	C_{i2000} (Pa)	$A_{2000,N}$ (µmol gN^{-1} s^{-1})	R_{light} (µmol m^{-2} s^{-1})	Leaf *T* (°C)	Chl (g m^{-2})
Lowland	SUC-05	8.8 ± 4.5	28.9 ± 2.9	38.5 ± 0.7	0.75 ± 0.08	4.6 ± 2.5	20.9 ± 6.1	156.5 ± 21.8	11.9 ± 5.1	1.2 ± 0.5	28.8 ± 0.5	0.73 ± 0.21
	TAM-05	9.5 ± 2.7	25.3 ± 2.6	38.0 ± 0.5	0.67 ± 0.06	4.8 ± 1.7	22.2 ± 3.6	147.5 ± 21.1	10.9 ± 2.1	0.7 ± 0.6	30.2 ± 0.7	
	JEN-11	7.3 ± 3.7	31.4 ± 2.9	38.9 ± 0.6	0.81 ± 0.07	4.1 ± 2.3	17.4 ± 7.5	171.7 ± 14.2	8.3 ± 3.9	1.1 ± 0.6	28.8 ± 0.4	0.69 ± 0.30
	ALP-01	7.5 ± 4.4	27.2 ± 3.4	39.2 ± 0.4	0.69 ± 0.09	3.9 ± 2.4	17.4 ± 6.1	146.5 ± 20.4	8.7 ± 3.0	0.7 ± 0.6	29.9 ± 0.6	0.58 ± 0.15
	SUC-01	7.8 ± 4.7	29.2 ± 4.3	38.9 ± 0.6	0.77 ± 0.08	3.8 ± 2.3	19.6 ± 6.2	157.4 ± 21.2	10.5 ± 3.4	1.1 ± 0.8	29.5 ± 1.0	0.64 ± 0.19
	JEN-12	8.5 ± 4.4	30.5 ± 2.8	38.9 ± 0.5	0.78 ± 0.07	4.5 ± 2.3	19.9 ± 6.8	161.5 ± 24.8	10.3 ± 3.1	1.0 ± 0.8	28.8 ± 0.4	0.57 ± 0.15
	ALP-03	6.7 ± 3.2	30.2 ± 2.5	39.2 ± 0.4	0.77 ± 0.07	4.3 ± 2.4	16.1 ± 6.2	165.3 ± 14.0	10.0 ± 3.8	1.0 ± 0.4	29.1 ± 0.6	0.54 ± 0.13
	CUZ-03	8.3 ± 3.4	25.5 ± 3.3	37.8 ± 0.5	0.67 ± 0.08	4.7 ± 2.2	19.2 ± 5.7	147.6 ± 24.0	10.8 ± 3.9	0.9 ± 0.4	29.9 ± 0.5	
	ALP-04	7.2 ± 3.7	25.4 ± 3.1	39.1 ± 0.3	0.65 ± 0.08	4.0 ± 2.3	18.3 ± 4.5	129.7 ± 27.8	10.7 ± 3.9	1.3 ± 0.8	30.9 ± 0.8	0.62 ± 0.14
	TAM-09	11.2 ± 2.3	26.5 ± 2.7	37.2 ± 0.5	0.71 ± 0.07	5.5 ± 1.8	20.9 ± 5.4	153.6 ± 18.6	10.2 ± 2.6	0.6 ± 0.4	29.1 ± 1.2	
