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Citation for published version:<br>Meir, P 2016, 'Leaf-level photosynthetic capacity in lowland Amazonian and high-1 elevation, Andean tropical moist forests of Peru', New Phytologist. https://doi.org/10.1111/nph. 14079

Digital Object Identifier (DOI):
10.1111/nph. 14079

Link:
Link to publication record in Edinburgh Research Explorer

## Document Version:

Peer reviewed version

Published In:
New Phytologist

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

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[^0]Number of References: 90

Abstract: 200 words
Introduction: 1279 words

Discussion: 2228 words

Number of Figures: 9 (plus 6 in Supporting Information and 5 in SM3)
Number of Tables: 3 (plus 7 in Supporting Information)

Number of Pages (text plus references): 30

Total Word count: 7658 (excluding Abstract, References, Figures and Tables)

Materials and Methods: 1826 words

## 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 ( $V_{c \max }$ 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 $\mathrm{CO}_{2}{ }^{-}$ fixing enzyme, Rubisco.
- Area- and N -based rates of photosynthetic capacity at $25^{\circ} \mathrm{C}$ 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 $V_{\text {cmax }}$ and $J_{\max }$ but did not account for variations in photosynthetic N -use efficiency. At any given $\mathrm{Na}_{\mathrm{a}}$ 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 ( $A_{\text {sat }}$ ) (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 $A_{\text {sat }}$ (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 $A_{\text {sat }}$ 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 $A_{\text {sat }} \leftrightarrow[\mathrm{N}]$ 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 $A_{\text {sat }} \leftrightarrow[\mathrm{N}]$ 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 $\mathrm{CO}_{2}$ 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 $A_{\text {sat }}$ (Terashima et al., 1995; Bruijnzeel \& Veneklaas, 1998; Letts \& Mulligan, 2005), leading to declines in productivity (Girardin et al., 2010). $A_{\text {sat }}$ 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 $A_{\text {sat }}$
being constant with increasing elevation (Cordell et al., 1999), or declining with increasing elevation (Hikosaka et al., 2002; Wittich et al., 2012).

Rates of $A_{\text {sat }}$ are subject to variations in stomatal conductance $\left(g_{\mathrm{s}}\right)$ and the partial pressure of internal leaf $\mathrm{CO}_{2}\left(\mathrm{C}_{\mathrm{i}}\right)$ (Santiago \& Mulkey, 2003). Since variations in $\mathrm{C}_{\mathrm{i}}$ alter both $\mathrm{CO}_{2}$ uptake and photorespiratory $\mathrm{CO}_{2}$ 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. $V_{\text {cmax }}$ ). Positive correlations between $V_{\text {cmax }}$ 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 $V_{\text {cmax }} \leftrightarrow[N]$ relationship was observed (Coste et al., 2005; van de Weg et al., 2012; Dusenge et al., 2015). Although reports on $V_{\text {cmax }}$ are less widespread in the tropics than $A_{\text {sat }}$ the available data suggest that $V_{\text {cmax }}$ values, as well as $V_{\text {cmax }}$ per unit N (herein termed ' $V_{\text {cmax, }} \mathrm{N}^{\prime}$ ), 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) reanalysed data to show that $V_{\text {cmax }}$ 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 $V_{\text {cmax }}$ (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 $V_{\text {cmax }} \leftrightarrow[\mathrm{N}]$ relationship in TMFs due to the scarcity of data, both in lowland and upland TMFs. Comprehensive surveys of $V_{\text {cmax }}$ (and $J_{\text {max }}$ - maximum rate of electron transport) across lowland and upland TMFs are required to establish whether there are
generalized patterns of photosynthetic capacity in relation to environmental conditions and/or other leaf traits.

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

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

We examined variations in photosynthetic capacity and leaf traits across TMF canopies located at 18 sites along a 3,300-m elevation gradient stretching from lowland western Amazonia to the Andean tree line in Peru. The study
included 11 lowland sites in northern and southern Peru (elevation 117-223 m a.s.l.), and seven upland sites at elevations of 1527-3379 m a.s.l. in southern Peru. Our site selection enabled an assessment of the potential role of $P$-availability on photosynthetic performance across Amazonian-Andean TMF sites differing $>40-$ fold in total soil P. The upland sites were characterised by a floristically distinct assemblage of montane forest species, with the transition from lowland moist forests to upland montane forests coinciding with an increase in cloud formation (van de Weg et al., 2009; Bruijnzeel et al., 2011). In conjunction with the recent findings of the key role of P in modulating carbon investment (Quesada et al., 2012) and photosynthesis (Bloomfield et al., 2014b) of tropical trees, and that leaf $P$ varies predictably along soil $P$ and elevation gradients (Asner et al., 2014b), we addressed the following questions:
(1) Do tropical TMF species growing on low-P soils exhibit lower photosynthetic capacity and photosynthetic $N$ use efficiency than TMF trees growing on sites with higher P availability?
(2) Are there marked differences in $V_{\text {cmax }} J_{\text {max }}$ and $V_{\text {cmax, }}$ between lowland Amazonian and upland Andean TMFs?
(3) Are differences in $V_{\text {cmax }} J_{\text {max }}$ and $V_{\text {cmax, }, ~}$ linked to concomitant variations in other leaf traits and/or environmental variables?

## Materials and Methods

## Study sites

Field work was carried out in 18 one-hectare long-term monitoring plots in Peru which contribute to the ABERG and RAINFOR networks of permanent sample plots. The plots are arrayed along gradients of elevation ( 117 to 3379 m above sea level) and soil nutrient status (Table 1). For each site, climate data were obtained from Asner et al. (2014a) and Malhi et al. (in prep). Marked changes in species richness, canopy cover and tree height occur along the elevation gradient (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$15.5 \mathrm{~g} \mathrm{~N} \mathrm{~kg}^{-1}$ ), substantial variation in total soil [P] occurs across both the lowland (38-727 $\mathrm{mg} \mathrm{P} \mathrm{kg}^{-1}$ ) and upland sites ( $496-1631 \mathrm{mg} \mathrm{P} \mathrm{kg}^{-1}$ ) (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 $5300 \mathrm{~mm} \mathrm{a}^{-1}$. Mean annual temperature ranged from 8.0 to $18.8^{\circ} \mathrm{C}$ across the upland sites, and 24.4 to $26.6^{\circ} \mathrm{C}$ 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).
$\mathrm{CO}_{2}$ response curves of light-saturated photosynthesis ( $A \leftrightarrow C_{i}$ curves) (at $1800 \mu \mathrm{~mol}$ photons $\mathrm{m}^{-2} \mathrm{~s}^{-1}$ ) were performed within 30-60 minutes after branch detachment. $\mathrm{CO}_{2}$ concentrations inside the reference chamber ranged in a stepped sequence from 35 to $2000 \mu \mathrm{~mol} \mathrm{~mol}^{-1}$ (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 $25-28{ }^{\circ} \mathrm{C}$ ). 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 $V_{\text {cmax }}$ 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 $\mathrm{O}_{2}$ partial pressure, and to calculate intercellular $\mathrm{CO}_{2}\left(C_{\mathrm{i}}\right)$ values on a partial pressure basis.

Rates of $\mathrm{CO}_{2}$ exchange were corrected for diffusion through the gasket of the LI-6400 leaf chamber (Bruhn et al., 2002) prior to calculation of $V_{\text {cmax }}$ and $J_{\text {max }}$. Assuming infinite internal diffusion conductance $\left(g_{m}\right)$, Michaelis constants of Rubisco for $\mathrm{CO}_{2}\left(K_{\mathrm{c}}\right)$ and $\mathrm{O}_{2}\left(K_{\circ}\right)$ at a reference temperature $25^{\circ} \mathrm{C}$ 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 $36 \mathrm{~kJ} \mathrm{~mol}^{-1}$ for $K_{c}$ and $K_{0}$, respectively (Farquhar et al., 1980). Fitted parameters were then scaled to a reference temperature of $25^{\circ} \mathrm{C}$ using activation energies of 64.8 and $37.0 \mathrm{~kJ} \mathrm{~mol}^{-1}$ for $V_{\text {cmax }}$ and $J_{\text {max }}$, respectively (Farquhar et al., 1980). Finally, rates of $A$ obtained at ambient $\mathrm{CO}_{2}$ concentrations of 400 and $2000 \mu \mathrm{~mol} \mathrm{~mol}^{-1}$ ( $A_{400}$ and $A_{2000}$, respectively) were extracted from the $A \leftrightarrow C_{i}$ curves and reported separately.

As atmospheric $\mathrm{CO}_{2}$ was not always saturating for measurements of upland species (due to low atmospheric partial pressure, resulting in insufficient $\mathrm{CO}_{2}$-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 $J_{\text {max }}$ 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 $70^{\circ} \mathrm{C}$ for at least two days, the dry mass measured and leaf mass per unit
leaf area $\left(M_{\mathrm{a}}\right)$ 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 $-80{ }^{\circ} \mathrm{C}$ cryogenic field container for subsequent chlorophyll and Rubisco assays in the laboratory.

Chlorophyll content of each set of leaf discs was determined using a dualbeam scanning UV-VIS spectrometer (Lambda 25, Perkin-Elmer) after extraction of chlorophyll pigments from two frozen leaf discs ( $0.77 \mathrm{~cm}^{2}$ each) with $100 \%$ acetone and $\mathrm{MgCO}_{3}$, 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 $\mathrm{cm}^{2}$ 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- $\mathrm{HCl}, 0.5 \mathrm{mM}$ 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 $100^{\circ} \mathrm{C}$ to completely dissolve extracted protein, then clarified by centrifugation (14,000 $\times \mathrm{g}$; 10 min ; room temperature). The supernatant was used as the source of leaf protein.

Equivalent volumes of supernatant were diluted in $4 \times$ 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 $0.5 \%$ Tween20 (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 $16 \% \mathrm{~N}$ 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, $V_{\text {cmax }}$ 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 ( $n_{\mathrm{R}}$ ) was estimated from values of $V_{\text {cmax }}$ according to Harrison et al. (2009), with slight modification $\left[2.33 \mathrm{~mol} \mathrm{CO}_{2}\right.$ (mol Rubisco sites) $)^{-1} \mathrm{~s}^{-1}$ for the catalytic turnover number of Rubisco at $25^{\circ} \mathrm{C}$ (Harrison et al., 2009)]. We assumed all Rubisco was fully activated and mesophyll conductance was infinite. The allocation of N to electron transport components $\left(n_{\mathrm{E}}\right)$ was calculated from $J_{\text {max }}$ assuming 160 mol electrons (mol cytochrome $\left.f\right)^{-1} \mathrm{~s}^{-}$ ${ }^{1}$ and 8.85 mol N (mmol cytochrome $\left.f\right)^{-1}$ (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 $V_{\text {cmax }}$, and area-based rates of $J_{\text {max }}$, 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 ( $M_{\mathrm{a}}$, 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 $\mathrm{N}: \mathrm{P}$ 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] $\left(\mathrm{P}_{\mathrm{a}}\right)$ were positively correlated with soil $[\mathrm{P}]\left(\mathrm{r}^{2}=0.37, p<0.01\right)$ and elevation ( $r^{2}=0.48, p<0.01$ ). Weaker positive associations were observed for area-based leaf $[N]\left(N_{a}\right)$ with total soil $[N]\left(r^{2}=0.10, p<0.01\right)$ and elevation $\left(r^{2}=0.14, p<0.01\right)$.

