

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

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4 Nur H.A. Bahar<sup>1</sup>, F. Yoko Ishida<sup>2</sup>, Lasantha K. Weerasinghe<sup>1,5</sup>, Rossella Guerrieri<sup>3,4</sup>,  
5 Odhran S. O'Sullivan<sup>1</sup>, Keith J. Bloomfield<sup>1</sup>, Gregory P. Asner<sup>8</sup>, Roberta E. Martin<sup>8</sup>,  
6 Jon Lloyd<sup>2,6</sup>, Yadvinder Malhi<sup>7</sup>, Oliver L. Phillips<sup>9</sup>, Patrick Meir<sup>1,3</sup>, Norma Salinas<sup>7,10</sup>,  
7 Eric G. Cosio<sup>10</sup>, Tomas Domingues<sup>11</sup>, Carlos A. Quesada<sup>12</sup>, Felipe Sinca<sup>8</sup>, Alberto  
8 Escudero Vega<sup>10</sup>, Paola P. Zuloaga Ccorimanya<sup>13</sup>, Jhon del Aguila-Pasquel<sup>14,15</sup>,  
9 Katherine Quispe Huaypar<sup>10</sup>, Israel Cuba Torres<sup>10</sup>, Rosalbina Butrón Loayza<sup>16</sup>,  
10 Yulina Pelaez Tapia<sup>10</sup>, Judit Huaman Ovalle<sup>10</sup>, Benedict M. Long<sup>1, 17</sup>, John R.  
11 Evans<sup>1,17</sup> and Owen K. Atkin<sup>1,18,\*</sup>

12  
13 <sup>1</sup>Div Plant Sciences, Research School of Biology, The Australian National University,  
14 Canberra, ACT, 2601, Australia; <sup>2</sup>College of Marine and Environmental Sciences and  
15 Centre for Tropical Environmental and Sustainability Science, James Cook University,  
16 Cairns, Queensland, Australia; <sup>3</sup>School of Geosciences, University of Edinburgh,  
17 Edinburgh EH9 3JN, UK; <sup>4</sup>Earth Systems Research Center, University of New Hampshire,  
18 Morse Hall, 8 College Rd, Durham, NH 03824, USA; <sup>5</sup>Faculty of Agriculture, University of  
19 Peradeniya, Peradeniya 20400, Sri Lanka; <sup>6</sup>Dept Life Sciences, Imperial College London,  
20 Silwood Park Campus, SL5 7PY, UK; <sup>7</sup>Environmental Change Institute, School of  
21 Geography and the Environment, University of Oxford, South Parks Road, Oxford OX1  
22 3QY, UK; <sup>8</sup>Dept of Global Ecology, Carnegie Institution for Science, Stanford, CA 94305;  
23 <sup>9</sup>School of Geography, University of Leeds, Woodhouse Lane, Leeds LS9 2JT, UK;  
24 <sup>10</sup>Pontificia Universidad Católica del Perú, Seccion Quimica, Av Universitaria 1801, San  
25 Miguel, Lima, Perú; <sup>11</sup>Universidade de São Paulo, Faculdade de Filosofia Ciências e Letras  
26 de Ribeirão Preto, Brazil; <sup>12</sup>Instituto Nacional de Pesquisas da Amazonia (INPA), Manaus,  
27 Brazil; <sup>13</sup>Seccion Biología, Universidad Nacional de San Antonio Abad del Cusco, Av de la  
28 Cultura, No. 733, Cusco, Perú; <sup>14</sup>Instituto de Investigaciones de la Amazonia Peruana  
29 (IIAP), Av. José A. Quiñones km. 2.5, Apartado Postal 784, Iquitos, Perú; <sup>15</sup>School of Forest  
30 Resources and Environmental Science, Michigan Technological University, 1400  
31 Townsend Drive, Houghton, Michigan, 49931, USA; <sup>16</sup>Museo de Historia Natural,  
32 Universidad Nacional de San Antonio Abad del Cusco, Av de la Cultura, No. 733, Cusco,  
33 Perú; <sup>17</sup>ARC Centre of Excellence in Translational Photosynthesis, Research School of  
34 Biology, Building 134, The Australian National University, Canberra, ACT 2601, Australia;  
35 <sup>18</sup>ARC Centre of Excellence in Plant Energy Biology, Research School of Biology, Building  
36 134, The Australian National University, Canberra, ACT 2601, Australia.

37  
38 \* Author for correspondence: Owen Atkin, tel +61 (0)2 6125 5046, email:  
39 [Owen.Atkin@anu.edu.au](mailto:Owen.Atkin@anu.edu.au)

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55 **Summary**

56

- 57 • We examined whether variations in photosynthetic capacity are linked to  
58 variations in the environment and/or associated leaf traits for tropical  
59 moist forest (TMFs) in the Andes/western-Amazon regions of Peru.
- 60 • We compared photosynthetic capacity ( $V_{\text{cmax}}$  and  $J_{\text{max}}$ ), leaf mass, nitrogen  
61 and phosphorus per unit leaf area ( $M_a$ ,  $N_a$  and  $P_a$  respectively), and  
62 chlorophyll from 210 species at 18 field sites along a 3,300-m elevation  
63 gradient. Western-blotting was used to quantify abundance of the CO<sub>2</sub>-  
64 fixing enzyme, Rubisco.
- 65 • Area- and N-based rates of photosynthetic capacity at 25°C were higher in  
66 upland- than lowland-TMFs, underpinned by greater investment of N in  
67 photosynthesis in high-elevation trees. Soil [P] and leaf  $P_a$  were key  
68 explanatory factors for models of area-based  $V_{\text{cmax}}$  and  $J_{\text{max}}$  but did not  
69 account for variations in photosynthetic N-use efficiency. At any given  $N_a$   
70 and  $P_a$ , the fraction of N allocated to photosynthesis was higher in upland  
71 than lowland species. For a small subset of lowland TMF trees examined, a  
72 substantial fraction of Rubisco was inactive.
- 73 • These results highlight the importance of soil- and leaf-phosphorus in  
74 defining photosynthetic capacity of TMFs, with variations in N allocation  
75 and Rubisco activation state further influencing photosynthetic rates and  
76 N-use efficiency of these critically important forests.

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80 ribulose biphosphate regeneration, temperature, tropical forests

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## 84 Introduction

85

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

92 Early studies in lowland TMFs implicated low foliar P concentrations as a  
93 major influence on light-saturated net photosynthesis ( $A_{\text{sat}}$ ) (Reich & Walters,  
94 1994; Raaimakers *et al.*, 1995), with soil P being a major factor limiting Amazon  
95 productivity (Quesada *et al.*, 2012). Foliar P is crucial to the fine-tuning  $A_{\text{sat}}$   
96 (Fredeen *et al.*, 1989; Jacob & Lawlor, 1993) via regulation of key intermediates in  
97 carbon metabolism (e.g. ATP, NADPH and sugar phosphates including ribulose  
98 1,5-bisphosphate - RuBP). While the direct effect of P-limitation is primarily on  
99 RuBP regeneration, reductions in Rubisco activity also occur (Brooks, 1986; Jacobs  
100 & Lawlor, 1992; Loustau *et al.*, 1999). Although Meir *et al.* (2002; 2007) and Reich  
101 *et al.* (2009) showed that  $A_{\text{sat}}$  at a given leaf N concentration ( $[N]$ ) was less in  
102 lowland tropical trees than their temperate counterparts, the extent to which P  
103 limitations *per se* alter  $A_{\text{sat}} \leftrightarrow [N]$  relations within TMFs is uncertain (Bloomfield *et al.*,  
104 2014a; Domingues *et al.*, 2015). A further unknown is the extent to which large  
105 elevation gradients affect  $A_{\text{sat}} \leftrightarrow [N]$  relations in the tropics. Upland TMFs are more  
106 likely to be limited by N than their lowland counterparts (Tanner *et al.*, 1998).  
107 Upland TMFs also experience lower temperatures and atmospheric  $\text{CO}_2$  partial  
108 pressures, more frequent cloud cover and experience greater leaf wetness  
109 (Grubb, 1977; Vitousek, 1984; Girardin *et al.*, 2010; Bruijnzeel *et al.*, 2011). Such  
110 factors can limit  $A_{\text{sat}}$  (Terashima *et al.*, 1995; Bruijnzeel & Veneklaas, 1998; Letts &  
111 Mulligan, 2005), leading to declines in productivity (Girardin *et al.*, 2010).  $A_{\text{sat}}$  in  
112 upland TMFs have been documented (e.g. Quilici & Medina, 1998; Cordell *et al.*,  
113 1999; Hikosaka *et al.*, 2002; Letts & Mulligan, 2005; Rada *et al.*, 2009), showing  $A_{\text{sat}}$

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

116 Rates of  $A_{\text{sat}}$  are subject to variations in stomatal conductance ( $g_s$ ) and the  
117 partial pressure of internal leaf  $\text{CO}_2$  ( $C_i$ ) (Santiago & Mulkey, 2003). Since  
118 variations in  $C_i$  alter both  $\text{CO}_2$  uptake and photorespiratory  $\text{CO}_2$  release, it could  
119 potentially confound our understanding of how environmental gradients alter N  
120 investment in  $A$ . By contrast, variations in  $g_s$  have less impact on the fundamental,  
121 biochemical parameter of photosynthetic capacity – that being the maximum rate  
122 of carboxylation by Rubisco (i.e.  $V_{\text{cmax}}$ ). Positive correlations between  $V_{\text{cmax}}$  and  
123 leaf [N] have been reported for some tropical species (Carswell *et al.*, 2000; Meir  
124 *et al.*, 2002; Domingues *et al.*, 2005; Kumagai *et al.*, 2006; Meir *et al.*, 2007;  
125 Vårhammar *et al.*, 2015) – whereas in others no strong  $V_{\text{cmax}} \leftrightarrow [\text{N}]$  relationship was  
126 observed (Coste *et al.*, 2005; van de Weg *et al.*, 2012; Dusenge *et al.*, 2015).  
127 Although reports on  $V_{\text{cmax}}$  are less widespread in the tropics than  $A_{\text{sat}}$ , the  
128 available data suggest that  $V_{\text{cmax}}$  values, as well as  $V_{\text{cmax}}$  per unit N (herein termed  
129 ' $V_{\text{cmax,N}}$ '), are lower in lowland TMFs than their non-tropical counterparts (Carswell  
130 *et al.*, 2000; Meir *et al.*, 2002; Domingues *et al.*, 2007; Meir *et al.*, 2007; Domingues  
131 *et al.*, 2010; Walker *et al.*, 2014; Vårhammar *et al.*, 2015). Kattge *et al.* (2009) re-  
132 analysed data to show that  $V_{\text{cmax}}$  per unit N in TMFs growing on young, relatively  
133 high nutrient status soils was higher compared to their older, Ferralsol and Acrisol  
134 soil counterparts that are characterised by very low soil P availability (Quesada *et al.*  
135 *et al.*, 2010). These observations are consistent with laboratory studies showing  
136 reduced  $V_{\text{cmax}}$  (Lauer *et al.*, 1989; Loustau *et al.*, 1999) and reduced N allocation  
137 to Rubisco (Warren & Adams, 2002) under P-limited conditions. Increased  
138 allocation of N to non-photosynthetic components may also play a role  
139 (Domingues *et al.*, 2010; Lloyd *et al.*, 2013), as might inactivation of Rubisco (Stitt  
140 & Schulze, 1994). Yet, doubt remains regarding the general  $V_{\text{cmax}} \leftrightarrow [\text{N}]$   
141 relationship in TMFs due to the scarcity of data, both in lowland and upland TMFs.  
142 Comprehensive surveys of  $V_{\text{cmax}}$  (and  $J_{\text{max}}$  - maximum rate of electron transport)  
143 across lowland and upland TMFs are required to establish whether there are

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

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

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

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

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

- 186 (1) Do tropical TMF species growing on low-P soils exhibit lower photosynthetic  
187 capacity and photosynthetic N use efficiency than TMF trees growing on  
188 sites with higher P availability?
- 189 (2) Are there marked differences in  $V_{\text{cmax}}$ ,  $J_{\text{max}}$  and  $V_{\text{cmax,N}}$  between lowland  
190 Amazonian and upland Andean TMFs?
- 191 (3) Are differences in  $V_{\text{cmax}}$ ,  $J_{\text{max}}$  and  $V_{\text{cmax,N}}$  linked to concomitant variations in  
192 other leaf traits and/or environmental variables?

193

## 194 **Materials and Methods**

195

### 196 *Study sites*

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

204 substrates, as well as changes in growth temperature, cloud cover and light  
205 environment. In addition to marked inter-site differences in total soil [N] (0.6 -  
206 15.5 g N kg<sup>-1</sup>), substantial variation in total soil [P] occurs across both the lowland  
207 (38 - 727 mg P kg<sup>-1</sup>) and upland sites (496 - 1631 mg P kg<sup>-1</sup>) (Table 1). Soils at  
208 three of the lowland sites in northern Peru (JEN-12, ALP-30 and ALP-40) are  
209 notable for being low nutrient status arenosols/podzols ('white sands'). Among  
210 the lowland and upland sites, mean annual precipitation (MAP) values range from  
211 1560 to 5300 mm a<sup>-1</sup>. Mean annual temperature ranged from 8.0 to 18.8 °C  
212 across the upland sites, and 24.4 to 26.6 °C among the lowland sites.

213 At each site, tree climbers collected from dominant tree species upper  
214 canopy branches supporting leaves considered to typically be exposed to full  
215 sunlight for much of the day, but with little replication of individual species  
216 possible at any site. Each tree was initially identified to the genus-level and,  
217 whenever possible, to the species-level. A total of 353 individual trees drawn from  
218 210 species were sampled across the 18 sites. See SM1 in Supporting Information  
219 for further details.

220

### 221 *Leaf gas exchange measurements*

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

227 CO<sub>2</sub> response curves of light-saturated photosynthesis ( $A \leftrightarrow C_i$  curves) (at  
228 1800  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ ) were performed within 30–60 minutes after branch  
229 detachment. CO<sub>2</sub> concentrations inside the reference chamber ranged in a  
230 stepped sequence from 35 to 2000  $\mu\text{mol mol}^{-1}$  (see SM2 in Supporting  
231 Information for details). Block temperatures within the chamber were set to the  
232 prevailing day-time air temperature at each site (from 25–28 °C). The resultant  
233  $A \leftrightarrow C_i$  curves (examples shown in Fig. 1) were fitted following the model described  
234 by Farquhar *et al.* (1980) in order to calculate  $V_{\text{cmax}}$  and  $J_{\text{max}}$  on a leaf area basis –



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

238 Rates of  $CO_2$  exchange were corrected for diffusion through the gasket of  
239 the LI-6400 leaf chamber (Bruhn *et al.*, 2002) prior to calculation of  $V_{cmax}$  and  $J_{max}$ .  
240 Assuming infinite internal diffusion conductance ( $g_m$ ), Michaelis constants of  
241 Rubisco for  $CO_2$  ( $K_c$ ) and  $O_2$  ( $K_o$ ) at a reference temperature 25°C were assumed  
242 to be 40.4 Pa and 24.8 kPa, respectively (von Caemmerer *et al.*, 1994); these values  
243 were adjusted to actual leaf temperatures assuming activation energies of 59.4  
244 and 36 kJ mol<sup>-1</sup> for  $K_c$  and  $K_o$ , respectively (Farquhar *et al.*, 1980). Fitted parameters  
245 were then scaled to a reference temperature of 25°C using activation energies of  
246 64.8 and 37.0 kJ mol<sup>-1</sup> for  $V_{cmax}$  and  $J_{max}$ , respectively (Farquhar *et al.*, 1980). Finally,  
247 rates of  $A$  obtained at ambient  $CO_2$  concentrations of 400 and 2000  $\mu\text{mol mol}^{-1}$   
248 ( $A_{400}$  and  $A_{2000}$ , respectively) were extracted from the  $A \leftrightarrow C_i$  curves and reported  
249 separately.