	TAM-06	9.4 ± 3.5	26.7 ± 3.6	38.0 ± 0.6	0.70 ± 0.09	4.0 ± 1.7	22.6 ± 3.6	150.3 ± 21.5	9.1 ± 2.1	0.6 ± 1.0	29.9 ± 0.6	
Lowland mean		**8.2 ± 3.9** [a]	**28.4 ± 3.7** [a]	**38.6 ± 0.8** [a]	**0.74 ± 0.09** [a]	**4.3 ± 2.2** [a]	**19.2 ± 6.1** [a]	**155.2 ± 22.7** [a]	**10.1 ± 3.6** [a]	**1.0 ± 0.7** [a]	**29.4 ± 0.9** [a]	**0.62 ± 0.17** [a]
Upland	SPD-02	8.4 ± 2.7	21.0 ± 1.9	32.2 ± 0.3	0.65 ± 0.06	3.9 ± 1.4	25.3 ± 9.7	89.3 17.1	11.3 ± 5.2	1.0 ± 1.5	27.2 ± 0.5	0.78 ± 0.30
	SPD-01	8.6 ± 5.0	20.4 ± 2.4	33.2 ± 0.6	0.61 ± 0.07	3.8 ± 2.2	23.0 ± 8.6	95.2 16.5	10.5 ± 4.4	0.1 ± 0.8	27.3 ± 1.0	0.72 ± 0.23
	TRU-08	9.0 ± 3.7	20.4 ± 3.0	32.0 ± 0.5	0.64 ± 0.10	4.1 ± 1.7	19.9 ± 7.0	90.4 20.4	10.6 ± 3.8	1.1 ± 0.8	24.5 ± 0.5	0.59 ± 0.16
	ESP-01	4.9 ± 2.9	16.7 ± 2.4	28.5 ± 0.3	0.58 ± 0.09	2.3 ± 1.4	17.1 ± 7.7	55.1 11.9	8.1 ± 4.4	1.4 ± 0.6	26.9 ± 1.7	
	WAQ-01	6.1 ± 2.4	16.5 ± 2.2	27.9 ± 0.4	0.59 ± 0.08	2.3 ± 0.9	19.3 ± 8.9	58.0 17.9	7.1 ± 3.1	1.2 ± 0.8	26.6 ± 1.6	
	TRU-03	7.9 ± 3.2	17.6 ± 2.3	27.7 ± 0.3	0.63 ± 0.08	3.6 ± 1.7	25.2 ± 9.4	65.3 12.6	10.8 ± 3.6	1.2 ± 0.8	23.1 ± 0.8	0.60 ± 0.29
	TRU-01	7.8 ± 3.1	17.1 ± 2.1	26.3 ± 0.3	0.65 ± 0.08	3.5 ± 1.2	26.5 ± 8.6	58.8 11.7	11.5 ± 2.6	1.3 ± 0.7	23.0 ± 1.1	0.81 ± 0.22
Upland mean		**7.6 ± 3.6** [a]	**18.8 ± 3.0** [b]	**30.1 ± 2.6** [b]	**0.62 ± 0.08** [b]	**3.4 ± 1.7** [b]	**22.3 ± 8.9** [b]	**75.8 ± 22.8** [b]	**10.0 ± 4.3** [a]	**1.0 ± 1.0** [a]	**25.7 ± 2.1** [b]	**0.69 ± 0.25** [b]