Leaf mass per unit leaf area $\left(M_{\mathrm{a}}\right)$ varied widely, both among and within lowland ( $54-230 \mathrm{~g} \mathrm{~m}^{-2}$ ) and upland ( $60-249 \mathrm{~g} \mathrm{~m}^{-2}$ ) sites (Table 1 and Table S1). Although variations in $M_{\mathrm{a}}$ were not correlated with variations in soil $[P]$, there were significant (but weak) correlations between $M_{a}$ and total soil $[N]\left(r^{2}=0.04, p<0.01\right)$ and elevation ( $r^{2}=0.03, p<0.01$ ) (Table S2). Overall means of $M_{a}$ for the sampled upland species $\left(143 \pm 39 \mathrm{~g} \mathrm{~m}^{-2}\right)$ were significantly higher than that of the lowland species ( $132 \pm 35 \mathrm{~g} \mathrm{~m}^{-2}$; 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 $M_{a}\left(p<0.01, r^{2}=0.04\right.$; Table S2). Similarly, a weak positive $\mathrm{P}_{\mathrm{a}} \leftrightarrow M_{\mathrm{a}}$ relationship ( $p=0.003, r^{2}=0.04$; Table S3) was found among upland species (Fig 2B). Although no significant $\mathrm{P}_{\mathrm{a}} \leftrightarrow \mathrm{Ma}_{\mathrm{a}}$ relationship was found among lowland species (with leaf $P_{a}$ varying 20-fold; Table $S$ 1), 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 $\mathrm{CO}_{2}$ concentration of $400 ~ \mu \mathrm{~mol} \mathrm{~mol}^{-1}\left(A_{400, \mathrm{a}}\right)$, 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 $T s$ at the high elevation sites [overall means: lowland $29.4 \pm 0.9^{\circ} \mathrm{C}$; upland $25.7 \pm 2.1^{\circ} \mathrm{C}, p<0.05$ ] and lower intercellular $\mathrm{CO}_{2}$ partial pressure $\left(C_{i}\right)$ (overall means: lowland $28.4 \pm 3.7 \mathrm{~Pa}$; upland $18.8 \pm 3.0 \mathrm{~Pa}$, $p<0.05$ ) (Table S4). Assessed on a per unit leaf $N$ basis $\left(A_{400, N}\right)$, 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 $A_{400, \mathrm{~N}}$ decreased with decreasing mean annual temperature (MAT) (Figure S1D). Area-based rates of photosynthesis at elevated $\mathrm{CO}_{2}\left(A_{2000, a}\right)$ were higher in upland (17.1-26.5 $\mathrm{mmol} \mathrm{m}^{-2} \mathrm{~s}^{-1}$; Table S4) than lowland (16.1-22.6 $\mu \mathrm{mol} \mathrm{m} \mathrm{m}^{-2} \mathrm{~s}^{-1}$ ) 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 $\left(A_{2000, N}\right)$, 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 $\mathrm{CO}_{2}$ fixation by Rubisco ( $V_{c m a x, a}$ ) and photosynthetic electron transport ( $J_{\text {max, }}$ ), using values normalized to a measuring temperature of $25{ }^{\circ} \mathrm{C}$ (i.e. $V_{\text {cmax }, 2}{ }^{25}$ and $J_{\text {max }, ~}{ }^{25}$ ). Site mean values of $V_{c m a x, a}{ }^{25}$ and $J_{\text {max,a }}{ }^{25}$ were significantly higher in the upland class ( $V_{\text {cmax }, ~}{ }^{25}$ and $J_{\text {max }, a}{ }^{25}$ 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 $V_{\text {cmax, } N}$ at $25^{\circ} \mathrm{C}\left(V_{c m a x} N^{25}\right)$ 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 $V_{\text {cmax }}$ ), photosynthetic $N$ use efficiency was, on average, greater at high elevations. Importantly, considerable within-site variability was observed for all three parameters $\left(V_{\text {cmax } a^{2}}{ }^{25}, J_{\text {max,a }}{ }^{25}\right.$, and $\left.V_{\text {cmax }} \mathrm{N}^{25}\right)$ (Fig. 3; Table S 1 ), 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 $J_{\text {max }}{ }^{25}$ were strongly correlated with $V_{\text {cmax }, ~}{ }^{25}$, both for lowland ( $r^{2}=0.59$ ) and upland classifications $\left(r^{2}=0.75\right)$ (Fig. 4). Overall, the $J_{\text {max }, ~}{ }^{25} \leftrightarrow V_{\text {cmax, }}{ }^{25}$ relationship was similar in the two elevation groups, with mean $J_{\text {max }}{ }^{25}: V_{\text {cmax }, 2}{ }^{25}$ ratios being statistically equivalent in lowland and upland classes (Table 2). Importantly, marked differences in $J_{\text {max }, ~} 25: V_{c m a x, a}{ }^{25}$ ratios were observed among individuals (Figs 3 and 4), underpinned by fundamental differences in the $\mathrm{CO}_{2}$ response of net photosynthesis (e.g. Fig. 1B). In most leaves, $J_{\text {max }}{ }^{25}$ and $V_{\text {cmax }, ~}{ }^{25}$ co-varied, resulting in relatively constant $J_{\text {max }}{ }^{25}: V_{\text {cmax }} 25$ ratios, as illustrated by data from individual plants of Cecropia angustifolia and Glycydendron amazonicum where the $J_{\text {max }}{ }^{25}: V_{\text {cmax }, ~}^{25}$ ratio was 1.8 (Fig. 1 A and Fig. 4). However, some leaves exhibited high $V_{\text {cmax }^{2}}{ }^{25}$ but low $J_{\text {max }}{ }^{25}$ (Fig. 1B; individual of Schefflera sp., where $J_{\text {max }}{ }^{25}: V_{\text {cmax }^{2}}{ }^{25}=1.1$ ) while other leaves with a similar $V_{\text {cmax,a }}{ }^{25}$ had markedly higher $J_{\text {max }}{ }^{25}$ (e.g. the Citronella incarum individual in Fig. 1B) leading to a higher $J_{\text {max }, a}{ }^{25}: V_{\text {cmax }, a}{ }^{25}$ value (2.4). Such variations in $J_{\text {max }, a}{ }^{25}$ and $V_{\text {cmax, }^{25}}{ }^{25}$ 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, $V_{\text {cmax, }^{25}}{ }^{25}$ and $J_{\text {max, }}{ }^{25}$ exhibited positive correlations with soil P, soil N and elevation, and negative correlations with MAT (Table S2); the strength
of these relationships was greater for $J_{\text {max }, 2}{ }^{25}$ than $V_{\text {cmax }, ~}{ }^{25}$. Relationships with MAP were either weak $\left(J_{\text {max }}{ }^{25}\right)$ and not significant $\left(V_{c m a x}{ }^{25}\right)$ (Table S2). Across all sites, variations in $V_{\text {cmax }, ~}{ }^{25}$ and $J_{\text {max }}{ }^{25}$ were also correlated with leaf chemical composition traits (Table S2), with bivariate relationships being stronger against $\mathrm{P}_{\mathrm{a}}\left(p<0.01, r^{2}=0.11\right.$ for $V_{\text {cmax }, a}{ }^{25}, r^{2}=0.13$ for $J_{\text {max }}{ }^{25}$ ) than $N_{a}\left(p<0.01, r^{2}=0.05\right.$ for both $V_{\text {cmax, }}{ }^{25}$ and $J_{\text {max }}{ }^{25}$ ). Leaf $\mathrm{N}: P$ ratios exhibited weak, negative correlations
 S2). No significant relationship was found between $V_{c m a x, a}{ }^{25}$ and $M_{a}$, whereas the $J_{\text {max }, ~}{ }^{25} \leftrightarrow M_{\mathrm{a}}$ relationship was significant ( $p<0.05, \mathrm{r}^{2}=0.04$; Table S2).

When assessed among upland sites, no significant relationships were found between $V_{c m a x, a}{ }^{25}, M_{a}, N_{a}, P_{a}$ or $N: P$ ratio (Fig. 5A-D). For lowland sites, $V_{\text {cmax, }}{ }^{25}$ was positively related with $\mathrm{Pa}\left(p=0.013, \mathrm{r}^{2}=0.04\right.$; Table S3) and $\mathrm{Na}_{\mathrm{a}}$ ( $p=0.050, r^{2}=0.02$; Table S3), but not leaf $N: P$ ratio or $M_{a}$ (Fig 5A-D). The absence of a N:P effect for upland or lowland classes was consistent with SMA analyses comparing the slopes of $V_{\text {cmax }, ~}{ }^{25} \leftrightarrow N_{a}, V_{\text {cmax }, a}{ }^{25} \leftrightarrow P_{a}$ and $V_{\text {cmax }, ~}{ }^{25} \leftrightarrow M_{a}$ for the lowland class, split according to leaf $\mathrm{N}: \mathrm{P}$ ratios below and above 20 - this ratio generally being thought to be roughly indicative of the $N: P$ above which physiological processes are more likely to be limited by $P$ as opposed to $N$ (and vice versa) (Güsewell, 2004). No significant difference in slopes of the relationships were found ( $p>0.05$, data not shown). Similar patterns were observed for $J_{\text {max }}{ }^{25}$ (Fig. $5 \mathrm{E}-\mathrm{H}$ ), which was positively related with $\mathrm{Na}_{\mathrm{a}}\left(p=0.012, \mathrm{r}^{2}=0.05\right.$; Table S3) and $\mathrm{Pa}_{\mathrm{a}}\left(p=0.002, \mathrm{r}^{2}=0.08\right.$; Table S3) for the lowland class only.

Investigating whether variations in photosynthetic N use efficiency were related to $M_{\mathrm{a}}$, both across all sites (Table S2) and within each elevation class (Fig. 6A), there was no significant $V_{\text {cmax }, N^{25}} \leftrightarrow M_{\mathrm{a}}$ relationship across all 18 sites (Table S2) or within the upland elevation class (Table S3). Nevertheless, for the lowland class, a weak negative $V_{\text {cmax, }} N^{25} \leftrightarrow M_{\mathrm{a}}$ relationship was observed ( $p=0.01$; Table S3). On average, $V_{c m a x, N^{25}}$ at a given $M_{a}$ was higher in upland species than their lowland counterparts. With respect to foliar phosphorus, there was no significant relationship between $V_{\text {cmax, } \mathrm{N}^{25}}$ and leaf $\mathrm{Pa}_{\mathrm{a}}$ or with leaf $\mathrm{N}: \mathrm{P}$ when considering the
elevation classes separately. This conclusion was held for $V_{c m a x}, N^{25} \leftrightarrow P_{a}$ when combining upland and lowland data (Table S2). For $V_{\text {cmax, }} \mathrm{N}^{25} \leftrightarrow \mathrm{~N}: P$, combining upland and lowland data resulted in a weak significant relationship ( $p<0.05, r^{2}=$ 0.02; Table S2); similarly, relationships between $V_{\text {cmax, } \mathrm{N}^{25}}$ and soil P, soil N and elevation were relatively weak (Table S2). Collectively, these results show that the proportion of the variance in $V_{\text {cmax, }}{ }^{25}$ 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 $V_{\text {cmax, }}{ }^{25}$, we calculated the fraction of leaf N allocated to photosynthesis $\left(n_{\mathrm{A}}\right) ; n_{\mathrm{A}}$ is dependent on the allocation of leaf N to Rubisco $\left(n_{\mathrm{R}}\right)$, electron transport ( $n_{\mathrm{E}}$ ) and pigmentprotein complexes $\left(n_{\mathrm{P}}\right)$. Figure 7 shows that mean values of $n_{\mathrm{A}}$ and its underlying components exhibited relatively little variation across sites. Nevertheless, interspecific 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, $n_{\mathrm{E}}$ 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 $n_{\mathrm{P}}$. Overall, $n_{\mathrm{A}}$ 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 $\mathrm{N}_{\mathrm{a}}$ and $\mathrm{P}_{\mathrm{a}}$ (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 $n_{\mathrm{R}}$ obtained for these in vitro assays with that of the in vivo estimates derived from $V_{\text {cmax,a }}{ }^{25}$. 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 $n_{\mathrm{R}}$ 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 $V_{\text {cmax }, ~}{ }^{25}, J_{\text {max }} a^{25}$ and $V_{\text {cmax }, N}{ }^{25}$
We used linear mixed-effects to model variations in $V_{\text {cmax }, ~}{ }^{25}, J_{\text {max }}{ }^{25}$ and $V_{\text {cmax, }}{ }^{25}$; 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 $V_{\text {cmax,a }}{ }^{25}$ (model 6, Table S6) retained $P$ only, suggesting an increase of $V_{\text {cmax, }^{25}}$ as soil and foliar P increase (Table 3). A combination of sitelevel soil P and individual-level foliar P as fixed effects, and family as a random effect, explained $39 \%$ of the variation in $V_{\text {cmax, }}{ }^{25}$ (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 $V_{\text {cmax, }}{ }^{25}$, variations in $J_{\text {max, }}{ }^{25}$ were largely accounted for by a combination of site-level soil P and individual-level foliar P, with $J_{\text {max }, 2}{ }^{25}$ increasing with increasing soil and foliar P (Table 3); the final model explained $44 \%$ of the variation in $J_{\text {max, }}{ }^{25}$ (Fig. S5). The preferred model (determined by assessing the effect of dropping sequentially explanatory variables; Table S6) did not retain soil N , leaf $\mathrm{N}_{\mathrm{a}}, M_{a}$ or MAT (Table S6). For the random effects, family contributed 2.8\% to the unexplained variance (Table 3).

For $V_{\text {cmax, }}{ }^{25}$ (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 $V_{\text {cmax, }}{ }^{25}$ and $J_{\text {max }}{ }^{25}, V_{\text {cmax, }}{ }^{25}$ 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 $V_{\text {cmax }} \mathrm{N}^{25}$. 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 $V_{\text {cmax, }}{ }^{25} \leftrightarrow \mathrm{~N}_{\mathrm{a}}$ relationships, with lower rates of $V_{\text {cmax }}$ 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 $A \leftrightarrow \mathrm{~N}$ relationships is lower in the tropics than in colder arctic and temperate biomes. Our study supports such studies, with $V_{\text {cmax, }}{ }^{25}$ values for our upland and lowland TMFs (22.5 and $18.9 \mu \mathrm{~mol} \mathrm{CO} 2 \mathrm{~g} \mathrm{~N}^{-1} \mathrm{~s}^{-1}$, respectively) being markedly lower than reported for temperate broadleaved trees [34 $\mu \mathrm{mol} \mathrm{CO} 2 \mathrm{~g} \mathrm{~N}^{-1} \mathrm{~s}^{-1}$ (Kattge et al., 2009)].