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

260

### 261 *Leaf structure and chemistry determination*

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

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

270

### 271 *Chlorophyll and Rubisco measurements*

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

275 Chlorophyll content of each set of leaf discs was determined using a dual-  
276 beam scanning UV-VIS spectrometer (Lambda 25, Perkin-Elmer) after extraction  
277 of chlorophyll pigments from two frozen leaf discs (0.77 cm<sup>2</sup> each) with 100%  
278 acetone and MgCO<sub>3</sub>, as outlined in Asner *et al.* (2014b). Chlorophyll a:b ratios  
279 varied between 2.45 and 2.75, which is consistent with results of past studies on  
280 tropical trees in the Peruvian Amazon (Asner & Martin, 2011).

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

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

297 calibration series. Proteins were run on 4-12% NuPAGE Bis-Tris gels (Invitrogen -  
298 Life Technologies, Carlsbad, CA, USA) according to the manufacturer's  
299 instructions and transferred to Immobilon-P PVDF membranes (Merck Millipore,  
300 Kilsyth, Vic., Australia) using an XCell II Blot module (Invitrogen). Membranes were  
301 blocked with 5% skim milk powder in Tris-buffered saline containing 0.5% Tween-  
302 20 (TBS-T) and an antibody raised in rabbits against tobacco Rubisco (used at  
303 1:5,000) prepared by Spencer Whitney (Research School of Biology, Australian  
304 National University, Canberra). Secondary antibody (goat-anti-rabbit-alkaline  
305 phosphatase conjugate, Agrisera) was diluted 1:5,000. Blots were visualized using  
306 Attophos AP fluorescent substrate system (Promega, Madison, WI, USA) and  
307 imaged using a Versa-Doc (Bio-Rad, Hercules, CA, USA) imaging system. Blots  
308 were analysed using Quantity One software (Bio-Rad) and relative band densities  
309 of each protein determined from duplicate samples, and data averaged. Rubisco  
310 concentration was calculated from the large subunit (molecular mass of 55 kD  
311 and 16% N by weight).

312

### 313 *Estimation of N allocation in photosynthetic metabolism*

314 N allocation in three major components (pigment-protein complexes, electron  
315 transport and Rubisco) for all leaves was estimated from chlorophyll  
316 concentration,  $V_{\text{cmax}}$  and  $J_{\text{max}}$  respectively. N allocation to pigment-protein  
317 complexes ( $n_{\text{P}}$ ) was calculated by assuming 44 mol N per mol of chlorophyll  
318 (Evans, 1989). N allocation to Rubisco ( $n_{\text{R}}$ ) was estimated from values of  $V_{\text{cmax}}$   
319 according to Harrison *et al.* (2009), with slight modification [ $2.33 \text{ mol CO}_2 (\text{mol}$   
320  $\text{Rubisco sites})^{-1} \text{ s}^{-1}$  for the catalytic turnover number of Rubisco at 25 °C (Harrison  
321 *et al.*, 2009)]. We assumed all Rubisco was fully activated and mesophyll  
322 conductance was infinite. The allocation of N to electron transport components  
323 ( $n_{\text{E}}$ ) was calculated from  $J_{\text{max}}$  assuming  $160 \text{ mol electrons } (\text{mol cytochrome } f)^{-1} \text{ s}^{-1}$   
324  $^1$  and  $8.85 \text{ mol N } (\text{mmol cytochrome } f)^{-1}$  (Evans & Seemann, 1989). The proportion  
325 of total leaf N allocated to each photosynthetic component was calculated by  
326 dividing the N investment in each component by the N content per unit leaf area.

327

328 *Data analysis*

329 Log<sub>10</sub> transformations were carried out on leaf traits when necessary to ensure  
330 normality and minimize heterogeneity of residuals. Student *T*-tests (two-tailed)  
331 were used to compare overall means of lowland and upland species. Standardized  
332 major axis (SMA) estimation was used to describe the best-fit relationship  
333 between pairs of variables and to assess whether relationships differed between  
334 lowland vs upland elevation classes, using SMATR Version 2.0 software (Falster *et al.*,  
335 2006; Warton *et al.*, 2006). The decision to compare upland and lowland trait  
336 relationships reflects the strong elevation contrast in environments, phylogeny,  
337 floristic composition and forest structure (Gentry, 1988; van de Weg *et al.*, 2009;  
338 Asner *et al.*, 2014b). Significance of SMA regression was tested at  $\alpha = 0.05$ .

339 In addition to the above bivariate analyses, we also used a mixed-effects  
340 linear model combining fixed and random components (Pinheiro & Bates, 2000)  
341 to account for variability in area- and N-based rates of  $V_{\text{cmax}}$ , and area-based rates  
342 of  $J_{\text{max}}$ , where the linear mixed-effects model combined fixed and random  
343 components. This approach enabled the structured nature of the data set to be  
344 recognized, and for interactions between multiple terms to be considered. The  
345 fixed effect included continuous variables only: leaf traits ( $M_a$ , area-based leaf N  
346 and P), and environment variables (soil P and N concentration, mean annual  
347 temperature (MAT) and effective cation exchange capacity of soil (ECEC)). Model  
348 specification and validation was based on the protocols outlined in Zuur *et al.*  
349 (2009) and fitted using the *nlme* package (R package ver. 3.1–105, R Foundation  
350 for Statistical Computing, Vienna, Austria, R Development Core Team 2011).  
351 Details on the model selection process are provided in Table S6. Briefly,  
352 phylogeny (family/genus/species) were treated as random effects, placing focus  
353 on the variation contained within these terms, rather than mean values for each  
354 level. For the mixed-effects linear model, site variation was captured by soil and  
355 environmental factors considered in the fixed component; because of this, no site  
356 term was included in the random component. Model comparisons and the

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

360

## 361 **Results**

362

### 363 *Variations in leaf chemistry and structure*

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

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

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

387 correlation with  $M_a$  ( $p < 0.01$ ,  $r^2 = 0.04$ ; Table S2). Similarly, a weak positive  $P_a \leftrightarrow M_a$   
388 relationship ( $p = 0.003$ ,  $r^2 = 0.04$ ; Table S3) was found among upland species (Fig  
389 2B). Although no significant  $P_a \leftrightarrow M_a$  relationship was found among lowland  
390 species (with leaf  $P_a$  varying 20-fold; Table S1), mean values of  $P_a$  at a given  $M_a$   
391 were lower than their upland counterparts.

392

### 393 *Variations in photosynthetic metabolism*

394 Light-saturated rates of photosynthesis per unit leaf area, measured at the  
395 prevailing day-time air temperature ( $T$ ) at each site and at an atmospheric  $\text{CO}_2$   
396 concentration of  $400 \mu\text{mol mol}^{-1}$  ( $A_{400,a}$ ), differed among co-occurring species  
397 (Table S1). However, there was no significant difference between mean values of  
398  $A_{400,a}$  from lowland and upland classes (Table 2). This uniformity of  $A_{400,a}$  occurred  
399 despite significantly lower measuring  $T_s$  at the high elevation sites [overall means:  
400 lowland  $29.4 \pm 0.9^\circ\text{C}$ ; upland  $25.7 \pm 2.1^\circ\text{C}$ ,  $p < 0.05$ ] and lower intercellular  $\text{CO}_2$   
401 partial pressure ( $C_i$ ) (overall means: lowland  $28.4 \pm 3.7 \text{ Pa}$ ; upland  $18.8 \pm 3.0 \text{ Pa}$ ,  
402  $p < 0.05$ ) (Table S4). Assessed on a per unit leaf N basis ( $A_{400,N}$ ), average rates were  
403 lower at the upland sites compared to their lowland counterparts (Tables 2 and  
404 S4), reflecting higher leaf  $N_a$  for trees at high elevation (Table 1). Across sites,  
405 mean  $A_{400,N}$  decreased with decreasing mean annual temperature (MAT) (Figure  
406 S1D). Area-based rates of photosynthesis at elevated  $\text{CO}_2$  ( $A_{2000,a}$ ) were higher in  
407 upland ( $17.1\text{-}26.5 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ; Table S4) than lowland ( $16.1\text{-}22.6 \mu\text{mol m}^{-2} \text{ s}^{-1}$ )  
408 species ( $p < 0.05$ ). The higher values of  $A_{2000,a}$  at the upland sites were achieved  
409 despite the colder temperatures. On a per unit leaf N basis ( $A_{2000,N}$ ), average rates  
410 were similar for both elevation classifications (Table S4; Fig. S1E).

411 To explore differences in rates of the underlying components of net  
412 photosynthesis, we compared maximal area-based rates of  $\text{CO}_2$  fixation by  
413 Rubisco ( $V_{\text{cmax},a}$ ) and photosynthetic electron transport ( $J_{\text{max},a}$ ), using values  
414 normalized to a measuring temperature of  $25^\circ\text{C}$  (i.e.  $V_{\text{cmax},a}^{25}$  and  $J_{\text{max},a}^{25}$ ). Site  
415 mean values of  $V_{\text{cmax},a}^{25}$  and  $J_{\text{max},a}^{25}$  were significantly higher in the upland class  
416 ( $V_{\text{cmax},a}^{25}$  and  $J_{\text{max},a}^{25}$  were 36 and 45% higher, respectively, in the upland class;

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

427 Variations in  $J_{\text{max},\text{a}}^{25}$  were strongly correlated with  $V_{\text{cmax},\text{a}}^{25}$ , both for lowland  
428 ( $r^2 = 0.59$ ) and upland classifications ( $r^2 = 0.75$ ) (Fig. 4). Overall, the  
429  $J_{\text{max},\text{a}}^{25} \leftrightarrow V_{\text{cmax},\text{a}}^{25}$  relationship was similar in the two elevation groups, with mean  
430  $J_{\text{max},\text{a}}^{25} : V_{\text{cmax},\text{a}}^{25}$  ratios being statistically equivalent in lowland and upland classes  
431 (Table 2). Importantly, marked differences in  $J_{\text{max},\text{a}}^{25} : V_{\text{cmax},\text{a}}^{25}$  ratios were observed  
432 among individuals (Figs 3 and 4), underpinned by fundamental differences in the  
433  $\text{CO}_2$  response of net photosynthesis (e.g. Fig. 1B). In most leaves,  $J_{\text{max},\text{a}}^{25}$  and  
434  $V_{\text{cmax},\text{a}}^{25}$  co-varied, resulting in relatively constant  $J_{\text{max},\text{a}}^{25} : V_{\text{cmax},\text{a}}^{25}$  ratios, as  
435 illustrated by data from individual plants of *Cecropia angustifolia* and  
436 *Glycydendron amazonicum* where the  $J_{\text{max},\text{a}}^{25} : V_{\text{cmax},\text{a}}^{25}$  ratio was 1.8 (Fig. 1A and  
437 Fig. 4). However, some leaves exhibited high  $V_{\text{cmax},\text{a}}^{25}$  but low  $J_{\text{max},\text{a}}^{25}$  (Fig. 1B;  
438 individual of *Schefflera* sp., where  $J_{\text{max},\text{a}}^{25} : V_{\text{cmax},\text{a}}^{25} = 1.1$ ) while other leaves with a  
439 similar  $V_{\text{cmax},\text{a}}^{25}$  had markedly higher  $J_{\text{max},\text{a}}^{25}$  (e.g. the *Citronella incarum* individual  
440 in Fig. 1B) leading to a higher  $J_{\text{max},\text{a}}^{25} : V_{\text{cmax},\text{a}}^{25}$  value (2.4). Such variations in  $J_{\text{max},\text{a}}^{25}$   
441 and  $V_{\text{cmax},\text{a}}^{25}$  likely reflect intra- and/or inter-specific variations in relative  
442 allocation of N allocation to Rubisco versus electron transport/bioenergetics.

443

#### 444 *Bivariate relationships*

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

447 of these relationships was greater for  $J_{\max,a}^{25}$  than  $V_{\max,a}^{25}$ . Relationships with  
448 MAP were either weak ( $J_{\max,a}^{25}$ ) and not significant ( $V_{\max,a}^{25}$ ) (Table S2). Across all  
449 sites, variations in  $V_{\max,a}^{25}$  and  $J_{\max,a}^{25}$  were also correlated with leaf chemical  
450 composition traits (Table S2), with bivariate relationships being stronger against  
451  $P_a$  ( $p < 0.01$ ,  $r^2 = 0.11$  for  $V_{\max,a}^{25}$ ,  $r^2 = 0.13$  for  $J_{\max,a}^{25}$ ) than  $N_a$  ( $p < 0.01$ ,  $r^2 = 0.05$  for  
452 both  $V_{\max,a}^{25}$  and  $J_{\max,a}^{25}$ ). Leaf N:P ratios exhibited weak, negative correlations  
453 with  $V_{\max,a}^{25}$  and  $J_{\max,a}^{25}$  ( $p < 0.01$ ,  $r^2 = 0.08$  for  $V_{\max,a}^{25}$ ,  $r^2 = 0.06$  for  $J_{\max,a}^{25}$ ; Table  
454 S2). No significant relationship was found between  $V_{\max,a}^{25}$  and  $M_a$ , whereas the  
455  $J_{\max,a}^{25} \leftrightarrow M_a$  relationship was significant ( $p < 0.05$ ,  $r^2 = 0.04$ ; Table S2).

456 When assessed among upland sites, no significant relationships were  
457 found between  $V_{\max,a}^{25}$ ,  $M_a$ ,  $N_a$ ,  $P_a$  or N:P ratio (Fig. 5A-D). For lowland sites,  
458  $V_{\max,a}^{25}$  was positively related with  $P_a$  ( $p = 0.013$ ,  $r^2 = 0.04$ ; Table S3) and  $N_a$   
459 ( $p = 0.050$ ,  $r^2 = 0.02$ ; Table S3), but not leaf N:P ratio or  $M_a$  (Fig 5A-D). The absence  
460 of a N:P effect for upland or lowland classes was consistent with SMA analyses  
461 comparing the slopes of  $V_{\max,a}^{25} \leftrightarrow N_a$ ,  $V_{\max,a}^{25} \leftrightarrow P_a$  and  $V_{\max,a}^{25} \leftrightarrow M_a$  for the  
462 lowland class, split according to leaf N:P ratios below and above 20 - this ratio  
463 generally being thought to be roughly indicative of the N:P above which  
464 physiological processes are more likely to be limited by P as opposed to N (and  
465 vice versa) (Güsewell, 2004). No significant difference in slopes of the relationships  
466 were found ( $p > 0.05$ , data not shown). Similar patterns were observed for  $J_{\max,a}^{25}$   
467 (Fig. 5E-H), which was positively related with  $N_a$  ( $p = 0.012$ ,  $r^2 = 0.05$ ; Table S3) and  
468  $P_a$  ( $p = 0.002$ ,  $r^2 = 0.08$ ; Table S3) for the lowland class only.

469 Investigating whether variations in photosynthetic N use efficiency were  
470 related to  $M_a$ , both across all sites (Table S2) and within each elevation class (Fig.  
471 6A), there was no significant  $V_{\max,N}^{25} \leftrightarrow M_a$  relationship across all 18 sites (Table  
472 S2) or within the upland elevation class (Table S3). Nevertheless, for the lowland  
473 class, a weak negative  $V_{\max,N}^{25} \leftrightarrow M_a$  relationship was observed ( $p = 0.01$ ; Table S3).  
474 On average,  $V_{\max,N}^{25}$  at a given  $M_a$  was higher in upland species than their lowland  
475 counterparts. With respect to foliar phosphorus, there was no significant  
476 relationship between  $V_{\max,N}^{25}$  and leaf  $P_a$  or with leaf N:P when considering the



477 elevation classes separately. This conclusion was held for  $V_{\text{cmax,N}}^{25} \leftrightarrow P_a$  when  
478 combining upland and lowland data (Table S2). For  $V_{\text{cmax,N}}^{25} \leftrightarrow N:P$ , combining  
479 upland and lowland data resulted in a weak significant relationship ( $p < 0.05$ ,  $r^2 =$   
480  $0.02$ ; Table S2); similarly, relationships between  $V_{\text{cmax,N}}^{25}$  and soil P, soil N and  
481 elevation were relatively weak (Table S2). Collectively, these results show that the  
482 proportion of the variance in  $V_{\text{cmax,N}}^{25}$  accounted for by the above soil and leaf  
483 level parameters was negligible.