Table S5: Standardized major axis regression slopes and their confidence intervals for relationships comparing leaf traits of lowland (~126 species) and upland (~40 species) species, depicted in Figures 7 and S2 in the main text. Analysis undertaken using individual replicates. Coefficients of determination (r^2) and significance values (p) of each bivariate relationship are shown. Significantly different p values are shown in bold. 95% confidence intervals (CI) of SMA slopes and y-axis intercepts are shown in parentheses. Where SMA tests for common slopes revealed no significant differences between the two groups (i.e. $p>0{\cdot}05$), common slopes were used (with CI of the common slopes provided). Where there was a significant difference in the elevation (i.e. y-axis intercept) of the common-slope SMA regressions, values for the y-axis intercept are provided. Where appropriate, significant shifts along a common slope are indicated.

Bivariate relationship (y- vs. x-axis)	Group	r^2	p	Slope	Slope CI	Intercept	p	Common slope	Common slope CI	p	Common slope y-axis intercept	Shift along a common slope?
n_P vs. M_a	Lowland	0.012	0.258	-0.2421	(-0.292, -0.201)	57.02	0.072	-0.2172	(-0.187, -0.253)	0.698	53.600	No, p = 0.185
	Upland	0.002	0.719	-0.1797	(-0.231, -0.134)	47.64					52.945	
n_R vs. M_a	Lowland	0.042	**0.011**	-0.1217	(-0.143, -0.104)	24.841	0.482	-0.1176	(-0.104, -0.133)	<0.001	24.303	No, p = 0.794
	Upland	0.001	0.809	0.1110	(0.090, 0.137)	-5.861					27.171	
n_E vs. M_a	Lowland	0.023	0.087	-0.0279	(-0.033, -0.023)	6.362	0.249	-0.0296	(-0.026, -0.034)	<0.001	6.579	No, p = 0.227
	Upland	0.001	0.870	-0.0339	(-0.045, -0.026)	8.240					7.605	
n_P vs. N_a	Lowland	0.358	**<0.001**	-16.52	(-19.23, -14.18)	55.21	0.711	-16.76	(-14.73, -19.08)	0.017	55.676	Yes, p <0.001
	Upland	0.001	0.773	-17.43	(-22.36, -13.59)	60.53					59.063	
n_R vs. N_a	Lowland	0.171	**<0.001**	-7.876	(-9.127, -6.797)	24.29	0.101	-8.499	(-7.544, -9.564)	<0.001	25.515	No, p = 0.065
	Upland	0.094	**0.003**	-9.725	(-11.842, -7.987)	32.64					29.802	
n_E vs. N_a	Lowland	0.382	**<0.001**	-1.732	(-1.992, -1.506)	6.156	0.001					
	Upland	0.165	**0.002**	-3.039	(-3.889, -2.374)	10.278						
n_P vs. P_a	Lowland	0.154	**<0.001**	-225.4	(-268.6, -189.2)	42.22	0.002					
	Upland	0.028	0.186	-129.5	(-165.9, -101.1)	43.04						
n_R vs. P_a	Lowland	0.013	0.175	-90.48	(-106. 4, -76.96)	17.23	0.167	-84.48	(-74.36, -96.08)	<0.001	16.677	Yes, p <0.001
	Upland	0.030	0.106	-75.48	(92.97, -61.28)	23.26					24.851	
n_E vs. P_a	Lowland	0.050	**0.013**	-19.99	(-23.79, -16.80)	4.635	0.568	-20.60	-17.84 -23.75	<0.001	4.692	Yes, p = 0.001
	Upland	0.155	**0.003**	-21.89	(-28.19, -16.99)	7.047					6.824	
n_A vs. M_a	Lowland	0.070	**0.003**	-1.2405	(-1.471, -1.046)	2.143	0.085	-1.152	(-0.992, -1.345)	0.025	1.958	No, p = 0.742
(log-transformed)	Upland	0.002	0.794	-0.8934	(-1.233, -0.647)	1.475					2.026	
n_A vs. N_a	Lowland	0.445	**<0.001**	-1.078	(-1.231, -0.945)	-0.159	0.099	-1.129	(-0.999, -1.273)	<0.001	-0.145	No, p = 0.189
(log-transformed)	Upland	0.156	**0.011**	-1.403	(-1.881, -1.046)	0.037					-0.054	
n_A vs. P_a	Lowland	0.056	**0.008**	-0.556	(-0.661, -0.468)	-1.065	0.446	-0.576	(-0.495, -0.670)	<0.001	-1.086	Yes, p <0.001
(log-transformed)	Upland	0.100	**0.047**	-0.640	(-0.869, -0.471)	-0.957					-0.904	

Table S6: Stepwise selection process for the fixed component of linear mixed effect models: with $V_{cmax,a}^{25}$ and $J_{max,a}^{25}$ as the response variables. Continuous explanatory variables are N_a, P_a, M_a, total soil P and N, MAT and effective cation exchange capacity of soil. Given the large number of species in our dataset, we treated phylogeny as a random component within the model construct and so focused on phylogenetic variation rather than individual species mean values. Because of low replication at the species level, a simple random term of Family was found to perform just as well as the fully nested Family/Genus/Species. In choosing explanatory terms for the model's fixed component, we began by adopting a beyond-optimal model including those continuous variables suggested by our starting hypotheses, initial data exploration, and with care to avoid problems of collinearity - a limited number of two-way interactions were included (specifically N:P). A backward, stepwise selection process adopted the Maximum Likelihood method; the model's random component was held constant through these iterations. The effect of dropping sequential terms was tested by comparing the nested model variants. The model's random component was identical in all variants. Test parameters and statistics are DF (degrees of freedom), AIC (Akaike Information Criterion), BIC (Bayesian Information Criterion) and -2LL (-2 restricted Log Likelihood). The effect of dropping sequential terms was tested by comparing the nested model variants. The best predictive model, underlined, was selected based on a combination of low criteria score and simplicity, considering two-way interactions only. Because our final preferred model, arrived at by backward selection, was so parsimonious, we then tested the effect of adding selected terms and interactions not previously included – in no case did those additional terms improve model performance.For the J_{max} model, it was not thought necessary to include site average terms for leaf N and P, since those terms had proved so marginal in the equivalent V_{cmax} model selection steps.