How do our results compare with other analyses of photosynthetic capacity in tropical ecosystems? The range of $V_{\text {cmax, }}{ }^{25}\left(6-96 \mu \mathrm{~mol} \mathrm{~m}^{-2} \mathrm{~s}^{-1}\right.$; Table S1) and $J_{\text {max, }}{ }^{25}\left(21-176 \mu \mathrm{~mol} \mathrm{~m}{ }^{-2} \mathrm{~s}^{-1}\right.$; 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 $V_{\text {cmax, }}{ }^{25}\left(36 \pm 15 \mu \mathrm{~mol} \mathrm{~m}{ }^{-2} \mathrm{~s}^{-1}\right)$ was lower than previously reported tropical values: Carswell et al. (2000): $43 \mu \mathrm{~mol} \mathrm{~m} \mathrm{~m}^{-2} \mathrm{~s}^{-1}$; Domingues et al. (2007): $53 \mu \mathrm{~mol} \mathrm{~m}^{-2} \mathrm{~s}^{-1}$; Meir et al. (2007): 49-68 $\mu \mathrm{mol} \mathrm{m}^{-2} \mathrm{~s}^{-1}$; Kattge et al. (2009): $41 \mu \mathrm{~mol} \mathrm{~m}{ }^{-2} \mathrm{~s}^{-1}$ (non-oxisol); Bloomfield et al. (2014a): $63 \mu \mathrm{~mol} \mathrm{~m} \mathrm{~m}^{-2} \mathrm{~s}^{-1}$; Domingues et al. (2015): 39-46 $\mu \mathrm{mol} \mathrm{m} \mathrm{m}^{-2} \mathrm{~s}^{-1}$. By contrast, our mean $V_{\text {cmax }, 2}{ }^{25}$ values were higher than the values for lowland TMFs only growing on nutrient-poor, oxisol [ $29 ~ \mu \mathrm{~mol} \mathrm{~m}{ }^{-2} \mathrm{~s}^{-1}$ (Kattge et al., 2009)]. Since $J_{\text {max,a }}{ }^{25}$ was tightly correlated with $V_{\mathrm{cmax}, \mathrm{a}}{ }^{25}$ (Fig. 4), our estimates of $J_{\text {max }}{ }^{25}$ for lowland TMFs were also lower than those reported in above-mentioned studies. Rates of $V_{\text {cmax, }}{ }^{25}$ at our upland sites $\left(49 \pm 20 \mu \mathrm{~mol} \mathrm{~m}^{-2} \mathrm{~s}^{-1}\right)$ were similar to those reported by van de Weg et al. (2012): $56 \mu \mathrm{~mol} \mathrm{~m}{ }^{-2} \mathrm{~s}^{-1}$ 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 $V_{\text {cmax,a }}{ }^{25}$ 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: $38-727 \mathrm{mg} \mathrm{P} \mathrm{kg}^{-1}$; upland sites: $496-1631 \mathrm{mg} \mathrm{P} \mathrm{kg}{ }^{-1}$ ). Low $P$ availability can limit rates of photosynthesis via reduced maximal rates of RuBP regeneration (i.e. $J_{\text {max }}$ ), with maximal Rubisco activity (i.e. $V_{\text {cmax }}$ ) also often being reduced (Brooks, 1986; Jacobs \& Lawlor, 1992; Loustau et al., 1999). While the mechanisms responsible for reduced $V_{\text {cmax }}$ 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 $\mathrm{Pa}_{\mathrm{a}}$ 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 $V_{c m a x, a}{ }^{25}$ or $J_{\text {max }, ~}{ }^{25}$ ) and foliar $\mathrm{P}_{\mathrm{a}}$, and against soil [P] (Tables S2, S3). Across all 18 TMF sites, $V_{\text {cmax }, ~}{ }^{25}$ and $J_{\text {max, }}{ }^{25}$ also exhibited significant negative relationships with leaf $N: P$ (Table S2). Moreover, foliar $\mathrm{P}_{\mathrm{a}}$ and soil [P] emerged as significant explanatory variables in linear mixed-effect models of variations in photosynthetic capacity (Table 3), accounting for $\sim 40 \%$ of the observed variations in $V_{c m a x, a}{ }^{25}$ and $J_{\text {max }}{ }^{25}$. 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 $V_{\mathrm{cmax}, \mathrm{N}}$ and foliar [P] were highest in our upland trees, no significant $V_{c m a x, N} \leftrightarrow \mathrm{~Pa}_{\mathrm{a}}$ relationships were observed, either across all sites or within each elevation class. Furthermore, we could not identify key factors explaining variation in $V_{\text {cmax, }}$ 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 $V_{\mathrm{cmax}, \mathrm{N},}$ 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 $\mathrm{CO}_{2}$ 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 $\mathrm{CO}_{2}$ 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 nonmetabolic protein (Stitt \& Schulze, 1994; Warren et al., 2000). Viewed from this perspective, in vivo estimates of $V_{\text {cmax }}$ 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 $V_{\text {cmax, }} N^{25}$ were lower than that of trees growing in temperate environments (Kattge et al., 2009). Similarly, when compared at any given $M_{\mathrm{a}}$, in vivo estimates of $n_{\mathrm{R}}$ (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 $\left(g_{\mathrm{m}}\right)$ have on estimates of $V_{\text {cmax }}$ and the associated values of $n_{R}$.

## Additional factors influencing $V_{\text {cmax }}$ estimates

In our study, we have so far estimated in vivo rates of $V_{\text {cmax,a }}{ }^{25}$ assuming a common, single set of kinetic constants ( $K_{\mathrm{c}}$ and $K_{\mathrm{o}}$ ) for Rubisco (von Caemmerer et al., 1994) and associated activation energies ( $E_{\mathrm{a}}$ ) (Farquhar et al., 1980), as well as infinite $g_{\mathrm{m}}$. Such assumptions were made necessary in the absence of $K_{\mathrm{c}}, K_{\mathrm{o}}, E_{\mathrm{a}}$ and $g_{\mathrm{m}}$ values for tropical species. Application of different $K_{\mathrm{c}}$ and $K_{o}$ values, such as those reported by Bernacchi et al. (2002), would alter estimates of $V_{\text {cmax, }{ }^{25} \text { for }}$ all trees but would not alter relative differences among sites or elevational classes. By contrast, application of Bernacchi et al. (2002) $E_{\mathrm{a}}$ values for $K_{c}$ and $K_{0}(80.99$ and $23.72 \mathrm{~kJ} \mathrm{~mol}^{-1}$, respectively), and $V_{\text {cmax }}\left(65.3 \mathrm{~kJ} \mathrm{~mol}^{-1}\right)$ could potentially relative differences in $V_{\text {cmax,a }}{ }^{25}$ between upland and lowland trees, depending on the extent to which leaf temperatures differed among the sites. Similarly, replacement
of the Farquhar et al. (1980) $E_{\mathrm{a}}$ values of $V_{\mathrm{cmax}}$ and $J_{\max }$ (of 64.8 and $37.0 \mathrm{~kJ} \mathrm{~mol}^{-1}$, respectively) with those of Bernacchi et al. (2002) ( 65.3 and $43.9 \mathrm{~kJ} \mathrm{~mol}^{-1}$, respectively) could alter the relative differences in $V_{\text {cmax,a }}{ }^{25}$ and $J_{\text {max }, ~}{ }^{25}$ between upland and lowland sites. To check whether application of alternative $E_{a}$ values change our conclusions regarding site-to-site differences, we calculated $V_{\text {cmax,a }}{ }^{25}$ and $J_{\text {max }, ~}{ }^{25}$ using the respective activation energies of Farquhar et al. (1980) and Bernacchi et al. (2002). Use of the Bernacchi et al. (2002) $E_{a}$ values resulted in an average $10.6 \%$ increase in estimates of $V_{\text {cmax25 }}$ for lowland trees (Table S7), reflecting the fact that lowland leaf temperatures were near $30^{\circ} \mathrm{C}$ (Table S4). Upland estimates were less affected ( $3.5 \%$ increase; Table S7) as the average leaf temperature of upland group was $25.7^{\circ} \mathrm{C}$ (Table S4). Despite the increased estimates of $V_{\text {cmax25 }}$ for lowland trees when using $E_{\mathrm{a}}$ values from Bernacchi et al. (2002), there remained a significant difference between lowland and upland mean $V_{\text {cmax25 }}$ values (Table S7); the same was true for $J_{\text {max }, 2}{ }^{25}$ (Table S7). As a result, relationships between photosynthetic properties and site MAT and soil P were similar when using Farquhar et al. (1980) and Bernacchi et al. (2002) Ea values (Fig. S1). Thus, irrespective of which $E_{\mathrm{a}}$ values are used [see Medlyn et al. (2002) for further discussion the temperature dependence of these constants], we are confident that that mean values of $V_{\mathrm{cmax25}}$ and $J_{\text {max, }}{ }^{25}$ are indeed higher in the upland plants growing in the Peruvian Andes.

What impact might systematic differences in $g_{\mathrm{m}}$ between upland and lowland TMFs have on our results? If $g_{\mathrm{m}}$ was finite, but similar in upland and lowland TMF environments, then our conclusion that $V_{\text {cmax,a }}{ }^{25}$ is higher in upland species would hold (albeit with modified values). However, if $g_{m}$ was more limiting in lowland TMF trees than their upland counterparts, then calculation of $V_{\text {cmax }}$ using $A-C_{c}$ curves might fail to differentiate between the upland and lowland groups. A definitive assessment of this issue will require further work assessing $g_{\mathrm{m}}$ in tropical trees (e.g. using concurrent measurements of leaf as exchange and carbon isotope discrimination or chlorophyll fluorescence). Although $g_{m}$ tends to decrease with increasing $M_{a}$ (Flexas et al., 2008), the $M_{a}$ difference between
lowland and upland groups was small (Table 1). Given the potential for large variations in $g_{m}$ among species (at a given $M_{\mathrm{a}}$ ), it is unlikely that $g_{\mathrm{m}}$ would have been higher in the selected lowland TMF trees. Irrespective of the effect of elevation on $g_{\mathrm{m}}$, rates of $A_{40, \mathrm{a}}$ and $A_{200, \mathrm{a}}$ (measured at prevailing leaf $T \mathrm{~s}$ ) were surprisingly high in plants at the cooler, high elevation sites (Table S4). Given this and our extensive sample size, we feel confident that photosynthetic capacity at a standardised $T$ is likely larger in trees growing at high elevations in the Andes compared to those in the lowland regions of Amazonia, as proposed by van de Weg et al. (2012; 2014). Enhanced photosynthetic capacity at high altitude could help negate the inhibitory effects of low $T$ on leaf-level $\mathrm{CO}_{2}$ uptake, with the result that gross primary productivity (GPP) would not decline with increasing elevation as much as expected.

Recent modelling of C-exchange processes at a high elevation TMF site (3025 m a.s.l.) in Peru suggested that gross primary productivity (GPP) may be 2040\% lower compared to lowland TMFs (Girardin et al., 2014a; van de Weg et al., 2014); low $T$ appeared to be most important factor limiting GPP at high elevations (van de Weg et al., 2014). Our results suggest that the inhibitory effect of low $T$ on GPP of upland TMFs would be greater if photosynthetic capacity remained constant across the elevation gradient. Thus, the greater photosynthetic capacity of upland TMFs might contribute to GPP being relatively homeostatic across the Peruvian Amazon-Andes elevation gradient. Further work is needed to explore how elevation-dependent variations in photosynthetic capacity impact on current and future net primary productivity (NPP) of TMFs, when taking into account other NPP components (e.g. leaf area index, biomass allocation, litter fall, autotrophic respiration).

## Concluding statements

Our findings reveal greater photosynthetic capacity in Andean forest leaves compared to lowland western Amazonian leaves, underpinned by greater 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 $V_{\text {cmax }}$ 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.

## Acknowledgements

We thank R. Tupayachi, N. Jaramillo, F. Sinca, L. Carranza-Jimenez and the Spectranomics team for field and laboratory assistance. Measurements were made in plots inventoried and maintained by RAINFOR (www.rainfor.org) investigators from Peru. Access to the field sites was also facilitated by Gordon and Betty Moore Foundation grants (to O.P., Y.M., J.L., and G.A.). Foliar sampling, taxonomic determinations, and chemical analyses were supported by a grant from the Gordon and Betty Moore Foundation to the Carnegie Institution for Science. This work was also funded by grants/fellowships from the Australian Research Council (DP0986823, DP130101252, CE140100008 and FT0991448 to O.K.A.; and, FT110100457 to P.M.), and NERC grants (NE/C51621X/1 and NE/F002149/1 to P.M.). R.G. was supported by a Newton International Fellowship (funded by the Royal Society, the British Academy and the Royal Academy of Engineering). NHAB is funded by Malaysian government postgraduate scholarship.