484

#### 485 *Variation in N-allocation patterns*

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

499 There was considerable variability in  $n_A$  among lowland and upland species  
500 (0.1 to 0.6), with significant negative correlations being found with  $M_a$ ,  $N_a$  and  $P_a$   
501 for the lowland group (Fig. 8, Table S5). Similar significant correlations existed for  
502 the upland class but with the important caveat that upland species consistently  
503 exhibited higher  $n_A$  at a given  $N_a$  and  $P_a$  (Figs. 8 and S2; Table S5). Thus, while  
504 mean values of  $n_A$  were similar in upland and lowland species, the fraction of leaf  
505 N allocated to photosynthesis was greater in upland plants when comparisons  
506 were made at common leaf  $N_a$  and  $P_a$  values.

507

### 508 *Validation of Rubisco estimates by in vitro assays*

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

526

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

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

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

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

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

562

## 563 **Discussion**

564

### 565 *Regional and inter-biome context*

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

567 of  $V_{\text{cmax},a}^{25} \leftrightarrow N_a$  relationships, with lower rates of  $V_{\text{cmax}}$  per unit N in nutrient-poor,  
568 lowland tropical forests compared to lowland forests on more fertile soils, upland  
569 tropical forests and temperate broadleaf forests (Carswell *et al.*, 2000; Domingues  
570 *et al.*, 2007; Meir *et al.*, 2007; Kattge *et al.*, 2009; Domingues *et al.*, 2010; Mercado  
571 *et al.*, 2011; van de Weg *et al.*, 2012). Moreover, Reich *et al.* (2009) concluded that  
572 the slope of mass-based  $A \leftrightarrow N$  relationships is lower in the tropics than in colder  
573 arctic and temperate biomes. Our study supports such studies, with  $V_{\text{cmax},N}^{25}$   
574 values for our upland and lowland TMFs (22.5 and 18.9  $\mu\text{mol CO}_2 \text{ g N}^{-1} \text{ s}^{-1}$ ,  
575 respectively) being markedly lower than reported for temperate broadleaved  
576 trees [34  $\mu\text{mol CO}_2 \text{ g N}^{-1} \text{ s}^{-1}$  (Kattge *et al.*, 2009)].

577 How do our results compare with other analyses of photosynthetic  
578 capacity in tropical ecosystems? The range of  $V_{\text{cmax},a}^{25}$  (6–96  $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ; Table  
579 S1) and  $J_{\text{max},a}^{25}$  (21–176  $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ; Table S1) values from our study were wider  
580 than those reported for drier tropical sites in West Africa (Domingues *et al.*, 2010),  
581 perhaps reflecting environmental differences, or differences in the number of  
582 species sampled (210 here versus 39 in the West African study). For our lowland  
583 TMFs (which included three low nutrient status white sand sites in Northern Peru),  
584 the overall mean  $V_{\text{cmax},a}^{25}$  ( $36 \pm 15 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ) was lower than previously  
585 reported tropical values: Carswell *et al.* (2000): 43  $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ; Domingues *et al.*  
586 (2007): 53  $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ; Meir *et al.* (2007): 49–68  $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ; Kattge *et al.* (2009):  
587 41  $\mu\text{mol m}^{-2} \text{ s}^{-1}$  (non-oxisol); Bloomfield *et al.* (2014a): 63  $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ;  
588 Domingues *et al.* (2015): 39–46  $\mu\text{mol m}^{-2} \text{ s}^{-1}$ . By contrast, our mean  $V_{\text{cmax},a}^{25}$  values  
589 were higher than the values for lowland TMFs only growing on nutrient-poor,  
590 oxisol [29  $\mu\text{mol m}^{-2} \text{ s}^{-1}$  (Kattge *et al.*, 2009)]. Since  $J_{\text{max},a}^{25}$  was tightly correlated  
591 with  $V_{\text{cmax},a}^{25}$  (Fig. 4), our estimates of  $J_{\text{max},a}^{25}$  for lowland TMFs were also lower  
592 than those reported in above-mentioned studies. Rates of  $V_{\text{cmax},a}^{25}$  at our upland  
593 sites ( $49 \pm 20 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ) were similar to those reported by van de Weg *et al.*  
594 (2012): 56  $\mu\text{mol m}^{-2} \text{ s}^{-1}$  for the same Andean region, and fell mid-range of values  
595 reported in Dusenge *et al.* (2015) and Vårhammar *et al.* (2015) for high elevation  
596 tropical trees of Rwanda.

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

602

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

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

615 The hypothesis that photosynthetic capacity would be positively correlated  
616 with soil [P] and leaf  $P_a$  was supported by our results – a finding consistent with  
617 earlier studies on tropical species in South America, West Africa and Australia  
618 (Domingues *et al.*, 2007; Meir *et al.*, 2007; Kattge *et al.*, 2009; Domingues *et al.*,  
619 2010; Bloomfield *et al.*, 2014b). Among lowland sites alone, and the combination  
620 of lowland and upland sites together, significant positive relationships were  
621 observed between photosynthetic capacity (expressed either as  $V_{\text{cmax},a}^{25}$  or  $J_{\text{max},a}^{25}$ )  
622 and foliar  $P_a$ , and against soil [P] (Tables S2, S3). Across all 18 TMF sites,  $V_{\text{cmax},a}^{25}$   
623 and  $J_{\text{max},a}^{25}$  also exhibited significant negative relationships with leaf N:P (Table  
624 S2). Moreover, foliar  $P_a$  and soil [P] emerged as significant explanatory variables  
625 in linear mixed-effect models of variations in photosynthetic capacity (Table 3),  
626 accounting for ~40% of the observed variations in  $V_{\text{cmax},a}^{25}$  and  $J_{\text{max},a}^{25}$ . The

627 absence of mean annual temperature (MAT) in the preferred models suggest that,  
628 while growth temperature can affect photosynthetic capacity (Hikosaka *et al.*,  
629 2006; Sage & Kubien, 2007) and patterns of N investment, knowledge of growth  
630 temperature along the western Amazon-Andes elevation gradient is not required  
631 when data on leaf and soil P is available.

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

642

#### 643 *Activation state of Rubisco*

644 *In vitro* quantification in several lowland TMF species revealed that Rubisco  
645 content inferred from CO<sub>2</sub> response curves may have substantially  
646 underestimated absolute levels of this key protein (Fig. 9). When estimating  
647 Rubisco abundance from  $A \leftrightarrow C_i$  curves, Rubisco is assumed to be fully activated –  
648 however, there is growing evidence that Rubisco often operates at less than  
649 maximum activity or is in excess of CO<sub>2</sub> fixation requirements (Stitt & Schulze,  
650 1994; Warren *et al.*, 2000). Partial activation could be linked to limitations in sink  
651 demand for carbohydrates and/or co-limitation by other rock-derived nutrients  
652 such as calcium [e.g. Asner *et al.* (2014b)]. Inactive Rubisco might serve as a  
653 temporary N store - as such, Rubisco can act as both a metabolic and non-  
654 metabolic protein (Stitt & Schulze, 1994; Warren *et al.*, 2000). Viewed from this  
655 perspective, *in vivo* estimates of  $V_{\text{cmax}}$  provide insights into N investment into the  
656 *metabolically active* Rubisco, relevant when modelling gross primary productivity

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

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

674

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

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

687 of the Farquhar *et al.* (1980)  $E_a$  values of  $V_{\text{cmax}}$  and  $J_{\text{max}}$  (of 64.8 and 37.0 kJ mol<sup>-1</sup>,  
688 respectively) with those of Bernacchi *et al.* (2002) (65.3 and 43.9 kJ mol<sup>-1</sup>,  
689 respectively) could alter the relative differences in  $V_{\text{cmax},a}^{25}$  and  $J_{\text{max},a}^{25}$  between  
690 upland and lowland sites. To check whether application of alternative  $E_a$  values  
691 change our conclusions regarding site-to-site differences, we calculated  $V_{\text{cmax},a}^{25}$   
692 and  $J_{\text{max},a}^{25}$  using the respective activation energies of Farquhar *et al.* (1980) and  
693 Bernacchi *et al.* (2002). Use of the Bernacchi *et al.* (2002)  $E_a$  values resulted in an  
694 average 10.6% increase in estimates of  $V_{\text{cmax}25}$  for lowland trees (Table S7),  
695 reflecting the fact that lowland leaf temperatures were near 30°C (Table S4).  
696 Upland estimates were less affected (3.5% increase; Table S7) as the average leaf  
697 temperature of upland group was 25.7°C (Table S4). Despite the increased  
698 estimates of  $V_{\text{cmax}25}$  for lowland trees when using  $E_a$  values from Bernacchi *et al.*  
699 (2002), there remained a significant difference between lowland and upland mean  
700  $V_{\text{cmax}25}$  values (Table S7); the same was true for  $J_{\text{max},a}^{25}$  (Table S7). As a result,  
701 relationships between photosynthetic properties and site MAT and soil P were  
702 similar when using Farquhar *et al.* (1980) and Bernacchi *et al.* (2002)  $E_a$  values (Fig.  
703 S1). Thus, irrespective of which  $E_a$  values are used [see Medlyn *et al.* (2002) for  
704 further discussion the temperature dependence of these constants], we are  
705 confident that that mean values of  $V_{\text{cmax}25}$  and  $J_{\text{max},a}^{25}$  are indeed higher in the  
706 upland plants growing in the Peruvian Andes.

707         What impact might systematic differences in  $g_m$  between upland and  
708 lowland TMFs have on our results? If  $g_m$  was finite, but similar in upland and  
709 lowland TMF environments, then our conclusion that  $V_{\text{cmax},a}^{25}$  is higher in upland  
710 species would hold (albeit with modified values). However, if  $g_m$  was more limiting  
711 in lowland TMF trees than their upland counterparts, then calculation of  $V_{\text{cmax}}$   
712 using A-C<sub>c</sub> curves might fail to differentiate between the upland and lowland  
713 groups. A definitive assessment of this issue will require further work assessing  
714  $g_m$  in tropical trees (e.g. using concurrent measurements of leaf as exchange and  
715 carbon isotope discrimination or chlorophyll fluorescence). Although  $g_m$  tends to  
716 decrease with increasing  $M_a$  (Flexas *et al.*, 2008), the  $M_a$  difference between



717 lowland and upland groups was small (Table 1). Given the potential for large  
718 variations in  $g_m$  among species (at a given  $M_a$ ), it is unlikely that  $g_m$  would have  
719 been higher in the selected lowland TMF trees. Irrespective of the effect of  
720 elevation on  $g_m$ , rates of  $A_{40,a}$  and  $A_{200,a}$  (measured at prevailing leaf  $T_s$ ) were  
721 surprisingly high in plants at the cooler, high elevation sites (Table S4). Given this  
722 and our extensive sample size, we feel confident that photosynthetic capacity at  
723 a standardised  $T$  is likely larger in trees growing at high elevations in the Andes  
724 compared to those in the lowland regions of Amazonia, as proposed by van de  
725 Weg *et al.* (2012; 2014). Enhanced photosynthetic capacity at high altitude could  
726 help negate the inhibitory effects of low  $T$  on leaf-level  $\text{CO}_2$  uptake, with the result  
727 that gross primary productivity (GPP) would not decline with increasing elevation  
728 as much as expected.

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

742

### 743 *Concluding statements*

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

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

755

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771

## 772 **Author Contributions**

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774 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.,  
775 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.,  
776 I.C.T., R.B.L., Y.P.T., J.H.O. and O.K.A conducted fieldwork and/or analysed field-based  
777 data. N.H.A.B., F.Y.I., G.P.A., R.E.M., B.M.L. and J.R.E. performed laboratory experiments  
778 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.,  
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780

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1032 **Supporting Information**

1033 Additional supporting information may be found in the online version of this article.

1034

1035 SM1: Additional study site details

1036 SM2: Identification of outliers and  $A \leftrightarrow C_i$  curve methodological details

1037 SM3: Optimization of protocols for protein extraction from the leaves of recalcitrant tree  
1038 species

1039

1040 Table S1. Summary of species sampled at each site and their parameters

1041 Table S2. Pearson correlations for bivariate relationships among leaf traits and  
1042 environmental parameters

1043 Table S3. Standardized major axis regression slopes for relationships in Figs 2, 4, 5 & 6

1044 Table S4. Means  $\pm$  standard deviation of leaf physiology and chemistry, expressed on  
1045 area basis for each site

1046 Table S5. Standardized major axis regression slopes for relationships in Figs 8 & S2

1047 Table S6: Stepwise selection process for the fixed component of the linear mixed effect  
1048 model to determine the best predictive model given in Table 3

1049

1050 Figure S1. Plots of photosynthetic parameters against mean annual temperature and  
1051 soil [P] for each site

1052 Figure S2. Plots of %  $n_P$ , %  $n_R$ , and %  $n_E$ , in relation to  $M_a$ ,  $N_a$ , and  $P_a$

1053 Figure S3. Plots of fraction of leaf N allocated in Rubisco,  $n_R$  in relation to leaf mass per  
1054 unit leaf area,  $M_a$

1055 Figure S4. Stacked graph show  $n_E$ ,  $n_P$  and  $n_R$  (*in vivo* and *in vitro*) for individual leaves

1056 Figure S5. Plots for linear mixed-effects model goodness of fits, including fixed and  
1057 random terms for  $V_{c_{max,a}}^{25}$  and  $J_{max,a}^{25}$

1058 Figure S6: Comparison of  $V_{c_{max,a}}^{25}$  in upland and lowland plants calculated using  
1059 different activation energies



**Table 1: Description of the sampled Peruvian field sites.**

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

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

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

Leaf Traits	Leaf N <sub>a</sub> (g m <sup>-2</sup> )	Leaf P <sub>a</sub> (g m <sup>-2</sup> )	Leaf N:P	M <sub>a</sub> (g m <sup>-2</sup> )	A <sub>400,a</sub> (μmol m <sup>-2</sup> s <sup>-1</sup> )	A <sub>400,N</sub> (μmol gN <sup>-1</sup> s <sup>-1</sup> )	V <sub>cmax,a</sub> <sup>25</sup> (μmol m <sup>-2</sup> s <sup>-1</sup> )	J <sub>max,a</sub> <sup>25</sup> (μmol m <sup>-2</sup> s <sup>-1</sup> )	J <sub>max,a</sub> <sup>25</sup> :V <sub>cmax,a</sub> <sup>25</sup>	V <sub>cmax,N</sub> <sup>25</sup> (μmol gN <sup>-1</sup> s <sup>-1</sup> )	n <sub>A</sub>	n <sub>P</sub>	n <sub>R</sub>	n <sub>E</sub>
Lowland species	1.96 ± 0.52 <sup>a</sup>	0.09 ± 0.05 <sup>a</sup>	22.2 ± 8.6 <sup>a</sup>	132 ± 35 <sup>a</sup>	8.2 ± 3.9 <sup>a</sup>	4.3 ± 2.2 <sup>a</sup>	35.9 ± 14.6 <sup>a</sup>	66.7 ± 18.6 <sup>a</sup>	1.86 ± 0.40 <sup>a</sup>	18.9 ± 8.1 <sup>a</sup>	37 ± 1 <sup>a</sup>	24 ± 1 <sup>a</sup>	9.0 ± 4.0 <sup>a</sup>	2.8 ± 1.0 <sup>a</sup>
Upland species	2.31 ± 0.44 <sup>b</sup>	0.18 ± 0.06 <sup>b</sup>	13.5 ± 3.6 <sup>b</sup>	143 ± 39 <sup>b</sup>	7.6 ± 3.6 <sup>a</sup>	3.4 ± 1.7 <sup>b</sup>	48.8 ± 20.0 <sup>b</sup>	96.9 ± 36.9 <sup>b</sup>	1.92 ± 0.36 <sup>a</sup>	22.5 ± 9.4 <sup>b</sup>	38 ± 1 <sup>a</sup>	22 ± 1 <sup>a</sup>	10.5 ± 4.3 <sup>b</sup>	3.4 ± 1.4 <sup>b</sup>

Values expressed on area basis. Abbreviation: leaf N<sub>a</sub> = leaf nitrogen, leaf P<sub>a</sub> = leaf phosphorus, leaf N:P = leaf nitrogen to phosphorus ratio, M<sub>a</sub> = leaf mass per unit leaf area, A<sub>400,a</sub> = area-based light-saturated net photosynthesis measured at 400 μmol mol<sup>-1</sup> atmospheric [CO<sub>2</sub>], A<sub>400,N</sub> = area-based light-saturated net photosynthesis measured at 400 μmol mol<sup>-1</sup> atmospheric [CO<sub>2</sub>] per unit leaf nitrogen, V<sub>cmax,a</sub><sup>25</sup> = maximum carboxylation velocity of Rubisco normalised to 25°C, J<sub>max,a</sub><sup>25</sup> = maximum rate of electron transport normalised to 25°C, J<sub>max,a</sub><sup>25</sup>:V<sub>cmax,a</sub><sup>25</sup> = ratio of maximum Rubisco carboxylation velocity over maximum rate of electron transport, both normalised to 25°C, V<sub>cmax,N</sub><sup>25</sup> = ratio of maximum carboxylation velocity of Rubisco normalised to 25°C per unit leaf nitrogen, n<sub>A</sub> = total fraction of leaf N allocated in photosynthetic metabolism, n<sub>P</sub> = fraction of leaf N in pigment-protein complexes, n<sub>R</sub> = fraction of leaf N in Rubisco, and n<sub>E</sub> = fraction of leaf N in electron transport. Values are overall mean ± SD of leaf traits for lowland and upland sites. Significantly different means are indicated by different letters (*p* < 0.05).