Model	Fixed component	DF	AIC	BIC	-2LL
$V_{cmax,a}^{25}$					
1	log10(Soil P) + N_a + Site.N_a + P_a + Site.P_a + N_a.P_a	9	1663.5	1693.1	-822.7
2	log10(Soil P) + N_a + Site.N_a + P_a + Site.P_a + log10(Soil P).N_a	9	1664.0	1693.7	-823.0
3	log10(Soil P) + N_a + Site.N_a + P_a + Site.P_a	8	1663.2	1689.6	-823.6
4	log10(Soil P) + N_a + Site.N_a + P_a	7	1661.4	1684.4	-823.7
5	log10(Soil P) + N_a + P_a	6	1661.5	1681.3	-824.7
6	**log10(Soil P) + P_a**	5	**1659.7**	**1676.1**	**-824.8**
7	log10(Soil P) + P_a + MAT + P_a:MAT	7	1663.1	1686.1	-824.5
8	log10(Soil P) + P_a + MAT	6	1661.1	1680.9	-824.6
9	log10(Soil P) + P_a + SoilN	6	1658.9	1678.6	-823.4
10	log10(Soil P) + P_a + ECEC	6	1657.5	1677.2	-822.7
11	log10(Soil P) + P_a + M_a	6	1660.8	1680.5	-824.4
$J_{max,a}^{25}$					
1	log10(Soil P) + P_a + N_a + M_a + MAT + N_a.P_a	9	1361.1	1388.0	-671.5
2	log10(Soil P) + P_a + N_a + M_a + MAT + log10(Soil P).N_a	9	1358.7	1385.7	-670.4
3	log10(Soil P) + P_a + N_a + M_a + MAT	8	1360.3	1384.3	-672.2
4	log10(Soil P) + P_a + M_a + MAT	7	1358.3	1379.3	-672.2
5	log10(Soil P) + P_a + M_a	6	1357.3	1375.3	-672.6
6	**log10(Soil P) + P_a**	5	**1359.9**	**1374.9**	**-674.9**
7	log10(Soil P)	4	1363.4	1375.4	-677.7

Abbreviations: N_a = leaf nitrogen, P_a = leaf phosphorus, M_a = leaf mass per unit leaf area, Soil P = soil phosphorus, Soil N = soil nitrogen, MAT = mean annual temperature, ECEC = effective cation exchange capacity of soil. Environmental parameters at each site were obtained using site information from Quesada (*et al.* 2010; pers. comm. 2014), Asner *et al.* (2014a) and Malhi *et al.* (in prep.).

Table S7: Comparison of mean values of V_{cmax} and J_{max} at 25°C values (V_{cmax25} and J_{max25}, respectively) in upland and lowland plants calculated using different activation energies (E_a) for each parameter (i.e. V_{cmax} and J_{max}) , and K_c and K_o constants when calculating V_{cmax}. Here, we compare values calculated using E_a values reported by Farquhar *et al.* (1980) and Bernacchi *et al.* (2002). For Farquhar *et al.* (1980), E_a values of K_c and K_o used were 59.4 and 36.0 kJ mol^{-1}, respectively. For Bernacchi *et al.* (2002), the E_a values of K_c and K_o were 80.99 and 23.72 kJ mol^{-1}. For calculations made using Farquhar *et al.* (1980), we used E_a values for V_{cmax} and J_{max} of 64.8 and 37.0 kJ mol^{-1}, respectively; for Bernacchi *et al.* (2002), the E_a values for V_{cmax} and J_{max} were 65.3 and 43.9 kJ mol^{-1}, respectively. Values are overall mean ± SD of leaf traits for lowland and upland sites. Significantly different means are indicated by different letters (p<0.05).

Source of constants		$V_{cmax,a}^{25}$ (μmol m^{-2} s^{-1})	$J_{max,a}^{25}$ (μmol m^{-2} s^{-1})
Farquhar et al. (1980)	Lowland species	35.9 ± 14.6^{a}	66.7 ± 18.6^{a}
	Upland species	48.8 ± 20.0^{b}	96.9 ± 36.9^{b}
Bernacchi et al. (2002)	Lowland species	39.7 ± 15.6^{a}	64.7 ± 18.6^{a}
	Upland species	50.5 ± 18.5^{b}	96.6 ± 37.3^{b}

Figure S1: Plots of maximum carboxylation velocity of Rubisco normalised to 25°C, $V_{cmax,a}^{25}$ against (A) mean annual temperature (MAT) and (F) soil P concentration; maximum rate of electron transport normalised to 25°C, $J_{max,a}^{25}$ against (B) MAT and (G) soil P; ratio of $V_{cmax,a}^{25}$ over leaf N, $V_{cmax,N}^{25}$ against (C) MAT and (H) soil P; ratio of light-saturated net photosynthesis measured at 400 µmol mol $^{-1}$ atmospheric [CO_2] over leaf N, A_{400}:N against (D) MAT and (I) soil P; and ratio of light-saturated net photosynthesis measured at 2000 µmol mol $^{-1}$ atmospheric [CO_2] over leaf N, A_{2000}:N against (E) MAT and (J) soil P for each site. In (A)-(H), black circles (and solid regression lines) represent photosynthetic parameters calculated using constants of Farquhar *et al.* (1980) and grey circles (and dashed regression lines) represent parameters calculated using Bernacchi *et al.* constants (2002). R^2 values shown are for Farquhar *et al.* (1980) only regressions. Environmental parameters at each site were obtained using site information from Quesada (*et al.* 2010; pers. comm. 2014) and Asner *et al.* (2014a).