## 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 $A \leftrightarrow C_{\mathrm{i}}$ 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 $\pm$ 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, $n_{\mathrm{R}}$ 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 $V_{\text {cmax }, ~}{ }^{25}$ and $J_{\text {max, }, ~}{ }^{25}$

Figure S6: Comparison of $V_{\text {cmaxa }}{ }^{25}$ 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 <br> (m a.s.l.) | No. of species | MAT$\left({ }^{\circ} \mathrm{C}\right)$ | $\begin{aligned} & \text { MAP } \\ & (\mathrm{m}) \end{aligned}$ | Atm. Pressure (kPa) | Soil classification | Total soil |  | Leaf chemistry |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  |  |  |  |  |  |  |  | $\begin{gathered} {[\mathrm{N}]} \\ \left(\mathrm{g} \mathrm{~kg}^{-1}\right) \\ \hline \end{gathered}$ | $\begin{gathered} {[\mathrm{P}]} \\ \left(\mathrm{mg} \mathrm{~kg}^{-1}\right) \\ \hline \end{gathered}$ | $\begin{aligned} & \text { Leaf } N_{a} \\ & \left(\mathrm{~g} \mathrm{~m}^{-2}\right) \end{aligned}$ | $\begin{aligned} & \text { Leaf } \mathrm{Pa}_{a} \\ & \left(\mathrm{~g} \mathrm{~m}^{-2}\right) \end{aligned}$ | Leaf $\mathrm{N}: \mathrm{P}$ | $\begin{gathered} M_{\mathrm{a}} \\ \left(\mathrm{~g} \mathrm{~m}^{-2}\right) \end{gathered}$ |
| Lowland | SUC-05 | -3.2558 | -72.8942 | 132 | 20 | 26.2 | 2.75 | 100 | Alisols | 1.9 | 276 | $1.94 \pm 0.61$ | $0.06 \pm 0.04$ | $30.1 \pm 7.03$ | $129 \pm 31$ |
|  | TAM-05 | -12.8309 | -69.2705 | 223 | 8 | 24.4 | 1.90 | 99 | Cambisols | 1.6 | 256 | $2.14 \pm 0.27$ | $0.08 \pm 0.02$ | $28.6 \pm 9.49$ | $119 \pm 27$ |
|  | JEN-11 | -4.8781 | -73.6295 | 131 | 18 | 26.6 | 2.70 | 100 | Acrisols | 1.8 | 141 | $2.12 \pm 0.52$ | $0.06 \pm 0.02$ | $27.9 \pm 10.4$ | $144 \pm 37$ |
|  | ALP-01 | -3.9500 | -73.4333 | 120 | 18 | 25.2 | 2.69 | 100 | Gleysols | 0.6 | 110 | $1.90 \pm 0.40$ | $0.08 \pm 0.03$ | $26.2 \pm 8.62$ | $119 \pm 24$ |
|  | SUC-01 | -3.2519 | -72.9078 | 117 | 17 | 26.2 | 2.75 | 100 | Plinthosols | 1.7 | 305 | $1.81 \pm 0.63$ | $0.09 \pm 0.03$ | $22.1 \pm 4.99$ | $123 \pm 27$ |
|  | JEN-12 | -4.8990 | -73.6276 | 135 | 19 | 26.6 | 2.70 | 100 | Podzols | 6.9 | 133 | $1.97 \pm 0.52$ | $0.09 \pm 0.05$ | $21.9 \pm 10.42$ | $156 \pm 31$ |
|  | ALP-30 | -3.9543 | -73.4267 | 150 | 21 | 25.2 | 2.69 | 100 | Arenosols | 0.8 | 38 | $1.67 \pm 0.47$ | $0.09 \pm 0.04$ | $20.8 \pm 6.85$ | $145 \pm 46$ |
|  | CUZ-03 | -12.5344 | -69.0539 | 205 | 12 | 24.4 | 1.90 | 99 | Cambisols | 2.4 | 727 | $1.88 \pm 0.47$ | $0.10 \pm 0.04$ | $17.2 \pm 5.97$ | $109 \pm 18$ |
|  | ALP-40 | -3.9410 | -73.4400 | 142 | 12 | 26.3 | 2.76 | 100 | Podzols | 2.1 | 59 | $1.84 \pm 0.36$ | $0.10 \pm 0.02$ | $16.8 \pm 5.00$ | $171 \pm 50$ |
|  | TAM-09 | -12.8309 | -69.2843 | 219 | 13 | 24.4 | 1.90 | 99 | Alisols | 1.1 | 326 | $2.19 \pm 0.45$ | $0.14 \pm 0.03$ | $16.4 \pm 3.77$ | $105 \pm 21$ |
|  | TAM-06 | -12.8385 | -69.2960 | 215 | 13 | 24.4 | 1.90 | 99 | Alisols | 1.7 | 529 | $2.56 \pm 0.34$ | $0.17 \pm 0.04$ | $15.3 \pm 2.84$ | $126 \pm 26$ |
| Upland | SPD-02 | -13.0491 | -71.5365 | 1527 | 19 | 18.8 | 5.30 | 83 | Cambisols | 8.8 | 1631 | $2.23 \pm 0.45$ | $0.16 \pm 0.05$ | $15.4 \pm 4.05$ | $126 \pm 36$ |
|  | SPD-01 | -13.0475 | -71.5423 | 1776 | 21 | 17.4 | 5.30 | 85 | Cambisols | 11.9 | 1071 | $2.25 \pm 0.35$ | $0.16 \pm 0.04$ | $14.3 \pm 3.34$ | $124 \pm 29$ |
|  | TRU-08 | -13.0702 | -71.5559 | 1885 | 20 | 18.0 | 2.47 | 82 | Cambisols | 8.1 | 496 | $1.99 \pm 0.36$ | $0.12 \pm 0.05$ | $16.9 \pm 3.54$ | $165 \pm 38$ |
|  | ESP-01 | -13.1751 | -71.5948 | 2863 | 17 | 13.1 | 1.56 | 72 | Umbrisols | 14.8 | 981 | $2.39 \pm 0.50$ | $0.19 \pm 0.05$ | $12.7 \pm 1.78$ | $140 \pm 32$ |
|  | TRU-03 | -13.1097 | -71.5995 | 3044 | 13 | 11.8 | 1.78 | 71 | Umbrisols | 15.5 | 787 | $2.24 \pm 0.44$ | $0.21 \pm 0.04$ | $10.5 \pm 2.35$ | $164 \pm 40$ |
|  | WAQ-01 | -13.1908 | -71.5874 | 3045 | 13 | 11.8 | 1.56 | 72 | Umbrisols | 8.8 | 1414 | $2.68 \pm 0.42$ | $0.24 \pm 0.05$ | $11.5 \pm 2.16$ | $149 \pm 46$ |
|  | TRU-01 | -13.1136 | -71.6069 | 3379 | 16 | 8.0 | 1.98 | 67 | Umbrisols | 15.0 | 856 | $2.53 \pm 0.31$ | $0.21 \pm 0.04$ | $11.2 \pm 3.10$ | $151 \pm 49$ |

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 ( $\mathrm{N}_{\mathrm{a}}$ ) and phosphorus ( $\mathrm{P}_{\mathrm{a}}$ ), as well as the ratio of leaf $\mathrm{N}: \mathrm{P}$ and leaf mass per unit area, $M_{\mathrm{a}}$, 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 $\mathrm{Na}_{\mathrm{a}}$ <br> ( $\mathrm{g} \mathrm{m}^{-2}$ ) | Leaf $\mathrm{P}_{\mathrm{a}}$ <br> ( $\mathrm{g} \mathrm{m}^{-2}$ ) | Leaf $\mathrm{N}: \mathrm{P}$ | $\begin{gathered} M_{\mathrm{a}} \\ \left(\mathrm{~g} \mathrm{~m}^{-2}\right) \end{gathered}$ | A400,a ( $\mu \mathrm{mol} \mathrm{m} \mathrm{m}^{-2} \mathrm{~s}^{-1}$ ) | A400,N $\left(\mu \mathrm{mol} \mathrm{gN}{ }^{-1} \mathrm{~s}^{-1}\right)$ | $\begin{aligned} & \left.V_{\text {cmaxa, }{ }_{2}^{25}}^{(\mu \mathrm{mol} \mathrm{~m}}{ }^{-2} \mathrm{~s}^{-1}\right) \end{aligned}$ | $\begin{gathered} J_{\text {max }, \mathrm{a}}{ }^{25} \\ \left(\mu \mathrm{~mol} \mathrm{~m}^{-2} \mathrm{~s}^{-1}\right) \end{gathered}$ | $J_{\text {maxa }}{ }^{25}: V_{\text {cmaxa }}{ }^{25}$ | $\begin{gathered} V_{\text {cmax } \mathrm{N}^{25}} \\ \left(\mu \mathrm{~mol} \mathrm{gN}^{-1} \mathrm{~s}^{-1}\right) \end{gathered}$ | $n_{\text {A }}$ | $n_{P}$ | $n_{\text {R }}$ | $n_{\mathrm{E}}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Lowland species | $1.96 \pm 0.52^{\text {a }}$ | $0.09 \pm 0.05^{\text {a }}$ | $22.2 \pm 8.6^{\text {a }}$ | $132 \pm 35^{\text {a }}$ | $8.2 \pm 3.9^{\text {a }}$ | $4.3 \pm 2.2^{\text {a }}$ | $35.9 \pm 14.6^{\text {a }}$ | $66.7 \pm 18.6^{\text {a }}$ | $1.86 \pm 0.40^{\text {a }}$ | $18.9 \pm 8.1^{\text {a }}$ | $37 \pm 1^{\text {a }}$ | $24 \pm 1^{\text {a }}$ | $9.0 \pm 4.0^{\text {a }}$ | $2.8 \pm 1.0^{\text {a }}$ |
| Upland species | $2.31 \pm 0.44^{\text {b }}$ | $0.18 \pm 0.06^{\text {b }}$ | $13.5 \pm 3.6^{\text {b }}$ | $143 \pm 39^{\text {b }}$ | $7.6 \pm 3.6^{\text {a }}$ | $3.4 \pm 1.7^{\text {b }}$ | $48.8 \pm 20.0^{\text {b }}$ | $96.9 \pm 36.9^{\text {b }}$ | $1.92 \pm 0.36^{\text {a }}$ | $22.5 \pm 9.4{ }^{\text {b }}$ | $38 \pm 1^{\text {a }}$ | $22 \pm 1^{\text {a }}$ | $10.5 \pm 4.3^{\text {b }}$ | $3.4 \pm 1.4^{\text {b }}$ |

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 lightsaturated net photosynthesis measured at $400 \mu \mathrm{~mol} \mathrm{~mol}{ }^{-1}$ atmospheric $\left[\mathrm{CO}_{2}\right], A_{400, \mathrm{~N}}=$ area-based light-saturated net photosynthesis measured at $400 \mu \mathrm{~mol}$ mol ${ }^{-1}$ atmospheric [CO2] per unit leaf nitrogen, $V_{\text {cmax, }}{ }^{25}=$ maximum carboxylation velocity of Rubisco normalised to $25^{\circ} \mathrm{C}, J_{\text {max, }}{ }^{25}=$ maximum rate of electron transport normalised to $25^{\circ} \mathrm{C}$, $J_{\text {max, }}{ }^{25}: V_{\text {cmax, }}{ }^{25}=$ ratio of maximum Rubisco carboxylation velocity over maximum rate of electron transport, both normalised to $25^{\circ} \mathrm{C}, V_{\text {cmax, }} \mathrm{N}^{25}=$ ratio of maximum carboxylation velocity of Rubisco normalised to $25^{\circ} \mathrm{C}$ 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 $n_{\mathrm{E}}=$ fraction of leaf N in electron transport.
Values are overall mean $\pm$ 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 $V_{\text {cmaxa }}{ }^{25}$ and $J_{\text {maxa }}{ }^{25}$ as the response variables, each showing fixed and random effects.

| Final model $\left(\boldsymbol{V}_{\text {cmaxa }}{ }^{\mathbf{2 5}}\right)$ |  |  |  |
| :--- | ---: | ---: | ---: |
| Fixed effect | Estimate | S.E | t value |
| Intercept | 41.470 | 1.578 | 26.288 |
| $\log 10$ (Soil P) | 7.909 | 2.466 | 3.207 |
| Pa | 68.148 | 22.558 | 3.021 |
|  |  |  |  |
| Random effect |  | Variance | \% of total |
| Intercept variance: family | 45.568 | $2.49 \%$ |  |
| Residual error (within family) | 1783.626 | $97.51 \%$ |  |
|  |  |  | $100.00 \%$ |


| Final model $\left(\boldsymbol{J}_{\text {maxa }}{ }^{\mathbf{2 5}}\right)$ |  |  |  |
| :--- | ---: | ---: | ---: |
| Fixed effect | Estimate | S.E | t value |
| Intercept | 77.217 | 2.712 | 28.477 |
| log10 (Soil P) | 16.866 | 4.327 | 3.898 |
| Pa | 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 | 1645.6 | AIC | 1342.4 |
| :--- | :--- | :--- | :--- |
| BIC | 1662.0 | BIC | 1357.3 |


| $-2 L L$ | -817.8 | $-2 L L$ | -666.2 |
| :--- | :--- | :--- | :--- |

$$
\begin{aligned}
& V_{\text {cmax }^{2}}=41.47+\left(7.91 * \log 10[\text { SoilP] })+\left(68.15 * \mathrm{P}_{\mathrm{a}}\right)\right. \\
& J_{\text {max }_{\mathrm{a}}}{ }^{25}=77.22+(16.87 * \log 10[\text { SoilP }])+\left(94.48 * \mathrm{P}_{\mathrm{a}}\right)
\end{aligned}
$$