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

Final model ( $V_{c_{max,a}}^{25}$ )				Final model ( $J_{max,a}^{25}$ )			
Fixed effect	Estimate	S.E	t value	Fixed effect	Estimate	S.E	t value
Intercept	41.470	1.578	26.288	Intercept	77.217	2.712	28.477
log10 (Soil P)	7.909	2.466	3.207	log10 (Soil P)	16.866	4.327	3.898
$P_a$	68.148	22.558	3.021	$P_a$	94.483	40.245	2.348
Random effect		Variance	% of total	Random effect		Variance	% of total
Intercept variance: family		45.568	2.49%	Intercept variance: family		121.3	2.79%
Residual error (within family)		1783.626	97.51%	Residual error (within family)		4232.9	97.21%
			100.00%				100.00%
AIC	1645.6			AIC	1342.4		
BIC	1662.0			BIC	1357.3		
-2LL	-817.8			-2LL	-666.2		

$$V_{c_{max,a}}^{25} = 41.47 + (7.91 * \log_{10}[\text{SoilP}]) + (68.15 * P_a)$$
  

$$J_{max,a}^{25} = 77.22 + (16.87 * \log_{10}[\text{SoilP}]) + (94.48 * P_a)$$

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

## Figure Legends

**Figure 1: Fitted curves of the response of CO<sub>2</sub> assimilation rate,  $A$  (area-based) to intercellular CO<sub>2</sub> ( $C_i$ ) at saturating light for (A) a lowland species *Glycydendron amazonicum* (TAM-09) and an upland species *Cecropia angustifolia* (SPD-01) and (B) two upland species *Citronella incarum* (TRU-03) and *Schefflera* sp. (WAQ-01).** Closed circles are the measured rates of assimilation,  $A$ . Solid lines correspond to fitted response and dashed lines correspond to estimated response at high  $C_i$ .  $V_{\text{cmax}}$  (maximum Rubisco carboxylation capacity) was calculated from the curvature of dashed line and  $J_{\text{max}}$  (maximum electron transport rate) were calculated from the points where  $A$  saturated. Individual leaf was measured at varying temperature close to growth temperature, therefore  $V_{\text{cmax}}$  and  $J_{\text{max}}$  were then normalised to 25°C. CO<sub>2</sub> was not always saturating for most upland measurement due to low partial pressure and/or phosphate limitation.

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

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

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

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

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

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

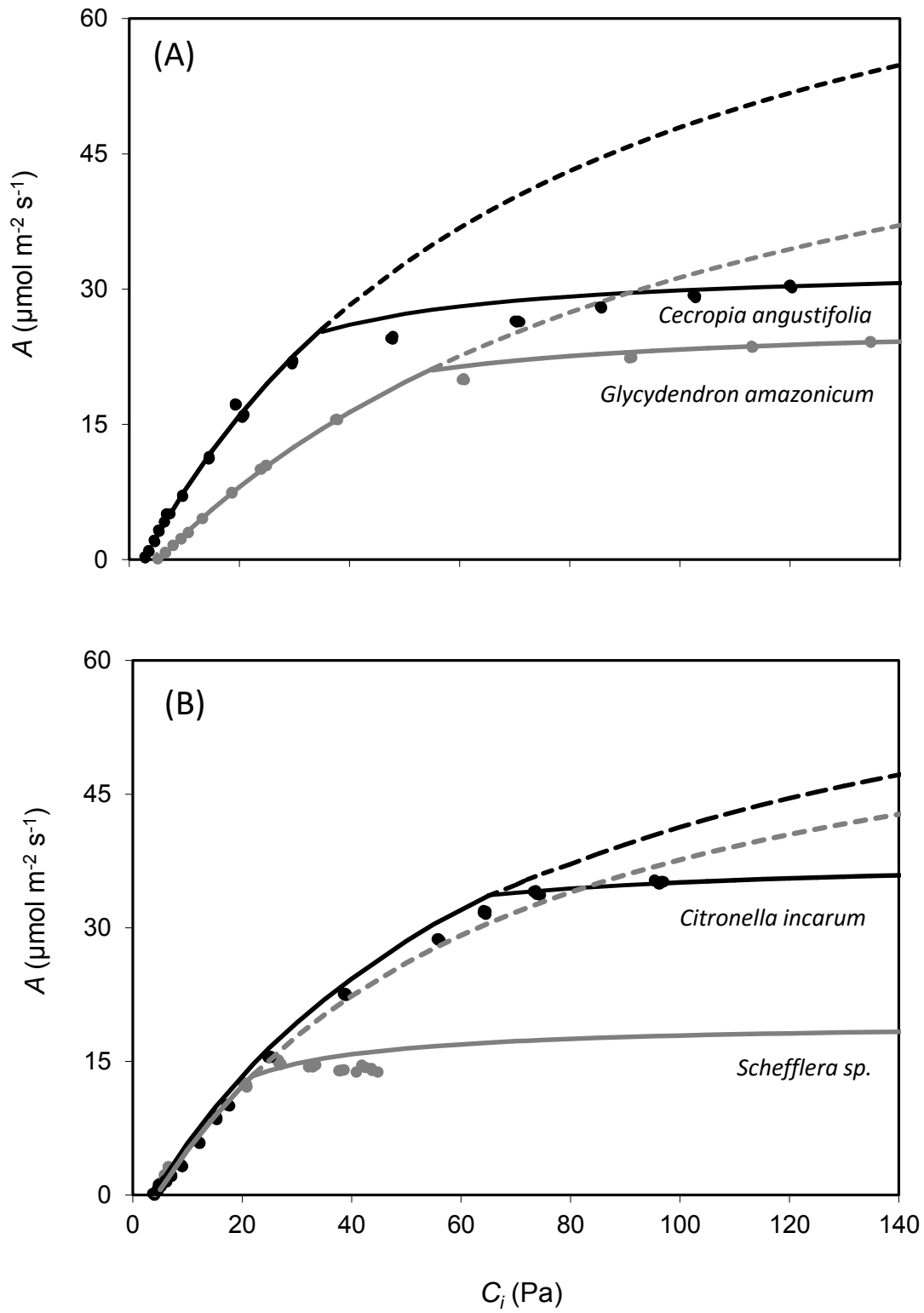
**Figure 7: Stacked graph show fraction of leaf N in pigment-protein complexes,  $n_P$ ; fraction of leaf N in electron transport,  $n_E$ ; fraction of leaf N in Rubisco;  $n_R$ , for each sites.**  $n_R$  was estimated from maximum carboxylation velocity of Rubisco (normalised to 25°C),  $V_{\text{cmax},a}^{25}$ ,  $n_E$  estimated from maximum electron transport rate (normalised to 25°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 N allocated in photosynthetic metabolism,  $n_A$  in relation to (A) leaf mass per unit leaf area,  $M_a$ , (B) leaf N-area,  $N_a$ , and (C) leaf P-area,  $P_a$ .** Data points represent individual leaf values (126 lowland species and 40 upland species). SMA tests for common slopes revealed no significant difference when comparing relationships between lowland and upland species, but with the elevation (i.e. y-axis intercept) of the bivariate relationship being higher in upland species than in lowland species. Symbols: closed symbols, lowland species; open symbols, upland species. SMA regressions: solid line, lowland species; dashed line, upland species. SMA regressions are given only when the relationships are significant ( $p < 0.05$ ), refer to Table S5.

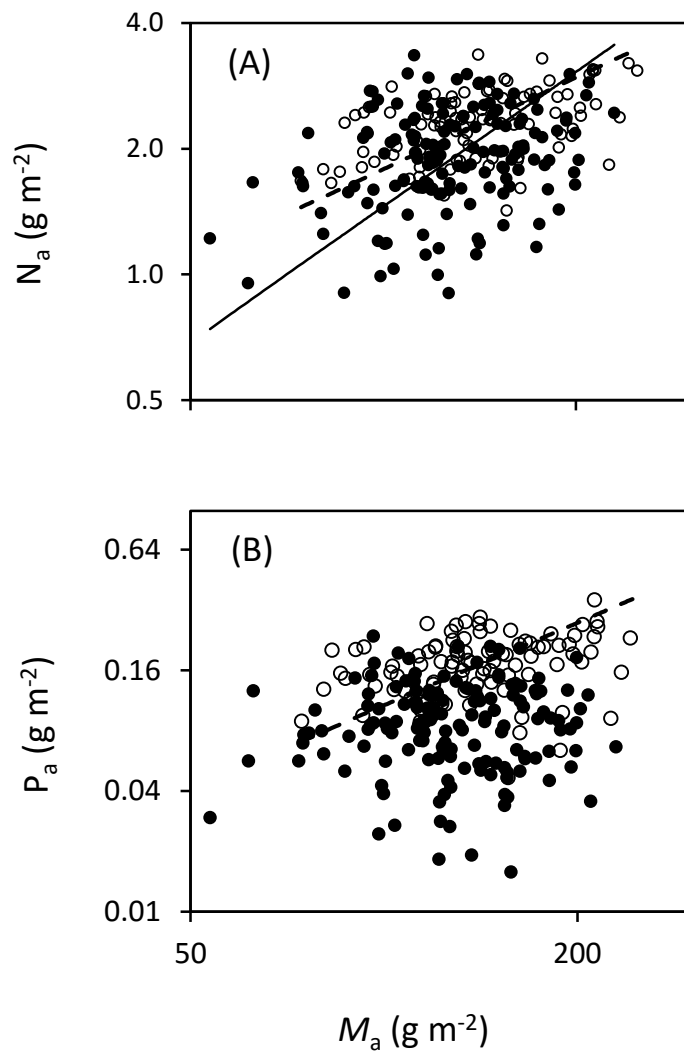
**Figure 9 (A): SDS-PAGE profile of native Rubisco extracted from frozen fresh leaf discs.** Individual bands show large subunits of Rubisco. The last five bands on the right side (A-E) correspond to 0.47, 0.54, 0.57, 0.78 and 1.21 g m<sup>-2</sup> of Rubisco of lowland species (*Licania unguiculata*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

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

Figure 1:



**Figure 2:**





**Figure 3:**

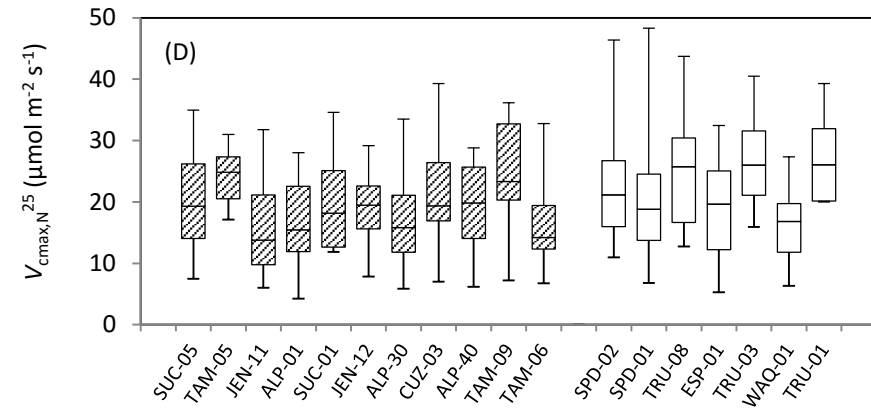
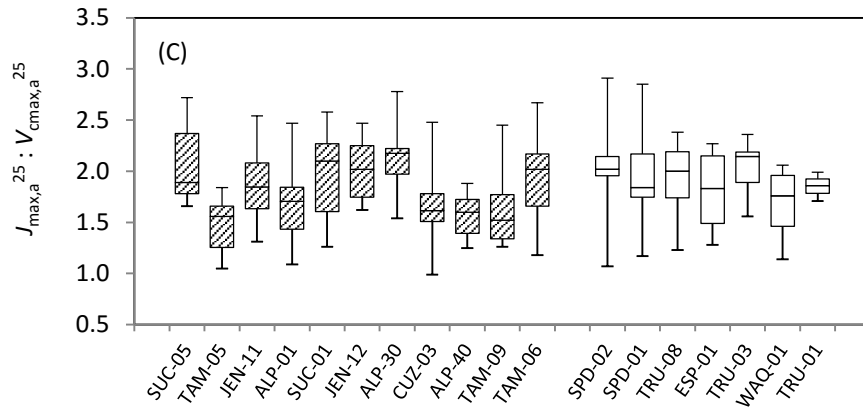
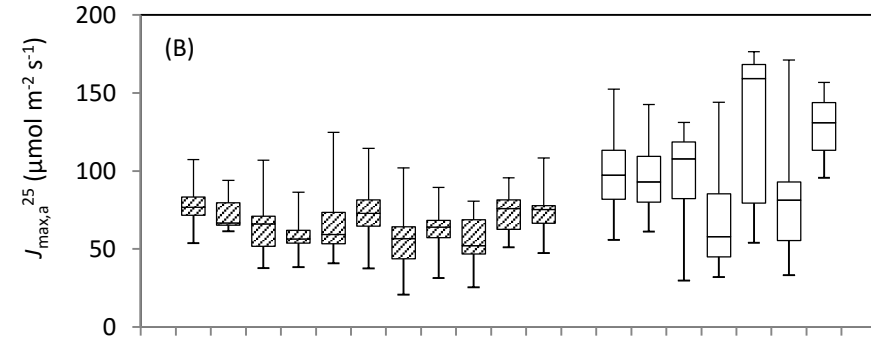
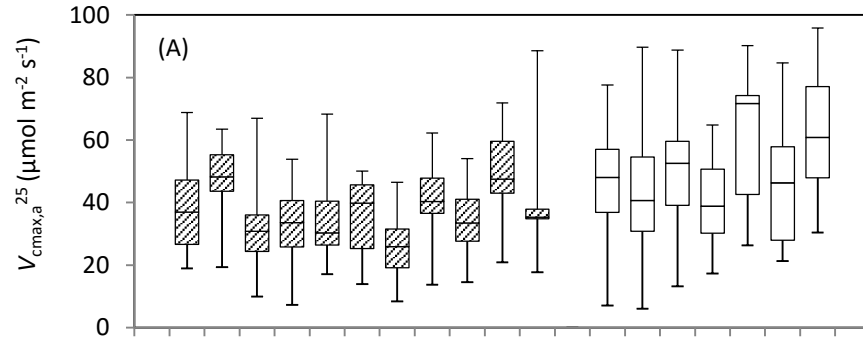


Figure 4:

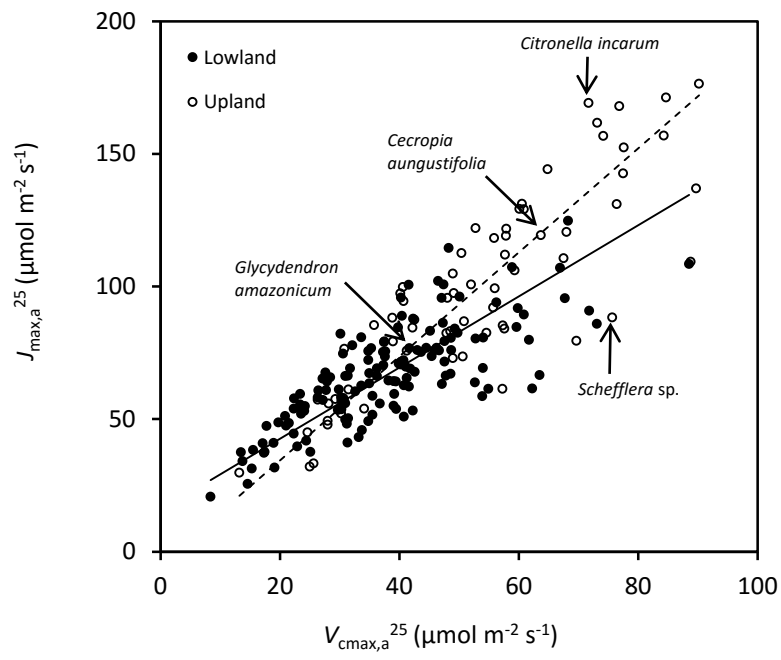


Figure 5:

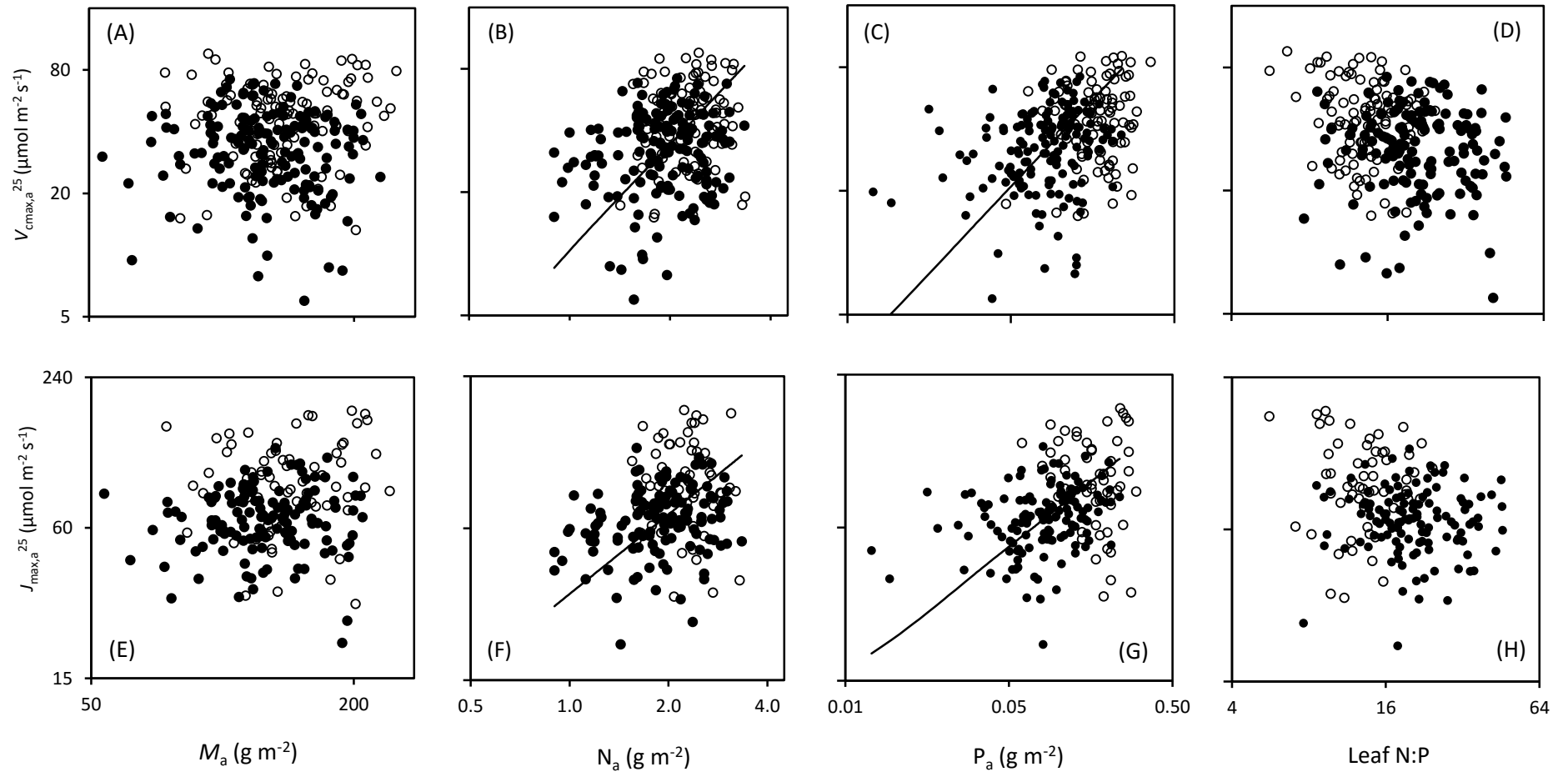


Figure 6:

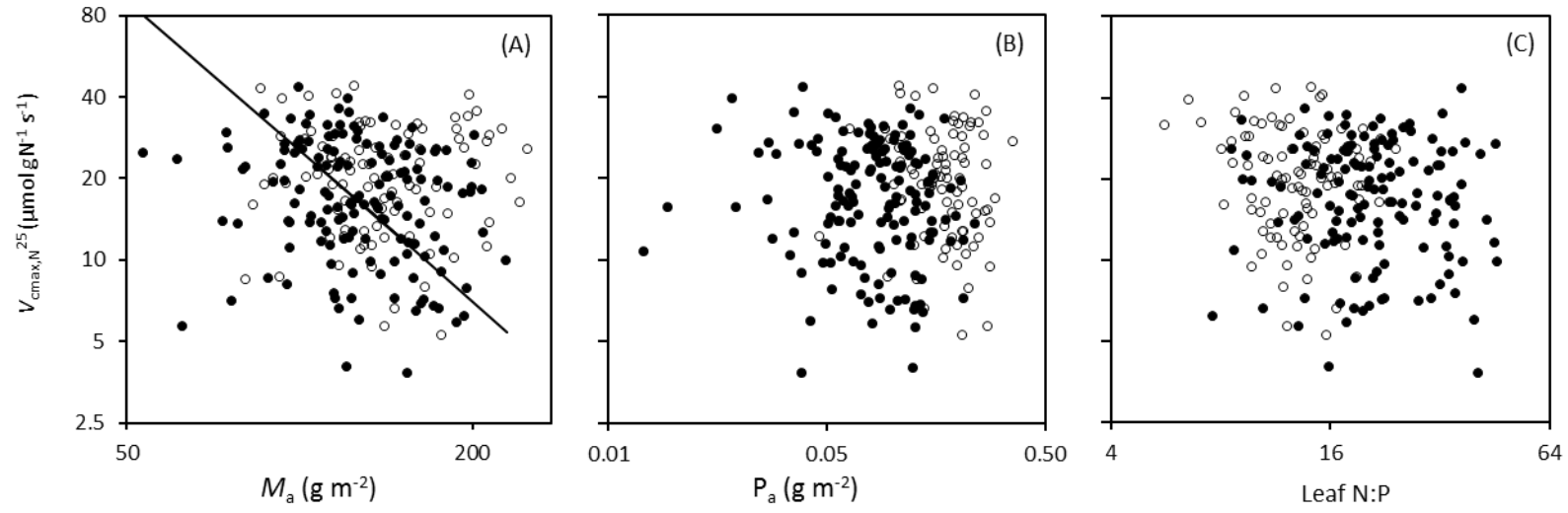


Figure 7:

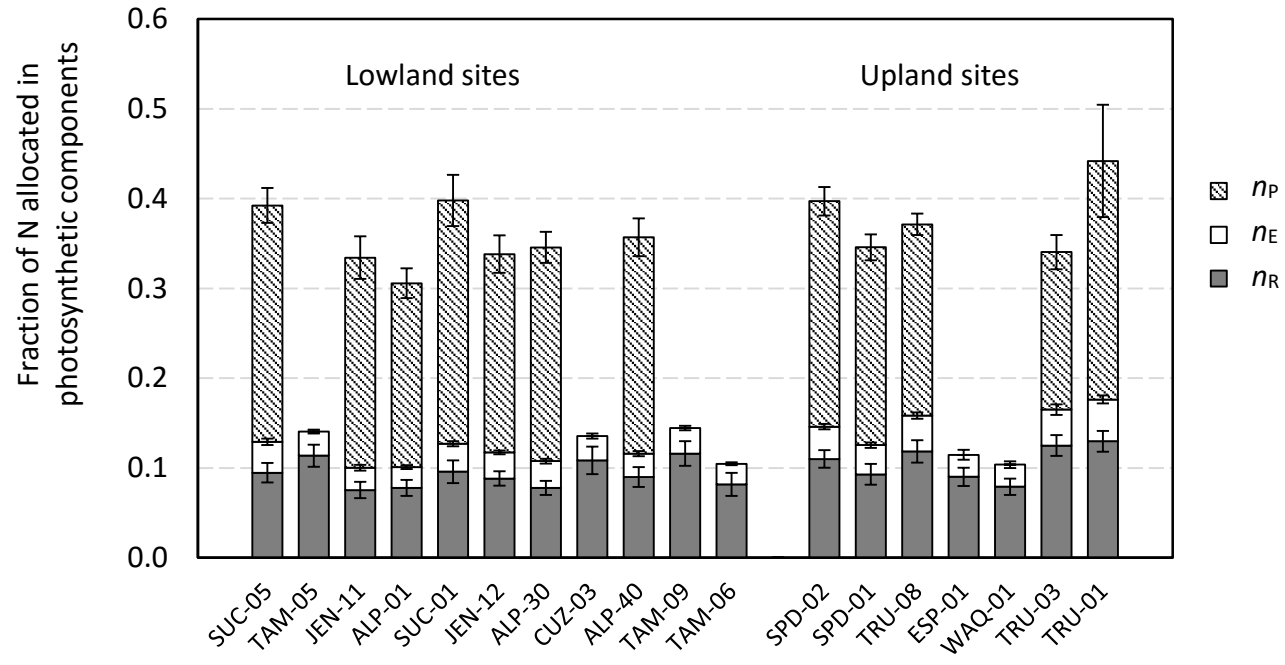


Figure 8:

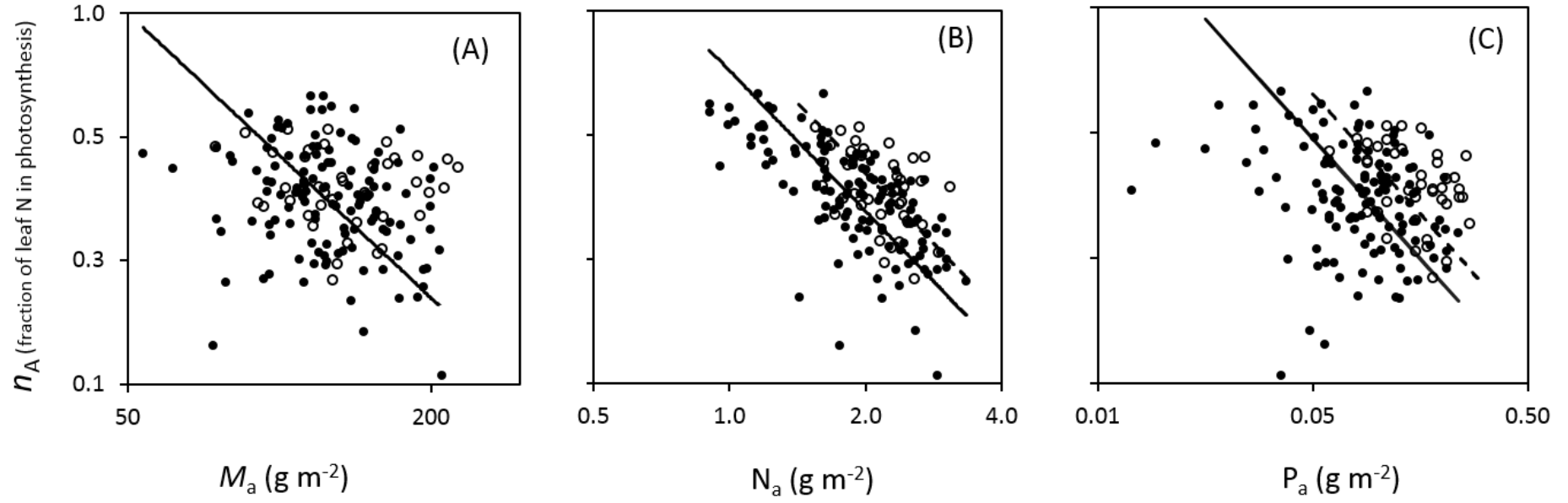
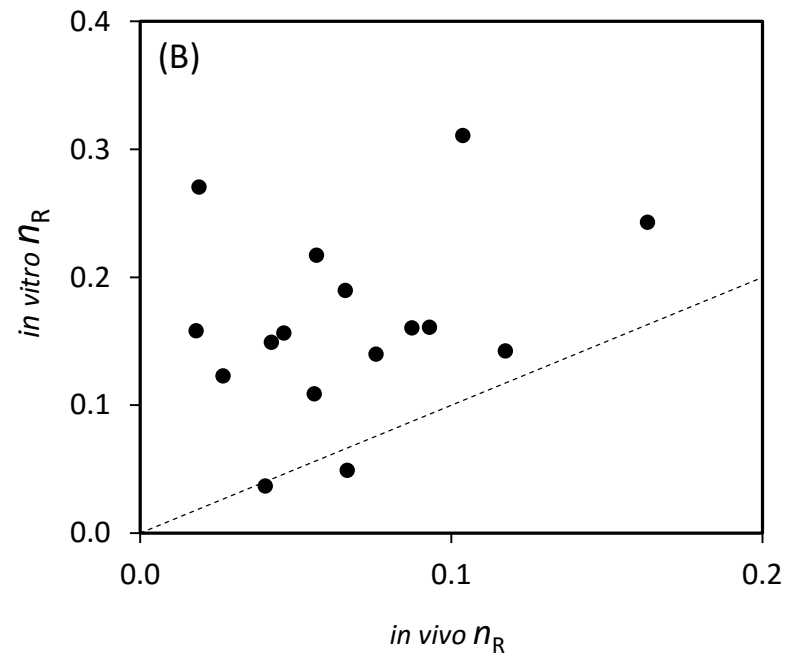
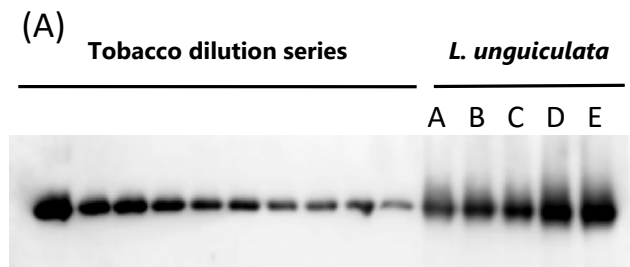


Figure 9:



## Supporting Information

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

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

### **SM1: Additional study site details**

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



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

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

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

where  $R_{\text{light}}$  is respiration in the light,  $\Gamma^*$  is the CO<sub>2</sub> compensation point in the absence of photorespiration (3.69 Pa at 25°C; von Caemmerer *et al.* (1994)),  $K_c$  and  $K_o$  are the effective Michaelis-Menten constants for CO<sub>2</sub> and O<sub>2</sub> at 25°C [40.4 Pa and 24.8 kPa,

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

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

The resultant  $O_2$  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 ( $E_a$ ) of  $K_c$  and  $K_o$  of 59.4 and 36 kJ mol<sup>-1</sup>, respectively (Farquhar *et al.*, 1980). These enzymatic kinetic constants were taken from von Caemmerer *et al.* (1994), assuming an infinite internal conductance.  $\Gamma^*$  at each leaf temperature was assumed to follow the temperature dependency reported by Brooks and Farquhar (1985). Rates of  $J_{max}$  were calculated using the electron-transport-limited equation of  $CO_2$  assimilation:

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

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

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

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

#### *Trouble-shooting using temperate and tropical evergreen species*

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

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

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

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

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

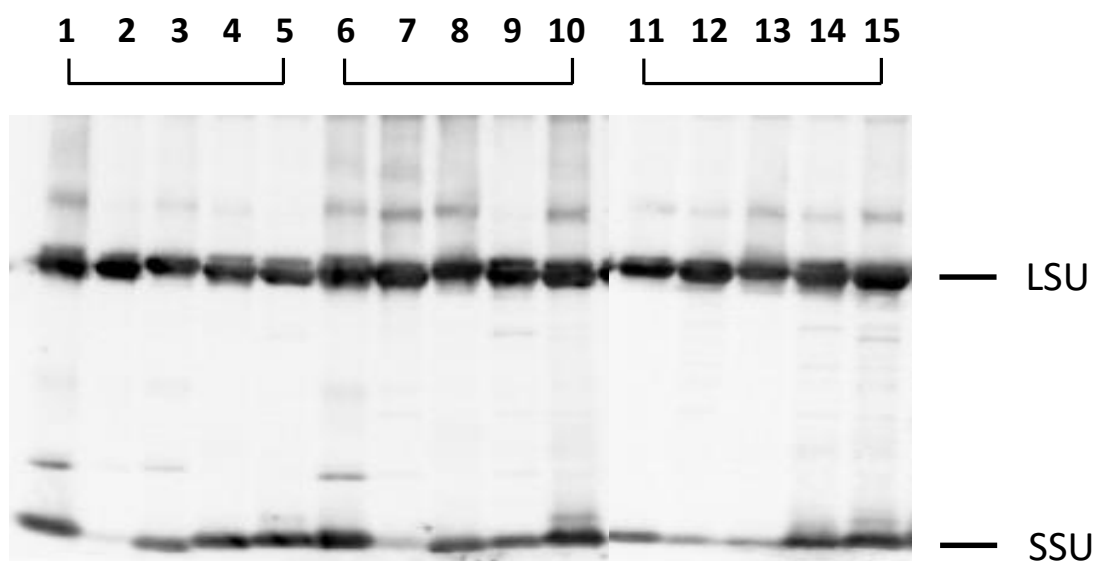
Analysis by SDS-PAGE and Western blotting was performed according to protocols described in *Materials and Methods: Chlorophyll and Rubisco measurements* in the main text. Based on this analysis, extraction with 100% methanol consistently provided the cleanest protein extracts as assessed by SDS-PAGE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

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

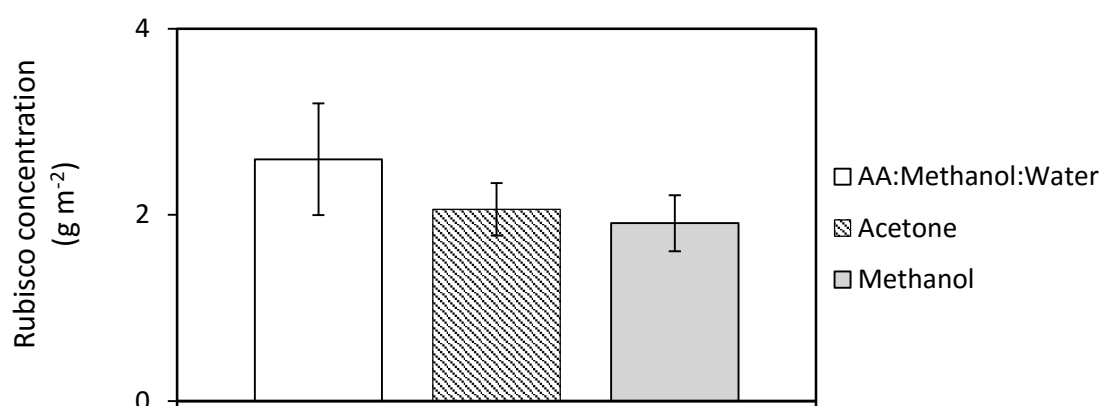
sample; a difference closely equivalent to the spike. This suggests that the Western blot antibody assay, typically designed for crop species, is compatible with temperate and tropical evergreen species and that the antibody used can successfully be applied to a variety of land plants (Kellogg & Juliano, 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*

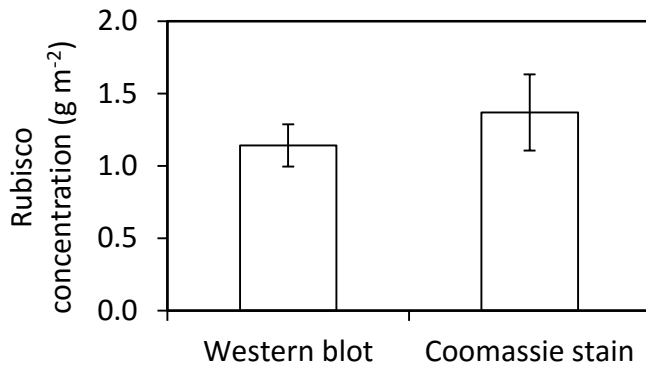
Leaf protein of lowland Peruvian tree species was extracted using a modified protocol as described above. After initial extraction of chlorophyll using 100% methanol, precipitated protein was further washed in hexane and acetone as described by Gaspar *et al.* (1997) and dissolved in PEB containing 5 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  $\mu\text{g}$  sample was required per lane to yield clear, unsaturated band with low background intensity (Fig. SM3.5).



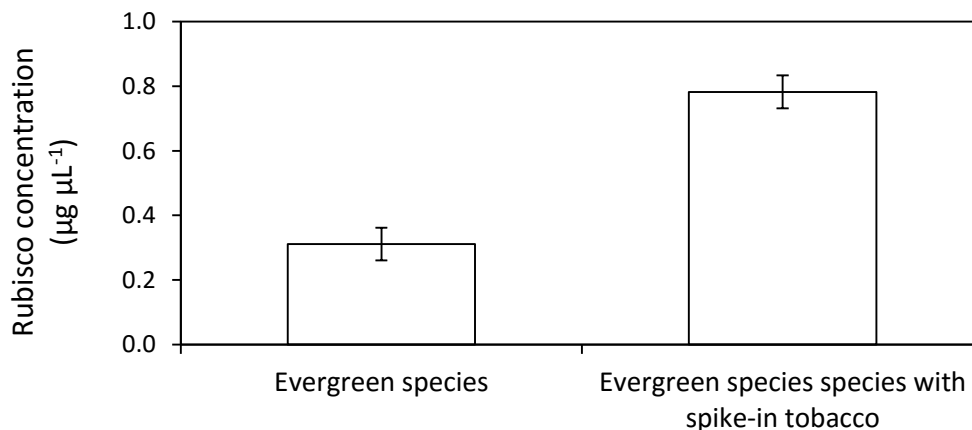
**Figure SM3.1: The effect of leaf extraction solvents on Rubisco western blot quality.** Typical western blot profile of Rubisco extracted from five temperate evergreen species after acetic acid, methanol and water (1:10:9) (1-5), 80% (v/v) acetone (6-10) and 100% methanol (11-15) clean-up, prior to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



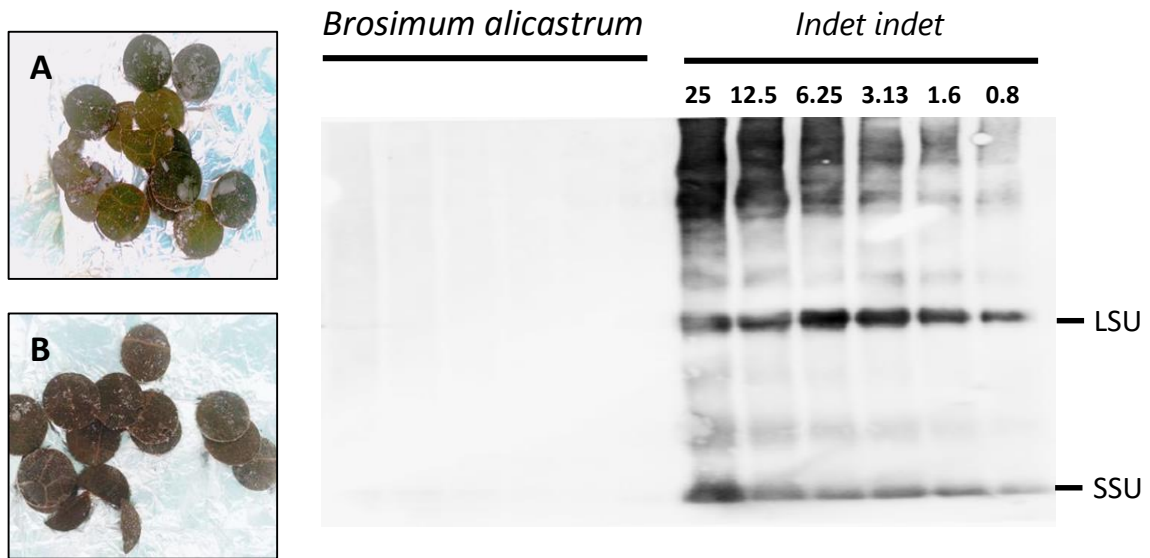
**Figure SM3.2: The effect of leaf extraction solvents on estimated Rubisco in protein extracts.** The graph shows estimated Rubisco concentration in leaves of five temperate evergreen species ( $\pm$  S.E.) after acetic acid (AA), methanol and water (1:10:9), 80% acetone and 100% methanol clean-up, 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 ( $0.5 \mu\text{g } \mu\text{L}^{-1}$ ). 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 (50mM EPPS [4-(2-hydroxyethyl)-1-piperazinepropanesulfonic acid]-NaOH, 1mM EDTA, 1% Polyvinylpolypyrrolidone (PVPP), 10mM DTT, 0.01% Triton, pH 7.8).



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



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

Abbreviations:  $M_a$  = leaf mass per unit leaf area, leaf  $N_a$  = leaf nitrogen, leaf  $P_a$  = leaf phosphorus,  $A_{400,a}$  = light-saturated net photosynthesis measured under 400  $\mu\text{mol mol}^{-1}$  atmospheric  $[\text{CO}_2]$ ,  $A_{2000,a}$  = light-saturated net photosynthesis measured under 2000  $\mu\text{mol mol}^{-1}$  atmospheric  $[\text{CO}_2]$ ,  $V_{c\text{max},a}^{25}$  = maximum carboxylation velocity of Rubisco normalised to 25°C,  $J_{\text{max},a}^{25}$  = maximum rate of electron transport normalised to 25°C,  $R_{\text{light}}$  = leaf respiration measured in the light at 400  $\mu\text{mol mol}^{-1}$  atmospheric  $[\text{CO}_2]$ , Leaf  $T$  = leaf temperature inside gas exchange cuvette, Chl = chlorophyll a and b content,  $n_E$  = fraction of leaf N in electron transport,  $n_R$  = fraction of leaf N in Rubisco,  $n_P$  = fraction of leaf N in pigment-protein complexes.

Site	Family	Genus	Species	$M_a$ (g m <sup>-2</sup> )	Leaf $N_a$ (g m <sup>-2</sup> )	Leaf $P_a$ (g m <sup>-2</sup> )	$A_{400,a}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	$A_{2000,a}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	$V_{c\text{max},a}^{25}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	$J_{\text{max},a}^{25}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	$R_{\text{light}}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	Leaf $T$ (°C)	Chl (g m <sup>-2</sup> )	$n_E$	$n_R$	$n_P$
SUC-05	<i>Urticaceae</i>	<i>Pourouma</i>	<i>bicolor</i>	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	<i>Chrysobalanaceae</i>	<i>Couepia</i>	<i>bracteosa</i>	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	<i>Burseraceae</i>	<i>Protium</i>	<i>paniculatum</i>	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	<i>Sapotaceae</i>	<i>Micropholis</i>	<i>guyanensis</i>	163	2.29	0.13	3.5	14.8	19.8	.	1.2	29.2	0.40	.	0.04	0.12
SUC-05	<i>Myristicaceae</i>	<i>Osteophloeum</i>	<i>platyspermum</i>	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	<i>Sapotaceae</i>	<i>Pouteria</i>	<i>caimito</i>	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	<i>Apocynaceae</i>	<i>Rhigospira</i>	<i>quadrangularis</i>	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	<i>Rubiaceae</i>	<i>Chimarrhis</i>	<i>gentryana</i>	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	<i>Sapotaceae</i>	<i>Pouteria</i>	<i>filipes</i>	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	<i>Chrysobalanaceae</i>	<i>Licania</i>	<i>latifolia</i>	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	<i>Moraceae</i>	<i>Naucleopsis</i>	<i>mello-barretoii</i>	115	2.53	0.07	4.1	14.5	19.0	.	1.2	29.6	1.09	.	0.04	0.30
SUC-05	<i>Rubiaceae</i>	<i>Ladenbergia</i>	<i>magnifolia</i>	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	<i>Myristicaceae</i>	<i>Virola</i>	<i>calophylla</i>	.	.	.	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	<i>Anacardiaceae</i>	<i>Tapirira</i>	<i>obtusa</i>	.	.	.	10.9	20.7	40.4	71.5	1.4	29.2	.	.	.	0.22
SUC-05	<i>Moraceae</i>	<i>Pseudolmedia</i>	<i>rigida</i>	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	<i>Apocynaceae</i>	<i>Parahancornia</i>	<i>peruviana</i>	137	1.47	0.02	5.4	16.7	23.2	.	1.2	28.4	0.87	.	0.07	0.41
SUC-05	<i>Humiriaceae</i>	<i>Humiriastrum</i>	<i>excelsum</i>	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	<i>Moraceae</i>	<i>Helicostylis</i>	<i>scabra</i>	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	<i>Lauraceae</i>	<i>Licaria</i>	<i>cannella</i>	181	.	0.06	11.7	20.6	44.5	76.8	1.2	28.0	.	0.02	.	.
TAM-05	<i>Ulmaceae</i>	<i>Ampelocera</i>	<i>edentula</i>	.	.	.	6.0	17.2	19.4	.	0.5	30.0	.	.	.	.
TAM-05	<i>Bixaceae</i>	<i>Bixa</i>	<i>arborea</i>	75	1.65	0.07	13.0	22.6	48.7	76.0	0.1	28.8	.	0.04	0.14	.
TAM-05	<i>Lauraceae</i>	<i>Ocotea</i>	<i>bofo</i>	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	<i>Sapotaceae</i>	<i>Pouteria</i>	<i>torta subsp. tuberculata</i>	117	2.05	0.10	6.8	25.9	45.2	83.3	1.3	30.4	.	0.03	0.10	.