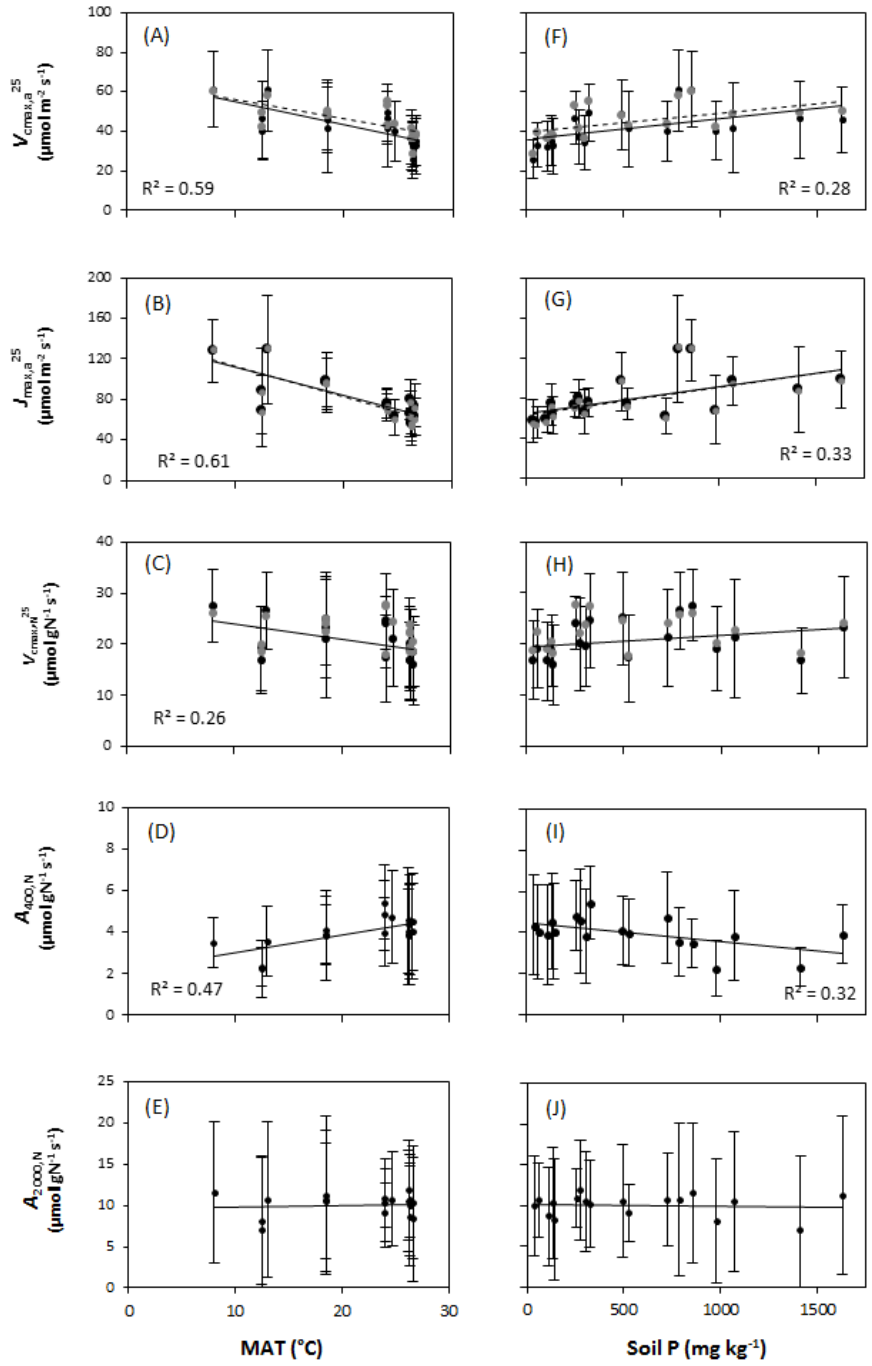


Figure S2: Plots of % of leaf N to pigment-protein complexes, n_P, % of leaf N to Rubisco, n_R, and % of leaf N to electron transport, n_E, in relation to (A) leaf mass per unit leaf area, M_a, (B) leaf N-area, N_a, and (C) leaf P-area, P_a. Data points represent individual leaf values (150 lowland species and 92 upland species).