Predictive equations for $V_{\text {cmaxa }}{ }^{25}$ and $J_{\operatorname{maxa}}{ }^{25}$ based on final preferred models are shown at the bottom. For the $V_{\text {cmaxa }}{ }^{25}$ and $J_{\text {maxa }}{ }^{25}$ 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 $\mathrm{CO}_{2}$ assimilation rate, $\boldsymbol{A}$ (area-based) to intercellular $\mathrm{CO}_{2}\left(C_{i}\right)$ 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 $\mathrm{C}_{\mathrm{i}} . V_{\text {cmax }}$ (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 $V_{c m a x}$ and $J_{\max }$ were then normalised to $25^{\circ} \mathrm{C}$. $\mathrm{CO}_{2}$ 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 $\mathbf{N}$-area, $\mathbf{N}_{\mathrm{a}}$ and (B) leaf $\mathbf{P}$-area, $\mathrm{P}_{\mathrm{a}}$ in relation to leaf mass per unit leaf area, $\boldsymbol{M}$ 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 $25^{\circ} \mathrm{C}, V_{\text {cmaxa }}{ }^{25}$, (B) maximum rate of electron transport normalised to $25^{\circ} \mathrm{C}$, $J_{\text {max }, ~}{ }^{25}$, (C) $J_{\text {max }, 25:} V_{\text {cmax }, 25}$ ratio, and (D) ratio of $V_{\text {cmax }, ~}{ }^{25}$ over leaf $\mathbf{N}, \boldsymbol{V}_{\text {cmax }} \mathbf{N}^{25}$ for each site. Values expressed on area basis. Sites are arranged according to decreasing leaf $\mathrm{N}: \mathrm{P}$ 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 $25^{\circ} \mathrm{C}\left(V_{\text {cmax a }}{ }^{\mathbf{2 5}}\right.$ ) against maximum rate of electron transport normalised to $\mathbf{2 5}{ }^{\circ} \mathrm{C}$ $\left(\boldsymbol{J}_{\text {max }} \mathbf{a}^{\mathbf{2 5}}\right.$ ). 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 $25^{\circ} \mathrm{C}\left(V_{\text {cmax }, ~}{ }^{25}\right)$ 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 $V_{c m a x a}{ }^{25} \leftrightarrow \mathrm{~N}_{\mathrm{a}}$,
$V_{\text {cmaxa }}{ }^{25} \leftrightarrow \mathrm{P}_{\mathrm{a}}$ and $V_{\text {cmax a }}{ }^{25} \leftrightarrow$ leaf $\mathrm{N}: \mathrm{P}$ relationships between lowland and upland species, but no significant difference when comparing slopes of $V_{\text {cmaxa }}{ }^{25} \leftrightarrow M_{a}$ relationships between lowland and upland species. Bottom panel shows log-log plots of maximum rate of electron transport normalised to $25^{\circ} \mathrm{C}\left(J_{\text {maxa }}{ }^{25}\right)$ 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 $J_{\text {max }}{ }^{25}$ 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 $V_{\text {cmaxa }}{ }^{25}$ to leaf $N\left(V_{c m a x}, N^{25}\right)$ in relation to (A) leaf mass per unit leaf area, $\mathbf{M}_{\mathrm{a}},(B)$ leaf $\mathbf{P}$-area, $\mathbf{P a}_{a}$ and (C) leaf $\mathbf{N}$ :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 $V_{\text {cmax }}{ }^{25} \leftrightarrow \mathrm{~Pa}_{\mathrm{a}}$ 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 $\mathbf{N}$ in pigment-protein complexes, $\boldsymbol{n}_{\mathrm{P}}$; fraction of leaf $\mathbf{N}$ in electron transport, $\boldsymbol{n}_{\mathrm{E}}$; fraction of leaf $\mathbf{N}$ in Rubisco; $\boldsymbol{n}_{\mathrm{R}}$, for each sites. $n_{R}$ was estimated from maximum carboxylation velocity of Rubisco (normalised to $25^{\circ} \mathrm{C}$ ), $V_{\mathrm{cmax}, \mathrm{a}}{ }^{25}, n_{\mathrm{E}}$ estimated from maximum electron transport rate (normalised to $25^{\circ} \mathrm{C}$ ), $J_{\text {max }} a^{25}$, 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 $\mathbf{N}$ allocated in photosynthetic metabolism, $n_{A}$ in relation to (A) leaf mass per unit leaf area, $M_{a}$, (B) leaf $N$-area, $\mathbf{N}_{\mathbf{a}}$, and (C) leaf P-area, $\mathbf{P a}_{\mathbf{a}}$. 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 $1.21 \mathrm{~g} \mathrm{~m}^{-2}$ of Rubisco of lowland species (Licania unguiculata from Chrysobalanaceae family), which then translate to $n_{\mathrm{R}}$
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 $25^{\circ} \mathrm{C}$ ), $V_{\text {cmax } a^{25}} . \mathrm{n}=16$

Figure 1:



Figure 2:



Figure 3:


Figure 4:


Figure 5:


Figure 6:


Figure 7:


Figure 8:




Figure 9:



## Supporting Information

## Authors: Bahar, Ishida, Weerasinghe et al. <br> 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, ALP30, 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

$\mathrm{CO}_{2}$ response curves of light-saturated photosynthesis (i.e. $A \leftrightarrow C_{i}$ curves) were quantified within 30-60 minutes after branch detachment, with $\mathrm{CO}_{2}$ concentrations inside the reference chamber ranging from 3.5 to $2000 \mu \mathrm{~mol} \mathrm{~mol}^{-1}$; initial measurements were made at $400 \mu \mathrm{~mol} \mathrm{~mol}^{-1}$, followed by decreases in $\mathrm{CO}_{2}$ to 300,200 , $150,125,100,75,50$ and $35 \mu \mathrm{~mol} \mathrm{~mol}^{-1}$; thereafter, $\mathrm{CO}_{2}$ concentrations were increased back to $400 \mu \mathrm{~mol} \mathrm{~mol}^{-1}$, and then to $600,900,1250,1500,1750$ and finally $2000 \mu \mathrm{~mol}$ $\mathrm{mol}^{-1}$. Block temperatures within the chamber were set to that of the prevailing daytime air temperature at each site (ranging from $25-28{ }^{\circ} \mathrm{C}$ depending on the site). A photosynthetic active radiation (PAR) flux density of $1800 \mu \mathrm{~mol} \mathrm{~m}^{-2} \mathrm{~s}^{-1}$, generated from an artificial light source (6400-02B Red/Blue LED Light Source, Li-Cor, Inc.), was used for all measurements. The resultant $A \leftrightarrow C_{\mathrm{i}}$ 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 $V_{\text {cmax }}$ and maximum rate of electron transport ( $J_{\max }$ ) on a leaf area basis. $V_{\text {cmax }}$ and $J_{\max }$ values at the prevailing leaf temperature were determined via minimizing the sum of squares of modelled vs observed estimates of net $\mathrm{CO}_{2}$ exchange at given $\mathrm{C}_{\mathrm{i}}$ values. This was done for both the $\mathrm{CO}_{2}$-limited and $\mathrm{CO}_{2}{ }^{-}$ 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. $V_{\text {cmax }}$ 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 $\mathrm{CO}_{2}$ values were fitted to the Rubisco-limited equation of photosynthesis:

$$
A=\left[\frac{V_{c \max }\left(C_{i}-\Gamma_{*}\right)}{\left(c_{i}+K_{c}\left(1+O / K_{o}\right)\right)}\right]-R_{\text {light }} \quad \text { (Eqn 1) }
$$

where $R_{\text {light }}$ is respiration in the light, $\Gamma *$ is the $\mathrm{CO}_{2}$ compensation point in the absence of photorespiration (3.69 Pa at $25^{\circ} \mathrm{C}$; von Caemmerer et al. (1994)), $K_{c}$ and $K_{o}$ are the effective Michaelis-Menten constants for $\mathrm{CO}_{2}$ and $\mathrm{O}_{2}$ at $25^{\circ} \mathrm{C}$ [40.4 Pa and 24.8 kPa ,
respectively, von Caemmerer et al. (1994)] and O is partial pressure of $\mathrm{O}_{2}$, corrected for atmospheric pressure at each altitude, according to:
$O_{2}$ partial pressure at site $=O_{2}$ partial pressure at sea level $\times \frac{\text { air pressure at site }}{\text { air pressure at sea level }}$ The resultant $\mathrm{O}_{2}$ partial pressures at each site were then used to modify estimates of $\Gamma^{*}$ 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 $\left(E_{\mathrm{a}}\right)$ of $K_{\mathrm{c}}$ and $K_{\circ}$ of 59.4 and $36 \mathrm{~kJ} \mathrm{~mol}^{-1}$, 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 $\mathrm{CO}_{2}$ assimilation:

$$
\begin{equation*}
A=\left[\frac{J_{\max }\left(C_{i}-\Gamma_{*}\right)}{\left(4 C_{i}+8 \Gamma_{*}\right)}\right]-R_{\text {light }} \tag{Eqn2}
\end{equation*}
$$

assuming that $A$ is limited by RuBP regeneration at higher concentrations of atmospheric $\mathrm{CO}_{2}$ (Fig. 1). As atmospheric $\mathrm{CO}_{2}$ was not always saturating for measurements of upland species (due to low atmospheric partial pressure), $J_{\text {max }}$ may have been underestimated in some cases and we excluded these $J_{\max }$ values from the Andean data set. Rates of $\mathrm{CO}_{2}$ exchange were corrected for diffusion through the gasket of the LI-6400 leaf chamber (Bruhn et al., 2002) prior to calculation of $V_{\text {cmax }}$ and $J_{\text {max. }}$. Fitted parameters were scaled to a reference temperature of $25^{\circ} \mathrm{C}$ using activation energies of 64.8 and $37.0 \mathrm{~kJ} \mathrm{~mol}^{-1}$ for $V_{\text {cmax }}$ and $J_{\text {max, }}$, respectively (Farquhar et al., 1980).

Alterations in stomatal conductance $\left(g_{s}\right)$ resulting from branch cutting were assumed to not affect the maximum carboxylation velocity of Rubisco ( $V_{\text {cmax }}$ ) (Miyazawa et $a l .$, 2011), except where $g_{s}$ declined to very low levels (Santiago \& Mulkey, 2003); in instances where $g_{\mathrm{s}}$ values fell below $0.04 \mathrm{~mol} \mathrm{~m}^{-2} \mathrm{~s}^{-1}$, 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 $2 \mu \mathrm{~mol} \mathrm{CO} 2 \mathrm{~g} \mathrm{~N}^{-1} \mathrm{~s}^{-1}$ 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 hardleaved 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) $100 \%(\mathrm{v} / \mathrm{v})$ 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, $0.1 \mathrm{mg} / \mathrm{mL}$ 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 cleanup 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 ( $0.5 \mu \mathrm{~g} \mathrm{LL}^{-1}$ ). The western blot assay estimated $0.31 \mu \mathrm{~g} \mu \mathrm{~L}-1$ Rubisco in the sample and $0.78 \mu \mathrm{~g} \mu \mathrm{~L}-1$ 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 $1.6 \mu \mathrm{~g}$ 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), $80 \%(\mathrm{v} / \mathrm{v})$ 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, $\sim 55 \mathrm{kDa}$ ) and small subunits (SSU, 15 kDa ). Greatest quality blots were consistently observed from $100 \%$ methanoltreated 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 ( $\pm$ 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 ( $\pm$ 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 ( $0.5 \mu \mathrm{~g} \mu \mathrm{~L}^{-1}$ ). 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 ( 50 mM EPPS [4-(2-hydroxyethyl)-1piperazinepropanesulfonic acid]-NaOH, 1mM EDTA, 1\% Polyvinylpolypyrrolidone (PVPP), 10 mM 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 $0.8 \mu \mathrm{~g}$ ) 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 $400 \mu \mathrm{~mol}$ mol ${ }^{-1}$ atmospheric $\left[C O_{2}\right], A_{2000, a}=$ light-saturated net photosynthesis measured under $2000 \mu \mathrm{~mol}^{\text {mol }}{ }^{-1}$ atmospheric $\left[\mathrm{CO}_{2}\right], V_{\text {cmaxa }}{ }^{25}=$ maximum carboxylation velocity of Rubisco normalised to $25^{\circ} \mathrm{C}$, $J_{\text {maxa }}{ }^{25}=$ maximum rate of electron transport normalised to $25^{\circ} \mathrm{C}$, Right = leaf respiration measured in the light at $400 \mu \mathrm{~mol}^{2} \mathrm{~mol}^{-1}$ atmospheric [ $\mathrm{CO}_{2}$ ], Leaf $T=$ leaf temperature inside gas exchange cuvette, $\mathrm{Chl}=\mathrm{chlorophyll}$ a and b content, $n_{E}=$ fraction of leaf N in electron transport, $n_{\mathrm{R}}=$ fraction of leaf N in Rubisco, $n_{\mathrm{P}}=$ fraction of leaf N in pigment-protein complexes.

| Site | Family | Genus | Species | $\begin{gathered} M_{\mathrm{a}} \\ \left(\mathrm{~g} \mathrm{~m}^{-2}\right) \\ \hline \end{gathered}$ | Leaf $\mathrm{Na}_{\mathrm{a}}$ $\qquad$ $\left(\mathrm{g} \mathrm{~m}^{-2}\right)$ | $\begin{array}{r} \text { Leaf } \mathrm{P}_{\mathrm{a}} \\ \left(\mathrm{~g} \mathrm{~m}^{-2}\right) \\ \hline \end{array}$ | $\begin{array}{r} A_{400, \mathrm{a}} \\ \left(\mathrm{mmolm}^{2} \mathrm{~s}^{1}\right) \end{array}$ | $\underset{\left(\mu \mathrm{molm} \mathrm{~m}^{2} \mathrm{~s}^{1}\right)}{A_{200, a}}$ | $\begin{gathered} V_{\text {cmax }, a^{2}} 25 \\ \left(\mu \mathrm{~mol} \mathrm{~m}^{2} \mathrm{~s}^{1}\right) \end{gathered}$ | $\begin{gathered} J_{\max , \mathrm{a}^{2}}^{25} \\ \left(\mathrm{\mu mol} \mathrm{~m}^{2} \mathrm{~s}^{1}\right) \end{gathered}$ | $\begin{array}{r} R_{\text {light }} \\ \left(\mu \mathrm{mol} \mathrm{~m}^{2} \mathrm{~s}^{1}\right) \end{array}$ | $\begin{array}{r} \hline \text { Leaf } T \\ \left({ }^{\circ} \mathrm{C}\right) \\ \hline \end{array}$ | $\begin{array}{r} \mathrm{ChI} \\ \left(\mathrm{~g} \mathrm{~m}^{-2}\right) \end{array}$ | $n_{\mathrm{E}}$ | $n_{R}$ | $n^{\prime}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 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. <br> 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 | $s p$ | 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 | $s p$ | 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 | $s p$. | 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 of | 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 | 11 ex | 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 | $s p$. | 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 | 11 x | 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 | 11 ex | 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 | 11 ex | 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: $\mathrm{N}_{\mathrm{a}}=$ leaf nitrogen, $\mathrm{P}_{\mathrm{a}}=$ leaf phosphorus, leaf $\mathrm{N}: \mathrm{P}=$ leaf nitrogen to phosphorus ratio, $\mathrm{M}_{\mathrm{a}}=$ leaf mass per unit leaf area, $\mathrm{Chl}=\mathrm{chlorophyll}$ a and b content, $V_{\mathrm{cmaxa}}{ }^{25}=$ maximum carboxylation velocity of Rubisco normalised to $25^{\circ} \mathrm{C}, J_{\text {max, }}{ }^{25}=$ maximum rate of electron transport normalised to $25^{\circ} \mathrm{C}, V_{N, 25}=$ ratio of maximum carboxylation velocity of Rubisco normalised to $25^{\circ} \mathrm{C}$ over leaf nitrogen, Soil $\mathrm{P}=$ soil phosphorus, Soil $\mathrm{N}=$ 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.