TAM-05	<i>Malvaceae</i>	<i>Huberodendron</i>	<i>switenioides</i>	95	2.17	0.12	10.6	20.5	54.9	61.4	0.4	30.4	.	0.02	0.12	.
TAM-05	<i>Melastomataceae</i>	<i>Miconia</i>	<i>pyrifolia</i>	155	2.27	0.05	11.9	28.7	56.3	94.0	1.6	30.6	.	0.03	0.12	.
TAM-05	<i>Elaeocarpaceae</i>	<i>Sloanea</i>	<i>brevipes</i>	125	2.05	0.08	11.5	20.7	63.5	66.6	1.3	31.0	.	0.03	0.15	.
JEN-11	<i>Sapotaceae</i>	<i>Micropholis</i>	<i>guyanensis</i>	156	.	0.05	2.5	22.1	32.1	77.8	2.2	29.5	.	0.02	.	.
JEN-11	<i>Olacaceae</i>	<i>Aptandra</i>	<i>liriosmoides</i>	165	2.35	0.11	5.3	15.7	18.2	.	1.0	29.5	0.98	.	0.04	0.29
JEN-11	<i>Lauraceae</i>	<i>Mezilaurus</i>	<i>synandra</i>	230	2.43	0.07	3.9	21.0	29.2	.	1.6	29.5	.	.	0.06	0.43
JEN-11	<i>Lecythidaceae</i>	<i>Eschweilera</i>	<i>coriacea</i>	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	<i>Vochysiaceae</i>	<i>Qualea</i>	<i>paraensis</i>	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	<i>Melastomataceae</i>	<i>Mouriri</i>	<i>nigra</i>	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	<i>Sapotaceae</i>	<i>Pouteria</i>	<i>guianensis</i>	163	1.78	0.05	4.9	16.1	24.2	.	1.1	28.9	0.71	.	0.06	0.27
JEN-11	<i>Goupiaceae</i>	<i>Goupia</i>	<i>glabra</i>	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	<i>Myristicaceae</i>	<i>Osteophloeum</i>	<i>platyspermum</i>	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	<i>Sapotaceae</i>	<i>Pouteria</i>	<i>platyphylla</i>	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	<i>Myrtaceae</i>	<i>Myrciaria</i>	<i>floribunda</i>	127	1.65	0.04	3.2	5.5	9.9	.	0.5	28.4	0.62	.	0.03	0.26
JEN-11	<i>Urticaceae</i>	<i>Pourea</i>	<i>bicolor</i>	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	<i>Chrysobalanaceae</i>	<i>Licania</i>	<i>indet</i>	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	<i>Lecythidaceae</i>	<i>Eschweilera</i>	<i>tessmannii</i>	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	<i>Apocynaceae</i>	<i>Couma</i>	<i>macrocarpa</i>	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	<i>Sapotaceae</i>	<i>Micropholis</i>	<i>guyanensis</i>	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	<i>Elaeocarpaceae</i>	<i>Sloanea</i>	<i>brevipes</i>	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	<i>Fabaceae</i>	<i>Dipteryx</i>	<i>micrantha</i>	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	<i>Sapotaceae</i>	<i>Pouteria</i>	<i>subrotata</i>	.	.	.	11.6	26.7	47.3	86.3	0.9	29.4	.	.	.	.
ALP-01	<i>Chrysobalanaceae</i>	<i>Licania</i>	<i>arachnoidea</i>	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	<i>Annonaceae</i>	<i>Guatteria</i>	<i>schomburgkiana</i>	125	2.20	0.07	2.9	22.1	32.4	.	2.0	29.7	0.47	.	0.07	0.15
ALP-01	<i>Olacaceae</i>	<i>Minuartia</i>	<i>guianensis</i>	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	<i>Myristicaceae</i>	<i>Iryanthera</i>	<i>lancifolia</i>	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	<i>Euphorbiaceae</i>	<i>Hevea</i>	<i>pauciflora</i>	121	1.96	0.12	0.9	4.5	8.3	.	1.2	30.5	0.52	.	0.02	0.18
ALP-01	<i>Olacaceae</i>	<i>Chaunochiton</i>	<i>kappleri</i>	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	<i>Ochnaceae</i>	<i>Cespedesia</i>	<i>spathulata</i>	119	1.86	0.10	4.2	22.5	30.0	.	1.2	30.0	0.58	.	0.08	0.21
ALP-01	<i>Fabaceae</i>	<i>Taralea</i>	<i>oppositifolia</i>	154	1.56	0.04	1.9	7.0	7.2	.	0.5	30.6	0.78	.	0.02	0.34
ALP-01	<i>Moraceae</i>	<i>Brosimum</i>	<i>rubescens</i>	114	1.61	0.07	2.9	12.0	15.5	38.3	0.9	30.2	.	0.02	0.05	.
ALP-01	<i>Fabaceae</i>	<i>Swartzia</i>	<i>polyphylla</i>	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	<i>Lepidobotryaceae</i>	<i>Ruptiliocarpon</i>	<i>caracolito</i>	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	<i>Clusiaceae</i>	<i>Caraipa</i>	<i>punctulata</i>	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	<i>Euphorbiaceae</i>	<i>Senefeldera</i>	<i>inclinata</i>	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	<i>Urticaceae</i>	<i>Pourouma</i>	<i>guianensis</i> subsp. <i>guianensi</i>	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	<i>Euphorbiaceae</i>	<i>Hevea</i>	<i>pauciflora</i>	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	<i>Fabaceae</i>	<i>Inga</i>	<i>striata</i>	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	<i>Myristicaceae</i>	<i>Virola</i>	<i>sebifera</i>	124	2.57	0.11	1.4	25.2	32.2	.	3.2	30.6	0.63	.	0.06	0.17
SUC-01	<i>Myristicaceae</i>	<i>Otoba</i>	<i>glycyarpa</i>	132	.	.	6.0	16.2	27.1	.	1.3	29.8	0.34	.	.	.
SUC-01	<i>Elaeocarpaceae</i>	<i>Sloanea</i>	<i>gladysiae</i>	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	<i>Sapotaceae</i>	<i>Pouteria</i>	<i>filipes</i>	113	1.89	0.09	3.3	18.0	26.5	.	1.7	27.8	0.46	.	0.07	0.16
SUC-01	<i>Urticaceae</i>	<i>Pourouma</i>	<i>bicolor</i>	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	<i>Lepidobotryaceae</i>	<i>Ruptiliocarpon</i>	<i>caracolito</i>	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	<i>Myristicaceae</i>	<i>Iryanthera</i>	<i>lancifolia</i>	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	<i>Lecythidaceae</i>	<i>Gustavia</i>	<i>hexapetala</i>	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	<i>Chrysobalanaceae</i>	<i>Licania</i>	<i>heteromorpha</i>	.	.	.	3.6	17.7	27.8	60.9	1.6	29.7	.	.	.	0.42
SUC-01	<i>Humiriaceae</i>	<i>Schistostemon</i>	<i>reticulatum</i> subsp. <i>reticula</i>	187	2.20	0.09	4.9	14.0	.	.	.	31.3	0.80	.	.	0.25
SUC-01	<i>Moraceae</i>	<i>Helicostylis</i>	<i>scabra</i>	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	<i>Sapindaceae</i>	<i>Talisia</i>	<i>sylvatica</i>	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	<i>Fabaceae</i>	<i>Inga</i>	<i>capitata</i>	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	<i>Lecythidaceae</i>	<i>Eschweilera</i>	<i>itayensis</i>	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	<i>Hypericaceae</i>	<i>Vismia</i>	<i>amazonica</i>	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	<i>Euphorbiaceae</i>	<i>Nealchornea</i>	<i>yapurensis</i>	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	<i>Olacaceae</i>	<i>Minquartia</i>	<i>guianensis</i>	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	<i>Combretaceae</i>	<i>Buchenavia</i>	<i>tomentosa</i>	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	<i>Apocynaceae</i>	<i>Macoubea</i>	<i>sprucei</i>	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	<i>Sapotaceae</i>	<i>Pouteria</i>	<i>lucumifolia</i>	175	1.32	0.13	1.0	9.1	13.9	.	1.5	28.8	0.61	.	0.05	0.32
JEN-12	<i>Clusiaceae</i>	<i>Caraipa</i>	<i>tereticaulis</i>	181	1.60	0.05	9.5	16.3	40.3	.	1.5	28.8	0.44	.	0.12	0.19
JEN-12	<i>Icacinaceae</i>	<i>Emmotum</i>	<i>floribundum</i>	.	.	.	9.2	26.6	45.8	75.9	-1.7	29.0	.	.	.	.
JEN-12	<i>Linaceae</i>	<i>Roucheria</i>	<i>columbiana</i>	.	.	.	5.2	13.2	17.1	.	0.7	28.8	.	.	.	0.36
JEN-12	<i>Euphorbiaceae</i>	<i>Micrandra</i>	<i>spruceana</i>	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	<i>Melastomataceae</i>	<i>Mouriri</i>	<i>nigra</i>	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	<i>Moraceae</i>	<i>Brosimum</i>	<i>utile</i> subsp. <i>ovatifolium</i>	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	<i>Clusiaceae</i>	<i>Tovomita</i>	<i>calophyllophylla</i>	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	<i>Apocynaceae</i>	<i>Aspidosperma</i>	<i>desmanthum</i>	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	<i>Lauraceae</i>	<i>Licaria</i>	<i>cannella</i>	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	<i>Malvaceae</i>	<i>Lueheopsis</i>	<i>althaeiflora</i>	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	<i>Burseraceae</i>	<i>Protium</i>	<i>polybotryum</i>	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	<i>Moraceae</i>	<i>Brosimum</i>	<i>rubescens</i>	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	<i>Moraceae</i>	<i>Pseudolmedia</i>	<i>rigida</i>	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	<i>Sapotaceae</i>	<i>Chrysophyllum</i>	<i>sanguinolentum</i>	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	<i>Euphorbiaceae</i>	<i>Alchornea</i>	<i>triplinervia</i>	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	<i>Apocynaceae</i>	<i>Parahancornia</i>	<i>peruviana</i>	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	<i>Sapotaceae</i>	<i>Micropholis</i>	<i>guyanensis</i> subsp. <i>guyanensi</i>	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	<i>Fabaceae</i>	<i>Tachigali</i>	<i>bracteosa</i>	151	2.48	0.15	4.4	22.9	31.5	.	1.9	29.6	0.84	.	0.06	0.23
ALP-30	<i>Moraceae</i>	<i>Brosimum</i>	<i>potabile</i>	158	2.57	0.14	5.6	16.5	21.9	.	1.5	29.4	0.44	.	0.04	0.12
ALP-30	<i>Elaeocarpaceae</i>	<i>Sloanea</i>	<i>floribunda</i>	.	.	0.06	5.6	13.6	21.0	47.5	1.1	29.2	.	0.02	0.05	0.24
ALP-30	<i>Euphorbiaceae</i>	<i>Micrandra</i>	<i>spruceana</i>	63	1.66	0.13	2.0	7.1	10.3	.	0.5	29.3	0.29	.	0.03	0.12
ALP-30	<i>Simaroubaceae</i>	<i>Simarouba</i>	<i>amara</i>	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	<i>Humiriaceae</i>	<i>Humiria</i>	<i>balsamifera</i>	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	<i>Lauraceae</i>	<i>Ocotea</i>	<i>aciphylla</i>	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	<i>Apocynaceae</i>	<i>Aspidosperma</i>	<i>desmanthum</i>	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	<i>Fabaceae</i>	<i>Diplotrapis</i>	<i>sp</i>	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	<i>Annonaceae</i>	<i>Guatteria</i>	<i>decurrens</i>	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	<i>Euphorbiaceae</i>	<i>Micrandra</i>	<i>elata</i>	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	<i>Lauraceae</i>	<i>Ocotea</i>	<i>myriantha</i>	166	2.00	0.06	4.6	14.3	18.0	.	0.5	30.5	0.46	.	0.04	0.16
ALP-30	<i>Apocynaceae</i>	<i>Aspidosperma</i>	<i>excelsum</i>	159	1.88	0.12	3.9	21.4	25.9	.	1.4	29.5	0.69	.	0.07	0.25
ALP-30	<i>Myrtaceae</i>	<i>Calyptanthes</i>	<i>bipennis</i>	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	<i>Lauraceae</i>	<i>Aniba</i>	<i>perutilis</i>	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	<i>Fabaceae</i>	<i>Macrolobium</i>	<i>microcalyx</i>	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	<i>Myristicaceae</i>	<i>Virola</i>	<i>pavonis</i>	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	<i>Chrysobalanaceae</i>	<i>Licania</i>	<i>unguiculata</i>	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	<i>Anacardiaceae</i>	<i>Tapirira</i>	<i>guianensis</i>	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	<i>Linaceae</i>	<i>Roucheria</i>	<i>schomburgkii</i>	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	<i>Icacinaceae</i>	<i>Emmotum</i>	<i>floribundum</i>	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	<i>Moraceae</i>	<i>Pseudolmedia</i>	<i>laevis</i>	95	1.48	0.08	10.0	19.9	39.4	64.2	0.6	29.9	.	0.03	0.13	.
CUZ-03	<i>Sapotaceae</i>	<i>Pouteria</i>	<i>torta</i> subsp. <i>glabra</i>	138	2.01	0.11	10.0	19.8	52.7	63.8	1.2	30.4	.	0.03	0.12	.
CUZ-03	<i>Moraceae</i>	<i>Poulsenia</i>	<i>armata</i>	119	1.59	0.12	6.8	23.5	46.3	76.8	1.4	29.9	.	0.04	0.14	.
CUZ-03	<i>Combretaceae</i>	<i>Terminalia</i>	<i>oblonga</i>	130	2.26	0.14	5.5	20.0	41.3	65.5	1.4	30.0	.	0.02	0.09	.