SMA regressions: solid line, lowland species; dashed line, upland species. SMA regressions are given only when the relationships are significant (p<0.05) and when lowland and upland shared similar slopes, refer to Table S5. Analyses were performed on percentage instead of fraction of N to meet the requirement of SMA analyses.

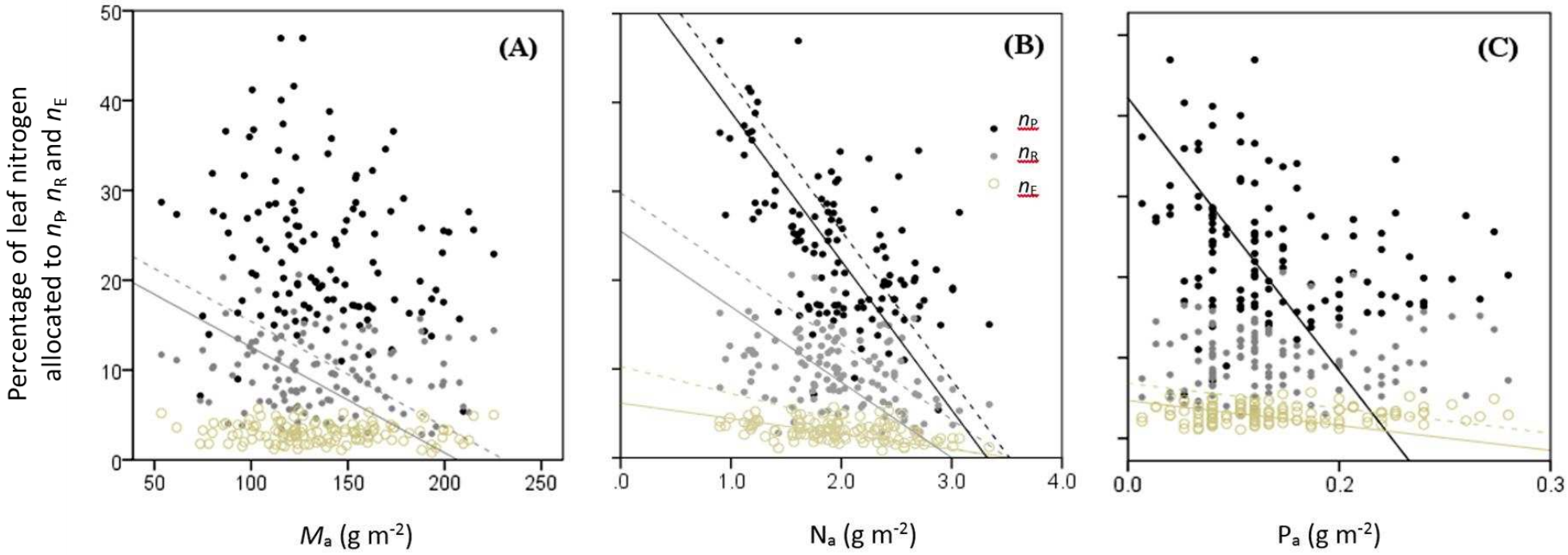


Figure S3: Plots of fraction of leaf N allocated in Rubisco, n_R in relation to leaf mass per unit leaf area, M_a, for (A) 16 lowland species for where both *in vivo* and *in vitro* estimates were available; and (B) 150 lowland and 92 upland species for where *in vivo* data was available. Black circles in Fig S3A are *in vivo* n_R derived from maximum carboxylation velocity of Rubisco (normalised to 25°C) (i.e. a subset of those in Fig S3B). Grey circles in Fig S3A are *in vitro* n_R derived from Rubisco western blot assay. n_R in Fig 3B is derived from maximum carboxylation velocity of Rubisco (normalised to 25°C), $V_{cmax,a}^{25}$. In both figures, the line shown is inferred from the global relationship between photosynthetic rate per unit leaf N and M_a (Hikosaka, 2004; Wright *et al.*, 2004), the equation $n_R = M_a^{-0.435}$ given in Harrison *et al.* (2009)