|  | Na | $\mathrm{Pa}_{\mathrm{a}}$ | Leaf $\mathrm{N}: \mathrm{P}$ | Ma | Chl | $V_{\text {cmax,a }}{ }^{25}$ | $J_{\text {max }, ~} 25$ | $V_{\text {cmax, } \mathrm{N}^{25}}$ | Soil P | Soil N | Elevation | MAT | MAP |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| $\mathrm{Na}_{\mathrm{a}}$ ( $\mathrm{g} \mathrm{m}^{-2}$ ) | $\begin{gathered} 1 \\ (248) \end{gathered}$ | $\underset{(240)}{0.613^{* *}}$ | $\begin{gathered} -0.208^{* *} \\ (232) \end{gathered}$ | $\begin{gathered} 0.353^{* *} \\ (246) \end{gathered}$ | $\underset{(171)}{0.370 * *}$ | $\begin{gathered} 0.226 * * \\ (246) \end{gathered}$ | $\begin{gathered} 0.227^{* *} \\ (184) \end{gathered}$ | $\underset{(242)}{-0.297^{* *}}$ | $\begin{gathered} 0.356^{* *} \\ (248) \end{gathered}$ | $\underset{(248)}{0.319^{* *}}$ | $\underset{(248)}{0.368^{* *}}$ | $\begin{gathered} -0.375 * * \\ (248) \end{gathered}$ | $\begin{array}{r} -0.041 \\ (248) \end{array}$ |
| $\begin{aligned} & \mathrm{Pa} \\ & \left(\mathrm{~g} \mathrm{~m}^{-2}\right) \end{aligned}$ |  | $\begin{gathered} 1 \\ (248) \end{gathered}$ | $\begin{gathered} -0.769 * * \\ (227) \end{gathered}$ | $\begin{gathered} 0.188^{* *} \\ (246) \end{gathered}$ | $\underset{(170)}{0.229^{* *}}$ | $\begin{gathered} 0.331^{* *} \\ (241) \end{gathered}$ | $\begin{gathered} 0.366 * * \\ (186) \end{gathered}$ | $\begin{array}{r} -0.013 \\ (234) \end{array}$ | $\begin{gathered} 0.611^{* *} \\ (248) \end{gathered}$ | $\begin{gathered} 0.623^{* *} \\ (248) \end{gathered}$ | $\begin{array}{r} 0.694^{\star *} \\ (248) \end{array}$ | $\begin{gathered} -0.711^{* *} \\ (248) \end{gathered}$ | $\begin{array}{r} -0.004 \\ (248) \end{array}$ |
| Leaf $\mathrm{N}: \mathrm{P}$ |  |  | $\begin{gathered} 1 \\ (245) \end{gathered}$ | $\begin{array}{r} -0.085 \\ (232) \end{array}$ | $\begin{array}{r} -0.047 \\ (159) \end{array}$ | $\underset{(243)}{-0.280 * *}$ | $\underset{(177)}{-0.244^{* *}}$ | $\underset{(227)}{-0.157^{*}}$ | $\begin{gathered} -0.476 * * \\ (245) \end{gathered}$ | $\underset{(245)}{-0.512 * *}$ | $\underset{(245)}{-0.539 * *}$ | $\underset{(245)}{0.551^{* *}}$ | $\begin{array}{r} -0.020 \\ (245) \end{array}$ |
| $M_{a}$ <br> ( $\mathrm{g} \mathrm{m}^{-2}$ ) |  |  |  | $\begin{gathered} 1 \\ (274) \end{gathered}$ | $0.157^{*}$ <br> (185) | $\begin{array}{r} 0.077 \\ (272) \end{array}$ | $\underset{(199)}{0.196 * *}$ | $\begin{array}{r} -0.095 \\ (240) \end{array}$ | $\begin{array}{r} -0.029 \\ (274) \end{array}$ | $\begin{gathered} 0.195^{* *} \\ (274) \end{gathered}$ | $\underset{(274)}{0.194^{* *}}$ | $\underset{(274)}{-0.162 * *}$ | $\begin{array}{r} -0.111 \\ (274) \end{array}$ |
| Chl $\left(\mathrm{g} \mathrm{~m}^{-2}\right)$ |  |  |  |  | $\begin{gathered} 1 \\ (185) \end{gathered}$ | $\begin{array}{r} -0.001 \\ (183) \end{array}$ | $\begin{array}{r} 0.085 \\ (133) \end{array}$ | $\begin{array}{r} -0.109 \\ (166) \end{array}$ | $\underset{(185)}{0.2855^{* *}}$ | $\begin{array}{r} 0.153^{*} \\ (185) \end{array}$ | $\begin{array}{r} 0.145 * \\ (185) \end{array}$ | $\begin{gathered} -0.151^{*} \\ (185) \end{gathered}$ | $\begin{array}{r} 0.239^{* *} \\ (185) \end{array}$ |
| $\begin{aligned} & \left.V_{\mathrm{cmax}, \mathrm{a}^{25}}^{(\mu \mathrm{molm}} \mathrm{m}^{-2} \mathrm{~s}^{-1}\right) \end{aligned}$ |  |  |  |  |  | $\begin{gathered} 1 \\ (283) \end{gathered}$ | $\begin{aligned} & 0.840 * * \\ & (209) \end{aligned}$ | $\begin{gathered} 0.810^{* *} \\ (242) \end{gathered}$ | $\begin{gathered} 0.287^{* *} \\ (290) \end{gathered}$ | $\begin{gathered} 0.354^{* *} \\ (290) \end{gathered}$ | $\begin{array}{r} 0.384^{* *} \\ (283) \end{array}$ | $\begin{gathered} -0.399 * * \\ (283) \end{gathered}$ | $\begin{array}{r} -0.070 \\ (283) \end{array}$ |
| $\begin{aligned} & \left.J_{\left(\mu \mathrm{mox}, \mathrm{a}^{-2}\right.} \mathrm{s}^{-1}\right) \end{aligned}$ |  |  |  |  |  |  | $\begin{gathered} 1 \\ (209) \end{gathered}$ | $\begin{gathered} 0.629^{* *} \\ (182) \end{gathered}$ | $\begin{gathered} 0.373^{* *} \\ (209) \end{gathered}$ | $\begin{gathered} 0.475^{* *} \\ (209) \end{gathered}$ | $\begin{array}{r} 0.461^{* *} \\ (209) \end{array}$ | $\begin{gathered} -0.462 * * \\ (209) \end{gathered}$ | $\begin{array}{r} 0.152^{*} \\ (209) \end{array}$ |
| $\begin{aligned} & V_{\mathrm{cmax}^{2} \mathrm{~N}^{25}} \\ & (\mu \mathrm{~mol} \mathrm{gN} \end{aligned}$ |  |  |  |  |  |  |  | $\begin{gathered} 1 \\ (242) \end{gathered}$ | $\begin{array}{r} 0.143^{*} \\ (242) \end{array}$ | $\underset{(242)}{0.201^{* *}}$ | $\begin{array}{r} 0.186 * * \\ (242) \end{array}$ | $\begin{array}{r} -0.198 * * \\ (242) \end{array}$ | $\begin{aligned} & 0.028 \\ & (242) \end{aligned}$ |
| Soil P <br> ( $\mathrm{mg} \mathrm{kg}{ }^{-1}$ ) |  |  |  |  |  |  |  |  | $\begin{gathered} 1 \\ (292) \end{gathered}$ | $\begin{gathered} 0.681^{* *} \\ (292) \end{gathered}$ | $\begin{array}{r} 0.716^{* *} \\ (292) \end{array}$ | $\underset{(292)}{-0.720 * *}$ | $\begin{array}{r} 0.380 * * \\ (292) \end{array}$ |
| Soil N ( $\mathrm{g} \mathrm{kg}^{-1}$ ) |  |  |  |  |  |  |  |  |  | $\begin{gathered} 1 \\ (292) \end{gathered}$ | $\begin{array}{r} 0.921^{* *} \\ (292) \end{array}$ | $\underset{(292)}{-0.902 * *}$ | $\begin{aligned} & 0.104 \\ & (292) \end{aligned}$ |
| Elevation (m a.s.l.) |  |  |  |  |  |  |  |  |  |  | $\begin{gathered} 1 \\ (292) \end{gathered}$ | $\underset{(292)}{-0.992^{* *}}$ | $\begin{array}{r} -0.068 \\ (292) \end{array}$ |
| $\begin{aligned} & \text { MAT } \\ & \left({ }^{\circ} \mathrm{C}\right) \end{aligned}$ |  |  |  |  |  |  |  |  |  |  |  | $\begin{gathered} 1 \\ (292) \end{gathered}$ | $\begin{aligned} & 0.070 \\ & (292) \end{aligned}$ |
| MAP <br> (mm) |  |  |  |  |  |  |  |  |  |  |  |  | $\begin{gathered} 1 \\ (292) \\ \hline \end{gathered}$ |

[^1]Table S3: Standardized major axis regression slopes and their confidence intervals for log-log transformed relationships comparing leaf traits of lowland ( $\sim 173$ species) and upland ( $\sim 120$ 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 Cl 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 <br> Cl | $p$ | Common slope $y$-axis intercept | Shift along a common slope? |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Navs. $M_{\text {a }}$ | 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 |  |  |  |  |  |  |
| Pa vs. Ma | 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 |  |  |  |  |  |  |
| $V_{\text {cmaxa }}{ }^{25}$ vs. $M_{\text {a }}$ | 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, $\mathrm{p}<0.001$ |
|  | Upland | 0.014 | 0.212 | 1.642 | (1.362, 1.981) | -1.863 |  |  |  |  | -1.999 |  |
| $V_{\text {cmaxa }}{ }^{25} \text { vs. } \mathrm{Na}_{\mathrm{a}}$ | 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 |  |  |  |  |  |  |
| $V_{\text {cmaxa }}{ }^{25} \mathrm{vs}. . \mathrm{Pa}^{\text {a }}$ | 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 |  |  |  |  |  |  |
| $V_{\text {cmaxa }}{ }^{25} \text { vs. leaf } \mathrm{N}: \mathrm{P}$ | 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 |  |  |  |  |  |  |
| $J_{\operatorname{maxa}}{ }^{25} \text { vs. } M_{\mathrm{a}}$ | 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 |  |  |  |  |  |  |
| $J_{\text {maxa }}{ }^{25} \mathrm{vs} . \mathrm{N}_{\mathrm{a}}$ | 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 |  |  |  |  |  |  |
| $J_{\text {maxa }}{ }^{25}$ vs. Pa | 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 |  |  |  |  |  |  |
| $J_{\max }{ }^{25} \text { vs. leaf N:P }$ | 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 |  |  |  |  |  |  |
| $V_{\text {cmax } \times N^{25}} \text { vs. } M_{a}$ | 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 |  |
| $V_{\mathrm{cmax}} \mathrm{~N}^{25} \text { vs. } \mathrm{Pa}_{\mathrm{a}}$ | 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 |  |  |  |  |  |  |
| $V_{\text {cmax }} N^{25} \text { vs. leaf } N: P$ | 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, $\mathrm{p}<0.001$ |
|  | Upland | 0.020 | 0.185 | -1.709 | (-2.105, -1.388) | 3.185 |  |  |  |  | 2.903 |  |
| $J_{\text {maxa }}{ }^{25}$ vs. ${ }^{-1} V_{\text {cmax }}{ }^{25}$ | 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 $\pm$ 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 $400 \mu \mathrm{~mol} \mathrm{~mol}{ }^{-1}$ atmospheric [ $\mathrm{CO}_{2}$ ]; $\mathrm{C}_{\mathrm{i} 400,}$, intercellular $\mathrm{CO}_{2}$ partial pressure at $400 \mu \mathrm{~mol}$ mol ${ }^{-1}$ atmospheric [CO ${ }_{2}$; $C_{a 400,}$ atmospheric $\mathrm{CO}_{2}$ partial pressure at $400 \mu \mathrm{~mol} \mathrm{~mol}^{-1}$ atmospheric $\left[\mathrm{CO}_{2}\right] ; \mathrm{C}_{4400}: \mathrm{C}_{\mathrm{a} 400}$, ratio of intercellular to atmospheric $\mathrm{CO}_{2}$ at $400 \mu \mathrm{~mol} \mathrm{~mol}^{-1}$ [CO2]; $A_{400}: \mathrm{N}^{2}$, ratio of light-saturated net photosynthesis measured under $400 \mu \mathrm{~mol} \mathrm{~mol}^{-1}$ atmospheric $\left[\mathrm{CO}_{2}\right]$ over leaf $\mathrm{N} ; A_{2000, \mathrm{a}}$, light-saturated net photosynthesis measured under $2000 \mu \mathrm{~mol} \mathrm{~mol}^{-1}$ atmospheric [CO2]; $\mathrm{C}_{\mathrm{i} 2000}$, intercellular $\mathrm{CO}_{2}$ at $2000 \mu \mathrm{~mol}$ $\mathrm{mol}^{-1}$ atmospheric [CO2]; $A_{2000}: \mathrm{N}$, ratio of light-saturated net photosynthesis measured under $2000 \mu \mathrm{~mol} \mathrm{~mol}^{-1}$ atmospheric [CO2] over leaf $\mathrm{N} ; \mathrm{R}_{\mathrm{d}}$, leaf dark respiration measured at $400 \mu \mathrm{~mol}$ mol ${ }^{-1}$ atmospheric [CO2]; Leaf $T$, leaf temperature inside gas exchange cuvette; Chl, chlorophyll a and b content.