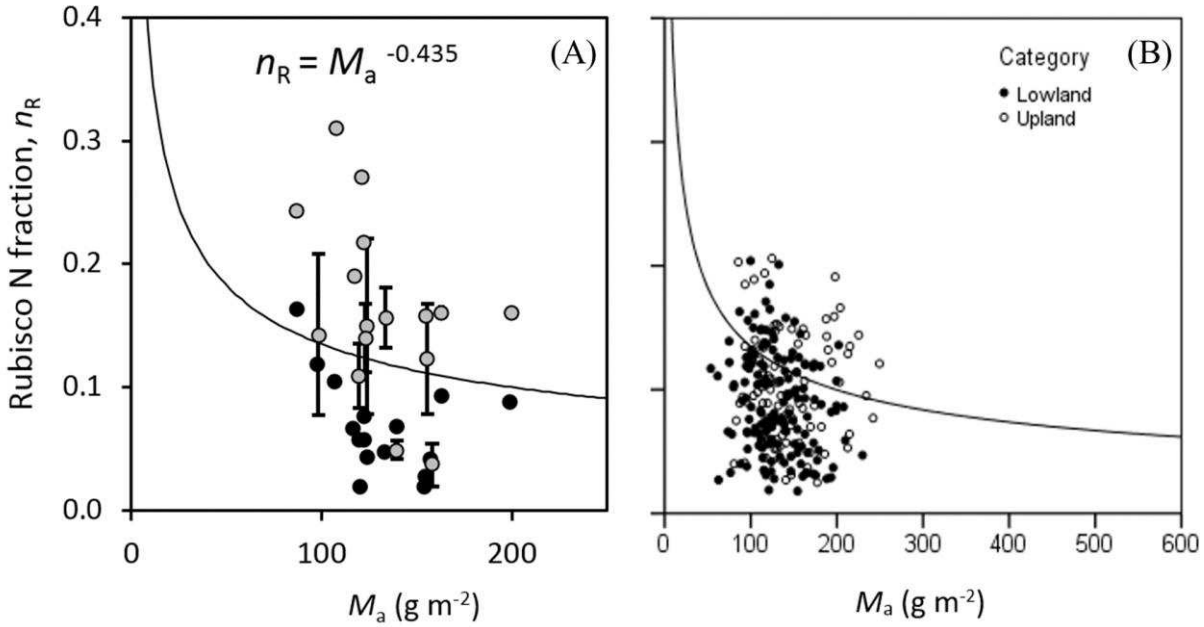


Figure S4: Stacked graph show n_E, n_P and n_R for individual leaves. Individual leaf is arranged first according to sites with increasing soil P (soil P value in mg kg^{-1} depicted underneath site code), then according to decreasing leaf N:P within each site. Leaf N:P for individual leaf is provided on top of the bar. n_E was estimated from maximum electron transport rate (normalised to 25°C), $J_{max,a}^{25}$ and n_P estimated from chlorophyll concentration. Grey panel depicts *in vitro* n_R estimated from Rubisco western blot assay, where black mark within grey panel indicates *in vivo* n_R derived from maximum carboxylation velocity of Rubisco (normalised to 25°C), $V_{cmax,a}^{25}$. Horizontal axis shows family of individual leaf.