|  | Sites | $A_{400, \mathrm{a}}$ $\left(\mu \mathrm{mol} \mathrm{m}^{-2} \mathrm{~s}^{-1}\right)$ | $\overline{C_{i 400}}$ (Pa) | $C_{\mathrm{a} 400}$ <br> (Pa) | $C_{\text {i400: }} C_{\text {a } 400}$ | $A_{400, \mathrm{~N}}$ <br> $\left(\mu \mathrm{mol} \mathrm{gN}^{-1} \mathrm{~s}^{-1}\right)$ | $A_{2000, \mathrm{a}}$ <br> ( $\mu \mathrm{mol} \mathrm{m}{ }^{-2} \mathrm{~s}^{-1}$ ) | $C_{i 2000}$ $(\mathrm{Pa})$ | $A_{2000, \mathrm{~N}}$ $\left(\mu \mathrm{mol} \mathrm{gN}^{-1} \mathrm{~s}^{-1}\right)$ | $\begin{aligned} & R_{\text {light }} \\ & (\mu \mathrm{mol} \mathrm{~m} \\ & \\ & \left(\mathrm{mos}^{-1}\right) \end{aligned}$ | Leaf $T$ <br> ( ${ }^{\circ} \mathrm{C}$ ) | $\begin{aligned} & \mathrm{Chl} \\ & \left(\mathrm{~g} \mathrm{~m}^{-2}\right) \\ & \hline \end{aligned}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Lowland | SUC-05 | $8.8 \pm 4.5$ | $28.9 \pm 2.9$ | $38.5 \pm 0.7$ | $0.75 \pm 0.08$ | $4.6 \pm 2.5$ | $20.9 \pm 6.1$ | $156.5 \pm 21.8$ | $11.9 \pm 5.1$ | $1.2 \pm 0.5$ | $28.8 \pm 0.5$ | $0.73 \pm 0.21$ |
|  | TAM-05 | $9.5 \pm 2.7$ | $25.3 \pm 2.6$ | $38.0 \pm 0.5$ | $0.67 \pm 0.06$ | $4.8 \pm 1.7$ | $22.2 \pm 3.6$ | $147.5 \pm 21.1$ | $10.9 \pm 2.1$ | $0.7 \pm 0.6$ | $30.2 \pm 0.7$ |  |
|  | JEN-11 | $7.3 \pm 3.7$ | $31.4 \pm 2.9$ | $38.9 \pm 0.6$ | $0.81 \pm 0.07$ | $4.1 \pm 2.3$ | $17.4 \pm 7.5$ | $171.7 \pm 14.2$ | $8.3 \pm 3.9$ | $1.1 \pm 0.6$ | $28.8 \pm 0.4$ | $0.69 \pm 0.30$ |
|  | ALP-01 | $7.5 \pm 4.4$ | $27.2 \pm 3.4$ | $39.2 \pm 0.4$ | $0.69 \pm 0.09$ | $3.9 \pm 2.4$ | $17.4 \pm 6.1$ | $146.5 \pm 20.4$ | $8.7 \pm 3.0$ | $0.7 \pm 0.6$ | $29.9 \pm 0.6$ | $0.58 \pm 0.15$ |
|  | SUC-01 | $7.8 \pm 4.7$ | $29.2 \pm 4.3$ | $38.9 \pm 0.6$ | $0.77 \pm 0.08$ | $3.8 \pm 2.3$ | $19.6 \pm 6.2$ | $157.4 \pm 21.2$ | $10.5 \pm 3.4$ | $1.1 \pm 0.8$ | $29.5 \pm 1.0$ | $0.64 \pm 0.19$ |
|  | JEN-12 | $8.5 \pm 4.4$ | $30.5 \pm 2.8$ | $38.9 \pm 0.5$ | $0.78 \pm 0.07$ | $4.5 \pm 2.3$ | $19.9 \pm 6.8$ | $161.5 \pm 24.8$ | $10.3 \pm 3.1$ | $1.0 \pm 0.8$ | $28.8 \pm 0.4$ | $0.57 \pm 0.15$ |
|  | ALP-03 | $6.7 \pm 3.2$ | $30.2 \pm 2.5$ | $39.2 \pm 0.4$ | $0.77 \pm 0.07$ | $4.3 \pm 2.4$ | $16.1 \pm 6.2$ | $165.3 \pm 14.0$ | $10.0 \pm 3.8$ | $1.0 \pm 0.4$ | $29.1 \pm 0.6$ | $0.54 \pm 0.13$ |
|  | CUZ-03 | $8.3 \pm 3.4$ | $25.5 \pm 3.3$ | $37.8 \pm 0.5$ | $0.67 \pm 0.08$ | $4.7 \pm 2.2$ | $19.2 \pm 5.7$ | $147.6 \pm 24.0$ | $10.8 \pm 3.9$ | $0.9 \pm 0.4$ | $29.9 \pm 0.5$ |  |
|  | ALP-04 | $7.2 \pm 3.7$ | $25.4 \pm 3.1$ | $39.1 \pm 0.3$ | $0.65 \pm 0.08$ | $4.0 \pm 2.3$ | $18.3 \pm 4.5$ | $129.7 \pm 27.8$ | $10.7 \pm 3.9$ | $1.3 \pm 0.8$ | $30.9 \pm 0.8$ | $0.62 \pm 0.14$ |
|  | TAM-09 | $11.2 \pm 2.3$ | $26.5 \pm 2.7$ | $37.2 \pm 0.5$ | $0.71 \pm 0.07$ | $5.5 \pm 1.8$ | $20.9 \pm 5.4$ | $153.6 \pm 18.6$ | $10.2 \pm 2.6$ | $0.6 \pm 0.4$ | $29.1 \pm 1.2$ |  |
|  | TAM-06 | $9.4 \pm 3.5$ | $26.7 \pm 3.6$ | $38.0 \pm 0.6$ | $0.70 \pm 0.09$ | $4.0 \pm 1.7$ | $22.6 \pm 3.6$ | $150.3 \pm 21.5$ | $9.1 \pm 2.1$ | $0.6 \pm 1.0$ | $29.9 \pm 0.6$ |  |
| Lowland mean |  | $8.2 \pm 3.9{ }^{\text {a }}$ | $28.4 \pm 3.7{ }^{\text {a }}$ | $38.6 \pm 0.8^{\text {a }}$ | $0.74 \pm 0.09^{\text {a }}$ | $4.3 \pm 2.2^{\text {a }}$ | $19.2 \pm 6.1^{\text {a }}$ | $155.2 \pm 22.7^{\text {a }}$ | $10.1 \pm 3.6^{\text {a }}$ | $1.0 \pm 0.7{ }^{\text {a }}$ | $29.4 \pm 0.9{ }^{\text {a }}$ | $0.62 \pm 0.17^{\text {a }}$ |
|  | SPD-02 | $8.4 \pm 2.7$ | $21.0 \pm 1.9$ | $32.2 \pm 0.3$ | $0.65 \pm 0.06$ | $3.9 \pm 1.4$ | $25.3 \pm 9.7$ | 89.317 .1 | $11.3 \pm 5.2$ | $1.0 \pm 1.5$ | $27.2 \pm 0.5$ | $0.78 \pm 0.30$ |
| Upland | SPD-01 | $8.6 \pm 5.0$ | $20.4 \pm 2.4$ | $33.2 \pm 0.6$ | $0.61 \pm 0.07$ | $3.8 \pm 2.2$ | $23.0 \pm 8.6$ | 95.216 .5 | $10.5 \pm 4.4$ | $0.1 \pm 0.8$ | $27.3 \pm 1.0$ | $0.72 \pm 0.23$ |
|  | TRU-08 | $9.0 \pm 3.7$ | $20.4 \pm 3.0$ | $32.0 \pm 0.5$ | $0.64 \pm 0.10$ | $4.1 \pm 1.7$ | $19.9 \pm 7.0$ | 90.420 .4 | $10.6 \pm 3.8$ | $1.1 \pm 0.8$ | $24.5 \pm 0.5$ | $0.59 \pm 0.16$ |
|  | ESP-01 | $4.9 \pm 2.9$ | $16.7 \pm 2.4$ | $28.5 \pm 0.3$ | $0.58 \pm 0.09$ | $2.3 \pm 1.4$ | $17.1 \pm 7.7$ | 55.111 .9 | $8.1 \pm 4.4$ | $1.4 \pm 0.6$ | $26.9 \pm 1.7$ |  |
|  | WAQ-01 | $6.1 \pm 2.4$ | $16.5 \pm 2.2$ | $27.9 \pm 0.4$ | $0.59 \pm 0.08$ | $2.3 \pm 0.9$ | $19.3 \pm 8.9$ | 58.017 .9 | $7.1 \pm 3.1$ | $1.2 \pm 0.8$ | $26.6 \pm 1.6$ |  |
|  | TRU-03 | $7.9 \pm 3.2$ | $17.6 \pm 2.3$ | $27.7 \pm 0.3$ | $0.63 \pm 0.08$ | $3.6 \pm 1.7$ | $25.2 \pm 9.4$ | 65.312 .6 | $10.8 \pm 3.6$ | $1.2 \pm 0.8$ | $23.1 \pm 0.8$ | $0.60 \pm 0.29$ |
|  | TRU-01 | $7.8 \pm 3.1$ | $17.1 \pm 2.1$ | $26.3 \pm 0.3$ | $0.65 \pm 0.08$ | $3.5 \pm 1.2$ | $26.5 \pm 8.6$ | 58.811 .7 | $11.5 \pm 2.6$ | $1.3 \pm 0.7$ | $23.0 \pm 1.1$ | $0.81 \pm 0.22$ |
| Upland mean |  | $7.6 \pm 3.6{ }^{\text {a }}$ | $18.8 \pm 3.0^{\text {b }}$ | $30.1 \pm 2.6^{\text {b }}$ | $0.62 \pm 0.08^{\text {b }}$ | $3.4 \pm 1.7{ }^{\text {b }}$ | $22.3 \pm 8.9{ }^{\text {b }}$ | $75.8 \pm 22.8{ }^{\text {b }}$ | $10.0 \pm 4.3^{\text {a }}$ | $1.0 \pm 1.0{ }^{\text {a }}$ | $25.7 \pm 2.1^{\text {b }}$ | $0.69 \pm 0.25{ }^{\text {b }}$ |

Table S5: Standardized major axis regression slopes and their confidence intervals for relationships comparing leaf traits of lowland ( $\sim 126$ species) and upland ( $\sim 40$ species) species, depicted in Figures 7 and $\mathbf{S 2}$ in the main text. Analysis undertaken using individual replicates. Coefficients of determination $\left(r^{2}\right)$ 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 Cl of the common slopes provided). Where there was a significant difference in the elevation (i.e. $y$-axis intercept) of the commonslope 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 | $\mathrm{r}^{2}$ | $p$ | Slope | Slope CI | Intercept | $p$ | Common slope | Common slope Cl | $p$ | Common slope y-axis intercept | Shift along a common slope? |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| $n_{\mathrm{P}}$ vs. $M_{\mathrm{a}}$ | 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 |  |
| $n_{\mathrm{R}}$ vs. $M_{\mathrm{a}}$ | 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, $\mathrm{p}=0.794$ |
|  | Upland | 0.001 | 0.809 | 0.1110 | (0.090, 0.137) | -5.861 |  |  |  |  | 27.171 |  |
| $n_{\mathrm{E}}$ Vs. $M_{\mathrm{a}}$ | 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, $\mathrm{p}=0.227$ |
|  | Upland | 0.001 | 0.870 | -0.0339 | $(-0.045,-0.026)$ | 8.240 |  |  |  |  | 7.605 |  |
| $n_{\mathrm{P}} \text { vs. } \mathrm{N}_{\mathrm{a}}$ | 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, $\mathrm{p}<0.001$ |
|  | Upland | 0.001 | 0.773 | -17.43 | (-22.36, -13.59) | 60.53 |  |  |  |  | 59.063 |  |
| $n_{\mathrm{R}}$ VS. $\mathrm{Na}_{\text {a }}$ | 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 |  |
| $n_{\mathrm{E}} \mathrm{VS} . \mathrm{Na}_{\mathrm{a}}$ | 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 |  |  |  |  |  |  |
| $n_{\mathrm{P}}$ vs. $\mathrm{Pa}_{\mathrm{a}}$ | 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 |  |  |  |  |  |  |
| $n_{\mathrm{R}} \mathrm{VS}$. Pa | 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, $\mathrm{p}<0.001$ |
|  | Upland | 0.030 | 0.106 | -75.48 | (92.97, -61.28) | 23.26 |  |  |  |  | 24.851 |  |
| $n_{\mathrm{E}} \text { vs. } \mathrm{Pa}_{\mathrm{a}}$ | Lowland | 0.050 | 0.013 | -19.99 | (-23.79, -16.80) | 4.635 | 0.568 | -20.60 | $\begin{array}{ll}-17.84 & -23.75\end{array}$ | <0.001 | 4.692 | Yes, $p=0.001$ |
|  | Upland | 0.155 | 0.003 | -21.89 | (-28.19, -16.99) | 7.047 |  |  |  |  | 6.824 |  |
| $n_{\text {A }}$ vs. $M_{\text {a }}$ | 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, $\mathrm{p}=0.742$ |
| (log-transformed) | Upland | 0.002 | 0.794 | -0.8934 | (-1.233, -0.647) | 1.475 |  |  |  |  | 2.026 |  |
| $n_{\text {A }}$ VS. $\mathrm{Na}_{\text {a }}$ | 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, $\mathrm{p}=0.189$ |
| (log-transformed) | Upland | 0.156 | 0.011 | -1.403 | (-1.881, -1.046) | 0.037 |  |  |  |  | -0.054 |  |
| $n_{\text {A }}$ vs. $\mathrm{Pa}_{\mathrm{a}}$ | 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, $\mathrm{p}<0.001$ |
| (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 $\boldsymbol{V}_{\text {cmax }, a^{25}}$ and $\boldsymbol{J}_{\text {max }, ~}{ }^{25}$ as the response variables. Continuous explanatory variables are $N_{a}, P_{a}, M_{a}$, total soil $P$ and $N, M A T$ 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 $\mathrm{N}: P$ ). 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 -2 LL ( -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 twoway 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 $V_{\text {cmax }}$ model selection steps.

| Model | Fixed component | DF | AIC | BIC | -2LL |
| :---: | :---: | :---: | :---: | :---: | :---: |
| $V_{\text {cmax, }}{ }^{25}$ |  |  |  |  |  |
| 1 | $\log 10\left(\right.$ Soil P) $+\mathrm{Na}_{\mathrm{a}}+$ Site $\cdot \mathrm{Na}_{\mathrm{a}}+\mathrm{Pa}_{\mathrm{a}}+$ Site. $\mathrm{Pa}_{\mathrm{a}}+\mathrm{Na}_{\mathrm{a}} \cdot \mathrm{Pa}_{\mathrm{a}}$ | 9 | 1663.5 | 1693.1 | -822.7 |
| 2 | $\log 10\left(\right.$ Soil P) $+\mathrm{Na}_{\mathrm{a}}+$ Site $\cdot \mathrm{Na}_{\mathrm{a}}+\mathrm{Pa}_{\mathrm{a}}+$ Site. $\mathrm{Pa}_{\mathrm{a}}+\log 10\left(\right.$ Soil P) $\cdot \mathrm{Na}_{\mathrm{a}}$ | 9 | 1664.0 | 1693.7 | -823.0 |
| 3 | $\log 10\left(\right.$ Soil P) $+\mathrm{N}_{\mathrm{a}}+$ Site $. \mathrm{Na}_{\mathrm{a}}+\mathrm{Pa}_{\mathrm{a}}+$ Site. $\mathrm{Pa}_{\mathrm{a}}$ | 8 | 1663.2 | 1689.6 | -823.6 |
| 4 | $\log 10\left(\right.$ Soil P) $+\mathrm{N}_{\mathrm{a}}+$ Site. $\mathrm{Na}_{\mathrm{a}}+\mathrm{Pa}$ | 7 | 1661.4 | 1684.4 | -823.7 |
| 5 | $\log 10\left(\right.$ Soil P) $+\mathrm{Na}_{\mathrm{a}}+\mathrm{Pa}_{\mathrm{a}}$ | 6 | 1661.5 | 1681.3 | -824.7 |
| 6 | $\underline{\log 10(\text { Soil P })+\mathrm{Pa}_{\text {a }}}$ | $\underline{5}$ | 1659.7 | 1676.1 | $\underline{-824.8}$ |
| 7 | $\log 10($ Soil P $)+\mathrm{Pa}_{\mathrm{a}}+\mathrm{MAT}+\mathrm{Pa}_{\mathrm{a}}:$ MAT | 7 | 1663.1 | 1686.1 | -824.5 |
| 8 | $\log 10\left(\right.$ Soil P) $+\mathrm{Pa}_{\mathrm{a}}+$ MAT | 6 | 1661.1 | 1680.9 | -824.6 |
| 9 | $\log 10($ Soil P) + Pa + SoilN | 6 | 1658.9 | 1678.6 | -823.4 |
| 10 | $\log 10\left(\right.$ Soil P) $+\mathrm{Pa}_{\mathrm{a}}+$ ECEC | 6 | 1657.5 | 1677.2 | -822.7 |
| 11 | $\log 10($ Soil P $)+\mathrm{Pa}_{\mathrm{a}}+\mathrm{Ma}_{a}$ | 6 | 1660.8 | 1680.5 | -824.4 |
| $J_{\text {max }, a^{25}}$ |  |  |  |  |  |
| 1 | $\log 10\left(\right.$ Soil P) $+\mathrm{Pa}+\mathrm{Na}_{\mathrm{a}}+\mathrm{Ma}_{a}+\mathrm{MAT}+\mathrm{Na}^{2} \cdot \mathrm{~Pa}$ | 9 | 1361.1 | 1388.0 | -671.5 |
| 2 | $\log 10\left(\right.$ Soil P) $+\mathrm{Pa}_{\mathrm{a}}+\mathrm{Na}_{\mathrm{a}}+M_{a}+\mathrm{MAT}+\log 10\left(\right.$ Soil P) $\cdot \mathrm{Na}_{\mathrm{a}}$ | 9 | 1358.7 | 1385.7 | -670.4 |
| 3 | $\log 10\left(\right.$ Soil P) $+\mathrm{Pa}_{\mathrm{a}}+\mathrm{Na}_{\mathrm{a}}+M_{a}+$ MAT | 8 | 1360.3 | 1384.3 | -672.2 |
| 4 | $\log 10\left(\right.$ Soil P) $+\mathrm{Pa}_{\mathrm{a}}+\mathrm{Ma}_{a}+$ MAT | 7 | 1358.3 | 1379.3 | -672.2 |
| 5 | $\log 10\left(\right.$ Soil P) $+\mathrm{Pa}+M_{a}$ | 6 | 1357.3 | 1375.3 | -672.6 |
| 6 | $\underline{\log 10(S o i l ~ P) ~+~ P a ~}$ | $\underline{5}$ | 1359.9 | 1374.9 | -674.9 |
| 7 | $\log 10($ Soil P) | 4 | 1363.4 | 1375.4 | -677.7 |

Abbreviations: $N_{a}=$ leaf nitrogen, $\mathrm{P}_{\mathrm{a}}=$ leaf phosphorus, $M_{a}=$ leaf mass per unit leaf area, Soil $\mathrm{P}=$ soil phosphorus, Soil $\mathrm{N}=$ 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 $V_{c \max }$ and $J_{\text {max }}$ at $25^{\circ} \mathrm{C}$ values ( $V_{\text {cmax } 25}$ and $J_{\text {max } 25}$, respectively) in upland and lowland plants calculated using different activation energies $\left(E_{a}\right)$ for each parameter (i.e. $\boldsymbol{V}_{\text {cmax }}$ and $\boldsymbol{J}_{\text {max }}$ ), and $\boldsymbol{K}_{\mathbf{c}}$ and $\boldsymbol{K}_{\mathbf{o}}$ constants when calculating $\boldsymbol{V}_{\text {cmax. }}$. Here, we compare values calculated using $E_{\mathrm{a}}$ values reported by Farquhar et al. (1980) and Bernacchi et al. (2002). For Farquhar et al. (1980), $E_{\mathrm{a}}$ values of $K_{\mathrm{c}}$ and $K_{\mathrm{o}}$ used were 59.4 and $36.0 \mathrm{~kJ} \mathrm{~mol}^{-1}$, respectively. For Bernacchi et al. (2002), the $E_{\mathrm{a}}$ values of $K_{\mathrm{c}}$ and $K_{\circ}$ were 80.99 and $23.72 \mathrm{~kJ} \mathrm{~mol}^{-1}$. For calculations made using Farquhar et al. (1980), we used $E_{\mathrm{a}}$ values for $V_{\text {cmax }}$ and $J_{\max }$ of 64.8 and $37.0 \mathrm{~kJ} \mathrm{~mol}^{-1}$, respectively; for Bernacchi et al. (2002), the $E_{\mathrm{a}}$ values for $V_{\text {cmax }}$ and $J_{\max }$ were 65.3 and $43.9 \mathrm{~kJ} \mathrm{~mol}^{-1}$, respectively. Values are overall mean $\pm$ SD of leaf traits for lowland and upland sites. Significantly different means are indicated by different letters ( $p<0.05$ ).

| Source of <br> constants |  | $V_{c m a x, a^{25}}$ <br> $(\mu \mathrm{~mol} \mathrm{~m}$ <br> $\left.\mathrm{s}^{-1}\right)$ | $J_{\text {max, }}{ }^{25}$ <br> $\left(\mu \mathrm{~mol} \mathrm{~m}^{-2} \mathrm{~s}^{-1}\right)$ |
| :--- | :--- | :---: | :---: |
| Farquhar et al. <br> (1980) | Lowland species | $35.9 \pm 14.6^{\mathrm{a}}$ | $66.7 \pm 18.6^{\mathrm{a}}$ |
|  | Upland species | $48.8 \pm 20.0^{\mathrm{b}}$ | $96.9 \pm 36.9^{\mathrm{b}}$ |
| Bernacchi et al. <br> $(2002)$ | Lowland species <br> Upland species | $39.7 \pm 15.6^{\mathrm{a}}$ | $64.7 \pm 18.6^{\mathrm{a}}$ |

Figure S1: Plots of maximum carboxylation velocity of Rubisco normalised to $25^{\circ} \mathrm{C}, \boldsymbol{V}_{\text {cmaxa }}{ }^{25}$ against (A) mean annual temperature (MAT) and ( $F$ ) soil $P$ concentration; maximum rate of electron transport normalised to $25^{\circ} \mathrm{C}$, $J_{\text {maxa }}{ }^{25}$ against (B) MAT and (G) soil P; ratio of $\boldsymbol{V}_{\text {cmaxa }}{ }^{25}$ over leaf $N, V_{\text {cmax }} \mathrm{N}^{25}$ against (C) MAT and (H) soil $P$; ratio of light-saturated net photosynthesis measured at $400 \mu \mathrm{~mol} \mathrm{~mol}^{-1}$ atmospheric $\left[\mathrm{CO}_{2}\right]$ over leaf $\mathrm{N}, \mathrm{A}_{400}: \mathrm{N}$ against (D) MAT and (I) soil P; and ratio of light-saturated net photosynthesis measured at $2000 \boldsymbol{\mu m o l} \mathrm{~mol}^{-1}$ atmospheric [ $\mathrm{CO}_{2}$ ] over leaf $\mathrm{N}, \boldsymbol{A}_{\mathbf{2 0 0 0}}: \mathrm{N}$ 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). $\mathrm{R}^{2}$ 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 $\mathbf{N}$ to pigment-protein complexes, $\boldsymbol{n}_{\mathbf{P}}$ \% of leaf $\mathbf{N}$ to Rubisco, $\boldsymbol{n}_{\mathbf{R}}$, and \% of leaf $\mathbf{N}$ to electron transport, $\boldsymbol{n}_{\mathrm{E}}$, in relation to (A) leaf mass per unit leaf area, $\boldsymbol{M}_{\mathrm{a}}$, (B) leaf $\mathbf{N}$-area, $\mathbf{N}_{\mathrm{a}}$, and (C) leaf $\mathbf{P}$-area, $\mathbf{P a}_{\mathrm{a}}$. 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 $\mathbf{N}$ allocated in Rubisco, $\boldsymbol{n}_{\mathbf{R}}$ 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) $\mathbf{1 5 0}$ lowland and $\mathbf{9 2}$ 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 $25^{\circ} \mathrm{C}$ ) (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 3 B is derived from maximum carboxylation velocity of Rubisco (normalised to $25^{\circ} \mathrm{C}$ ), $V_{\text {cmax, }}{ }^{25}$. 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 $\boldsymbol{n}_{\mathbf{E}}, \boldsymbol{n}_{\mathbf{P}}$ and $\boldsymbol{n}_{\mathbf{R}}$ for individual leaves. Individual leaf is arranged first according to sites with increasing soil $P$ (soil $P$ value in $\mathrm{mg} \mathrm{kg}^{-1}$ depicted underneath site code), then according to decreasing leaf $\mathrm{N}: \mathrm{P}$ within each site. Leaf $\mathrm{N}: \mathrm{P}$ for individual leaf is provided on top of the bar. $n_{\mathrm{E}}$ was estimated from maximum electron transport rate (normalised to $25^{\circ} \mathrm{C}$ ), $J_{\text {max }, ~}{ }^{25}$ 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 $25^{\circ} \mathrm{C}$ ), $V_{\text {cmax, }}{ }^{25}$. 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) $\boldsymbol{V}_{\text {cmax,a }}{ }^{\mathbf{2 5}}$; and, (B) $\boldsymbol{J}_{\text {max, }}{ }^{\mathbf{2 5}}$. Measured values of $V_{\text {cmax,a }}{ }^{25}$ and $J_{\text {max }}{ }^{25}$ are plotted against model predictions (using the 'best' predictive models detailed in Table 3). For $V_{\text {cmax,a }}{ }^{25}$ and $J_{\text {max, }}{ }^{25}$ model, the fixed component explanatory variables were: soil $P$ and leaf $P\left(P_{a}\right)$.

(B)


## Supporting information - References

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[^1]:    ** Correlation is significant at $p<0.01$

    * Correlation is significant at $p<0.05$