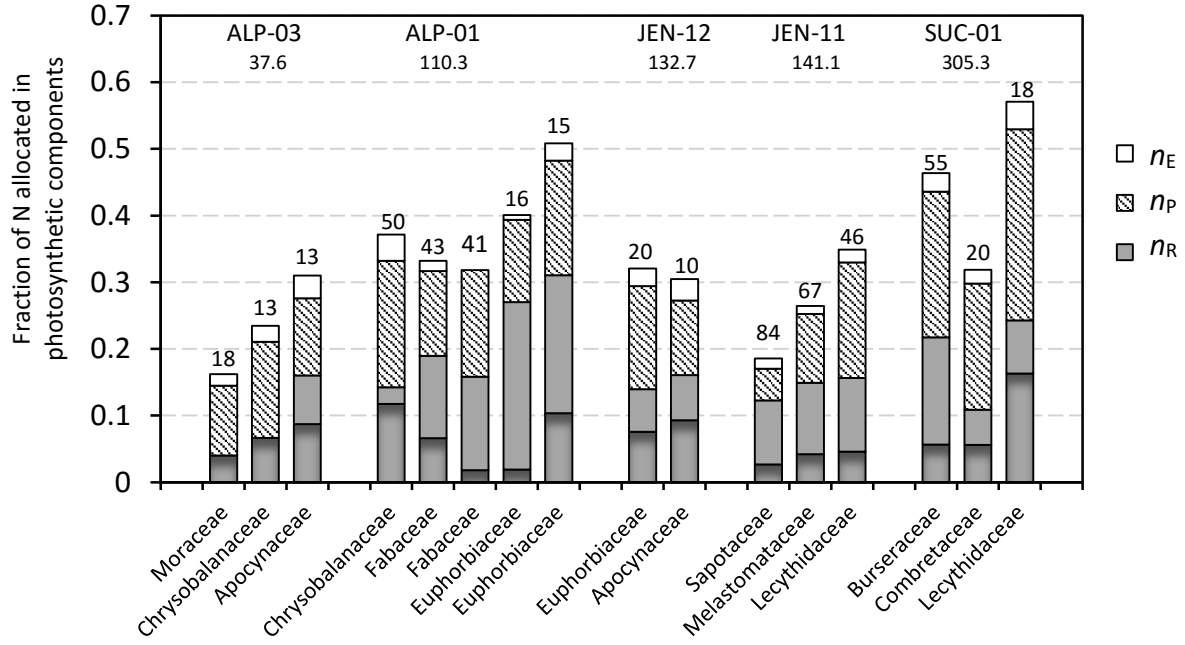
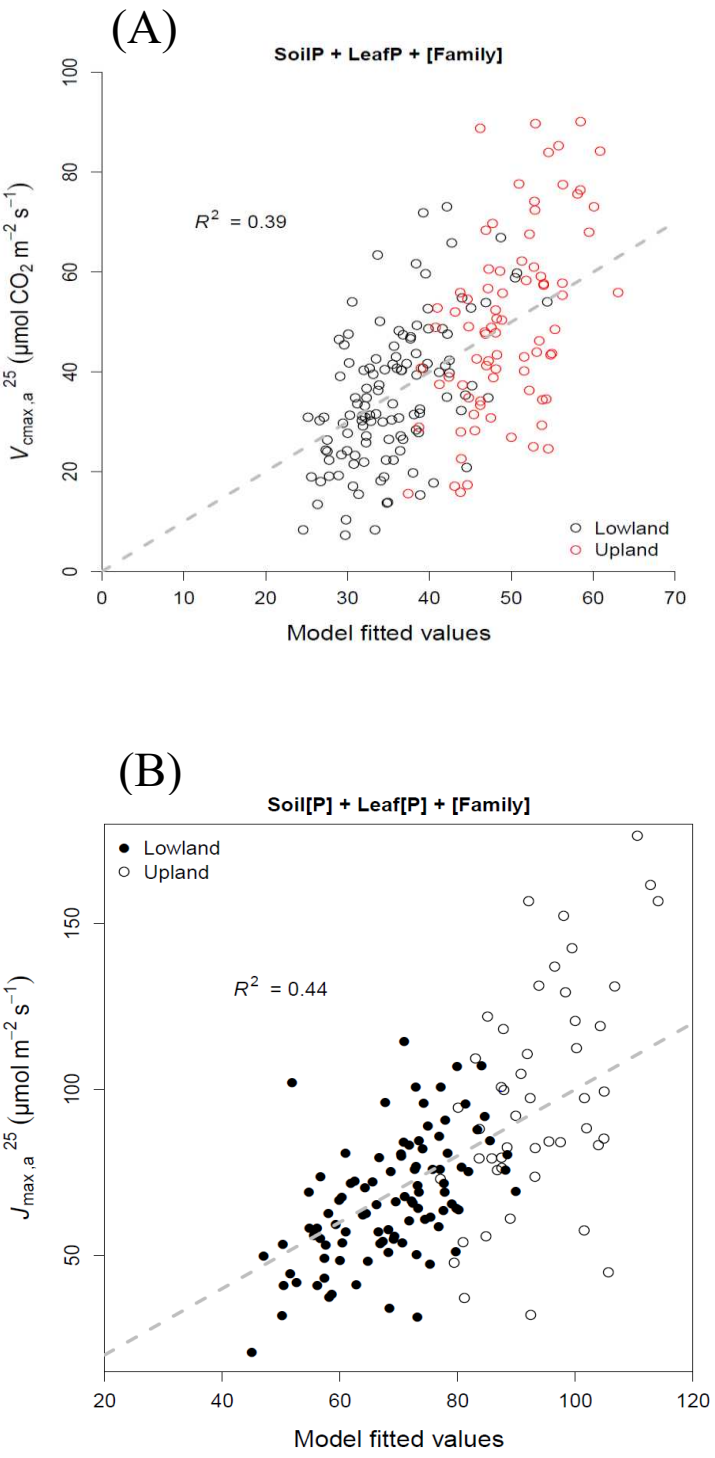


Figure S5: Plots for linear mixed-effects model goodness of fits, including fixed and random terms for (A) $V_{cmax,a}^{25}$; and, (B) $J_{max,a}^{25}$. Measured values of $V_{cmax,a}^{25}$ and $J_{max,a}^{25}$ are plotted against model predictions (using the 'best' predictive models detailed in Table 3). For $V_{cmax,a}^{25}$ and $J_{max,a}^{25}$ model, the fixed component explanatory variables were: soil P and leaf P (P_a).



Supporting information - References

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