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

TAM-06	<i>Fabaceae</i>	<i>Inga</i>	<i>alba</i>	.	.	.	7.3	22.0	35.0	67.3	0.7	30.3	.	.	.	.
TAM-06	<i>Moraceae</i>	<i>Ficus</i>	<i>schultesii</i>	151	2.30	0.15	13.2	23.0	47.6	71.6	0.9	30.8	.	0.02	0.10	.
TAM-06	<i>Fabaceae</i>	<i>Pterocarpus</i>	<i>rohrii</i>	.	.	.	7.1	24.8	28.7	.	1.0	30.2	.	.	.	.
TAM-06	<i>Moraceae</i>	<i>Pseudolmedia</i>	<i>laevis</i>	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	<i>Moraceae</i>	<i>Sorocea</i>	<i>pileata</i>	109	3.02	0.18	9.1	22.7	35.3	76.7	0.6	29.3	.	0.02	0.06	.
TAM-06	<i>Fabaceae</i>	<i>Dipteryx</i>	<i>alata</i>	112	2.34	0.14	16.4	26.4	73.1	86.0	1.2	29.9	.	0.03	0.15	.
TAM-06	<i>Moraceae</i>	<i>Sorocea</i>	<i>trophoides</i>	96	2.52	0.15	9.9	20.4	35.0	63.5	0.2	29.9	.	0.02	0.07	.
TAM-06	<i>Lecythidaceae</i>	<i>Bertolletia</i>	<i>excelsa</i>	151	2.70	0.20	14.8	.	88.6	108.4	-2.7	28.8	.	0.03	0.16	.
TAM-06	<i>Moraceae</i>	<i>Brosimum</i>	<i>sp.</i>	172	2.63	0.13	4.0	14.0	17.8	47.5	1.0	29.4	.	0.01	0.03	.
TAM-06	<i>Cannabaceae</i>	<i>Celtis</i>	<i>schippii</i>	131	2.93	0.21	9.8	23.0	34.8	75.6	0.8	29.5	.	0.02	0.06	.
TAM-06	<i>Moraceae</i>	<i>Clarisia</i>	<i>racemosa</i>	105	2.56	0.20	8.2	22.4	37.3	75.2	1.7	30.0	.	0.02	0.07	.
SPD-02	<i>Burseraceae</i>	<i>Protium</i>	<i>sagotianum</i>	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	<i>Phyllanthaceae</i>	<i>Hieronyma</i>	<i>macrocarpa</i>	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	<i>Sapotaceae</i>	<i>Chrysophyllum</i>	<i>sp.</i>	182	2.91	0.24	4.8	25.1	43.0	.	1.9	27.3	1.19	.	0.07	0.28
SPD-02	<i>Sapindaceae</i>	<i>Matayba</i>	<i>guianensis</i>	210	3.01	0.20	.	.	7.1	.	1.1	25.9	1.17	.	.	0.27
SPD-02	<i>Fabaceae</i>	<i>Inga</i>	<i>killipiana</i>	95	2.51	0.15	8.0	8.2	48.1	.	0.4	27.1	0.71	.	0.09	0.19
SPD-02	<i>Melastomataceae</i>	<i>Miconia</i>	<i>coelestis</i>	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	<i>Ebenaceae</i>	<i>sp1(1046WFR)</i>	<i>sp.</i>	108	1.69	0.13	5.8	19.9	34.9	.	0.6	27.8	0.86	.	0.10	0.35
SPD-02	<i>Burseraceae</i>	<i>Protium</i>	<i>nodulosum</i>	60	.	.	7.1	23.4	32.7	.	0.0	27.7	0.21	.	.	.
SPD-02	<i>Burseraceae</i>	<i>Protium</i>	<i>spruceanum cf</i>	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	<i>Lauraceae</i>	<i>Beilschmiedia</i>	<i>latifolia</i>	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	<i>Caryocaraceae</i>	<i>Caryocar</i>	<i>sp.</i>	120	1.85	0.14	5.3	16.0	22.6	.	0.2	26.9	0.56	.	0.06	0.21
SPD-02	<i>Araliaceae</i>	<i>Dendropanax</i>	<i>cuneatus</i>	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	<i>Aquifoliaceae</i>	<i>Ilex</i>	<i>sp.</i>	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	<i>Moraceae</i>	<i>Pseudolmedia</i>	<i>laevigata</i>	103	2.82	0.17	8.6	33.4	56.8	.	2.0	27.1	0.65	.	0.10	0.16
SPD-02	<i>Moraceae</i>	<i>*Ficus</i>	<i>americana subsp. guianensis</i>	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	<i>Sapotaceae</i>	<i>Pouteria</i>	<i>torta</i>	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	<i>Rubiaceae</i>	<i>Elaeagia</i>	<i>mariae</i>	.	.	.	11.4	31.9	58.0	121.7	0.3	27.3	.	.	.	0.27
SPD-02	<i>Cunoniaceae</i>	<i>Weinmannia</i>	<i>lechleriana</i>	116	1.67	0.11	5.6	36.5	68.4	.	6.1	26.7	0.81	.	0.19	0.33
SPD-02	<i>Lauraceae</i>	<i>Nectandra</i>	<i>sp.</i>	134	2.10	0.20	7.9	45.2	.	.	.	27.0	0.64	.	.	0.21
SPD-01	<i>Euphorbiaceae</i>	<i>Alchornea</i>	<i>anamariae</i>	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	<i>Lauraceae</i>	<i>Ocotea</i>	<i>cernua</i>	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	<i>Lauraceae</i>	<i>Endlicheria</i>	<i>chalsea</i>	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	<i>Brunelliaceae</i>	<i>Brunellia</i>	<i>stenoptera</i>	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	<i>Lauraceae</i>	<i>Endlicheria</i>	<i>macrophylla</i>	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	<i>Lauraceae</i>	<i>Licaria</i>	<i>cannella</i>	81	1.79	0.13	3.1	10.7	17.1	.	1.0	26.0	0.39		0.05	0.15
SPD-01	<i>Urticaceae</i>	<i>Cecropia</i>	<i>angustifolia</i>	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	<i>Euphorbiaceae</i>	<i>Hyeronima</i>	<i>moritziana</i>	117	2.42	0.20	10.2	21.7	33.4	.	1.4	25.9	1.07	.	0.07	0.30
SPD-01	<i>Meliaceae</i>	<i>Cabralea</i>	<i>canjerana</i>	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	<i>Urticaceae</i>	<i>Pourouma</i>	<i>bicolor subsp. scobina</i>	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	<i>Flacourtiaceae</i>	<i>sp5(1101KGC)</i>	<i>sp.</i>	93	1.80	0.10	4.5	10.1	15.6	.	0.1	27.5	0.34	.	0.04	0.13
SPD-01	<i>Chrysobalanaceae</i>	<i>Licania</i>	<i>sp.</i>	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	<i>Lauraceae</i>	<i>Endlicheria</i>	<i>sp.</i>	168	.	0.15	1.8	.	9.5	.	0.6	27.7	.	0.01	.	.
SPD-01	<i>Lauraceae</i>	<i>Nectandra</i>	<i>amazonum</i>	147	2.34	0.14	3.4	8.5	15.9	.	0.7	27.9	1.07	.	0.03	0.31
SPD-01	<i>Sapotaceae</i>	<i>Pouteria</i>	<i>sagotiana</i>	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	<i>Phyllanthaceae</i>	<i>Hieronyma</i>	<i>asperifolia</i>	166	2.66	0.22	3.5	26.1	36.3	.	2.2	28.2	0.70	.	0.06	0.18
SPD-01	<i>Hypericaceae</i>	<i>*Vismia</i>	<i>glaziovii</i>	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	<i>Anacardiaceae</i>	<i>*Tapirira</i>	<i>obtusa</i>	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	<i>Sapindaceae</i>	<i>Matayba</i>	<i>guianensis</i>	154	2.64	0.13	.	.	6.1	.	0.3	27.2	1.18	.	.	0.31
TRU-08	<i>Aquifoliaceae</i>	<i>Ilex</i>	<i>rimbachii</i>	194	.	.	7.7	12.2	40.3	70.6	1.2	24.2	0.56	.	.	.
TRU-08	<i>Anacardiaceae</i>	<i>Tapirira</i>	<i>obtusa</i>	140	.	.	11.9	22.3	59.3	106.1	1.0	24.0	0.48	.	.	.
TRU-08	<i>Myrtaceae</i>	<i>Siphoneugena</i>	<i>densiflora</i>	202	.	.	4.9	5.9	13.2	29.8	0.2	23.3	0.71	.	.	.
TRU-08	<i>Rubiaceae</i>	<i>Elaeagia</i>	<i>mariae</i>	138	.	.	10.6	24.1	57.7	112.0	0.7	24.3	0.44	.	.	.
TRU-08	<i>Lauraceae</i>	<i>Nectandra</i>	<i>laurel</i>	183	.	.	12.7	26.0	63.7	119.3	0.3	24.0	0.75	.	.	.
TRU-08	<i>Proteaceae</i>	<i>Panopsis</i>	<i>rubescens var. sprucei</i>	182	.	.	9.3	18.9	42.6	87.5	0.5	24.0	0.50	.	.	.
TRU-08	<i>Alzateaceae</i>	<i>Alzatea</i>	<i>verticillata subsp. vertici</i>	120	.	.	6.8	22.0	55.9	.	2.8	24.4	0.33	.	.	.
TRU-08	<i>Clethraceae</i>	<i>Clethra</i>	<i>fagifolia</i>	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	<i>Myrtaceae</i>	<i>Myrcia</i>	<i>fallax</i>	156	1.42	0.05	2.9	12.7	22.0	.	1.3	25.1	0.39	.	0.07	0.19
TRU-08	<i>Araliaceae</i>	<i>Schefflera</i>	<i>patula</i>	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	<i>Proteaceae</i>	<i>Roupala</i>	<i>monosperma</i>	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	<i>Moraceae</i>	<i>Ficus</i>	<i>americana</i>	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	<i>Lauraceae</i>	<i>Nectandra</i>	<i>cuspidata</i>	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	<i>Annonaceae</i>	<i>Guatteria</i>	<i>terminalis</i>	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	<i>Melastomataceae</i>	<i>Miconia</i>	<i>sp.</i>	136	2.03	0.11	7.6	25.1	52.4	.	1.6	24.9	0.80	.	0.12	0.27
TRU-08	<i>Myrtaceae</i>	<i>Myrcia</i>	<i>mollis</i>	.	2.15	0.11	7.4	18.3	35.8	85.4	1.2	24.6	.	0.03	0.08	0.17
TRU-08	<i>Rosaceae</i>	<i>Prunus</i>	<i>pleiantha</i>	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	<i>Hypericaceae</i>	<i>Vismia</i>	<i>schultesii</i>	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	<i>Euphorbiaceae</i>	<i>Alchornea</i>	<i>anamariae</i>	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	<i>Sapindaceae</i>	<i>Cupania</i>	<i>rubiginosa</i>	134	2.24	0.13	3.5	10.4	29.0	.	2.0	24.3	0.70	.	0.06	0.21
ESP-01	<i>Clethraceae</i>	<i>Clethra</i>	<i>scabra</i>	143	2.35	0.16	6.2	13.3	57.3	85.3	1.0	25.5	.	0.03	0.12	.
ESP-01	<i>Primulaceae</i>	<i>*Myrsine</i>	<i>coriacea</i>	125	2.29	0.20	6.7	20.7	47.7	.	1.2	26.5	.	.	0.11	.
ESP-01	<i>Rosaceae</i>	<i>Prunus</i>	<i>integrifolia</i>	141	2.86	0.25	6.9	12.7	34.4	.	0.8	26.7	.	.	0.06	.
ESP-01	<i>Myricaceae</i>	<i>Morella</i>	<i>pavonis</i>	115	2.29	0.11	8.5	34.9	64.8	144.1	1.8	27.0	.	0.05	0.13	.
ESP-01	<i>Brunelliaceae</i>	<i>Brunellia</i>	<i>cuzcoensis</i>	129	.	.	5.7	13.2	30.6	57.8	1.3	26.4	.	.	.	.
ESP-01	<i>Melastomataceae</i>	<i>Miconia</i>	<i>livida</i>	106	.	.	2.7	10.8	30.2	52.1	1.1	25.9	.	.	.	.
ESP-01	<i>Cunoniaceae</i>	<i>Weinmannia</i>	<i>pubescens</i>	132	1.87	0.15	2.8	20.9	38.8	88.1	1.6	26.6	.	0.04	0.10	.
ESP-01	<i>Primulaceae</i>	<i>*Myrsine</i>	<i>youngii</i>	120	2.27	0.18	6.4	15.4	43.6	32.1	1.5	26.8	.	0.01	0.09	.
ESP-01	<i>Lauraceae</i>	<i>Persea</i>	<i>buchtienii</i>	174	2.74	0.21	6.6	10.5	50.6	73.6	2.3	29.9	.	0.02	0.09	.
ESP-01	<i>Melastomataceae</i>	<i>Miconia</i>	<i>sp</i>	114	1.80	0.17	6.0	26.7	43.4	.	1.2	27.8	.	.	0.11	.
ESP-01	<i>Lauraceae</i>	<i>Cinnamomum</i>	<i>floccosum</i>	215	3.08	0.28	1.9	23.9	44.0	.	2.9	29.7	.	.	0.07	.
ESP-01	<i>Clethraceae</i>	<i>Clethra</i>	<i>sp.</i>	186	2.43	0.17	2.2	11.3	24.6	45.0	1.2	29.0	.	0.01	0.05	.
ESP-01	<i>Icacinaceae</i>	<i>Citronella</i>	<i>sp.</i>	177	3.29	0.21	2.8	8.4	17.3	37.2	0.9	26.6	.	0.01	0.03	.
ESP-01	<i>Melastomataceae</i>	<i>Miconia</i>	<i>theizans</i>	.	.	.	3.0	12.9	22.3	.	0.8	25.6	.	.	.	.
ESP-01	<i>Lauraceae</i>	<i>Ocotea</i>	<i>cernua</i>	110	1.69	0.12	2.6	19.2	46.3	.	2.1	24.5	.	.	0.13	.
WAQ-01	<i>Lauraceae</i>	<i>Ocotea</i>	<i>sp6(1674KGC)</i>	134	2.73	0.28	6.1	6.2	25.6	33.3	1.3	29.1	.	0.01	0.04	.
WAQ-01	<i>Araliaceae</i>	<i>Schefflera</i>	<i>sp.</i>	194	2.70	0.22	11.3	14.2	69.7	79.5	1.1	25.6	.	0.02	0.12	.
WAQ-01	<i>Myrsinaceae</i>	<i>Myrsine</i>	<i>coriacea</i>	141	3.36	0.27	4.0	17.9	21.3	.	0.3	28.5	.	.	0.03	.
WAQ-01	<i>Chloranthaceae</i>	<i>Hedyosmum</i>	<i>maximum</i>	130	2.37	0.20	5.4	12.1	28.0	49.3	1.2	28.3	.	0.02	0.06	.
WAQ-01	<i>Melastomataceae</i>	<i>Axinaea</i>	<i>sp.</i>	77	.	.	5.4	24.1	62.0	.	2.6	25.4	.	0.03	.	.
WAQ-01	<i>Escalloniaceae</i>	<i>Escallonia</i>	<i>paniculata</i>	130	2.58	0.27	10.4	25.9	57.9	119.1	1.4	24.7	.	0.04	0.11	.
WAQ-01	<i>Chletracae</i>	<i>Chletra</i>	<i>cuneata</i>	213	3.10	.	6.8	42.8	84.7	171.2	2.7	27.0	.	0.04	0.13	.
WAQ-01	<i>Lauraceae</i>	<i>Cinnamomum</i>	<i>floccosum</i>	141	2.88	0.30	6.8	17.6	48.6	83.1	1.9	27.3	.	0.02	0.08	.
WAQ-01	<i>Podocarpaceae</i>	<i>Podocarpus</i>	<i>oleifolius</i>	169	2.29	0.22	3.4	13.9	27.0	.	1.1	24.3	.	.	0.06	.
WAQ-01	<i>Melastomataceae</i>	<i>Miconia</i>	<i>coelestis</i>	139	1.90	0.14	3.1	15.1	29.3	57.5	0.4	27.4	.	0.02	0.07	.
WAQ-01	<i>Rubiaceae</i>	<i>Cinchona</i>	<i>officinalis</i>	87	2.30	0.15	5.3	25.2	43.4	.	-0.1	26.9	.	.	0.09	.
WAQ-01	<i>Styracaceae</i>	<i>Styrax</i>	<i>foveolaria</i>	242	3.20	0.23	5.3	17.1	57.6	84.1	1.1	24.8	.	0.02	0.09	.
WAQ-01	<i>Lauraceae</i>	<i>Persea</i>	<i>sp.</i>	147	2.76	0.27	6.0	18.3	46.3	.	1.3	27.0	.	.	0.08	.
TRU-03	<i>Cunoniaceae</i>	<i>Weinmannia</i>	<i>auriculata</i>	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	<i>Cardiopteridaceae</i>	<i>Citronella</i>	<i>incarum</i>	157	.	0.25	8.7	35.2	71.7	169.2	1.8	24.0	.	0.03	.	.
TRU-03	<i>Lauraceae</i>	<i>Persea</i>	<i>corymbosa</i>	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	<i>Primulaceae</i>	<i>Myrsine</i>	<i>sp.</i>	128	2.67	0.23	6.4	28.3	84.0	.	1.3	22.3	0.79	.	0.15	0.20



TRU-03	<i>Araliaceae</i>	<i>Schefflera</i>	<i>allicotantha</i>	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	<i>Aquifoliaceae</i>	<i>Ilex</i>	<i>biserrulata</i>	203	2.51	0.18	4.3	23.9	58.4	.	1.7	23.0	0.35	.	0.11	0.10
TRU-03	<i>Clethraceae</i>	<i>Clethra</i>	<i>cuneata</i>	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	<i>Aquifoliaceae</i>	<i>Ilex</i>	<i>sessiliflora</i>	197	2.15	0.19	9.1	35.6	72.5	.	1.4	22.7	0.36	.	0.16	0.12
TRU-03	<i>Primulaceae</i>	<i>Myrsine</i>	<i>coriacea</i>	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	<i>Clethraceae</i>	<i>Clethra</i>	<i>sp.</i>	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	<i>Pentaphragaceae</i>	<i>Freziera</i>	<i>karsteniana</i>	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	<i>Lauraceae</i>	<i>Persea</i>	<i>buchtienii</i>	146	1.82	0.16	9.1	17.4	37.4	.	0.0	22.4	0.43	.	0.10	0.16
TRU-01	<i>Melastomataceae</i>	<i>Miconia</i>	<i>cf. denticulata</i>	135	2.18	0.18	7.2	23.6	43.8	.	0.7	24.8	1.25	.	0.10	0.39
TRU-01	<i>Primulaceae</i>	<i>Myrsine</i>	<i>andina</i>	120	2.27	0.21	.	.	59.1	.	1.4	24.2	.	.	0.12	.
TRU-01	<i>Melastomataceae</i>	<i>Miconia</i>	<i>setulosa</i>	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	<i>Melastomataceae</i>	<i>Miconia</i>	<i>media</i>	145	2.75	0.20	5.9	26.7	55.4	.	1.8	22.8	.	.	0.10	.
TRU-01	<i>Asteraceae</i>	<i>Senecio</i>	<i>sp</i>	93	2.44	.	10.1	40.6	95.8	.	1.9	22.8	.	.	0.19	.
TRU-01	<i>Symplocaceae</i>	<i>Symplocos</i>	<i>psiloclada</i>	234	2.37	0.16	5.9	20.2	47.6	.	0.8	21.8	0.72	.	0.10	0.21
TRU-01	<i>Melastomataceae</i>	<i>Miconia</i>	<i>atofusca</i>	155	2.93	0.19	10.9	39.9	85.3	.	1.0	22.6	.	.	0.14	.
TRU-01	<i>Clethraceae</i>	* <i>Clethra</i>	<i>cuneata</i>	227	2.74	0.27	10.9	31.0	81.6	156.9	1.1	22.4	.	0.05	0.14	.
TRU-01	<i>Cunoniaceae</i>	<i>Weinmannia</i>	<i>microphylla</i>	75	.	.	4.3	32.0	64.8	.	3.3	23.4	.	.	.	.
TRU-01	<i>Aquifoliaceae</i>	<i>Ilex</i>	<i>sessiliflora</i>	171	.	.	9.5	30.4	71.1	.	1.1	23.5	0.74	.	.	.
TRU-01	<i>Symplocaceae</i>	<i>Symplocos</i>	<i>quitensis</i>	174	.	.	11.6	33.2	62.5	.	0.5	22.5	0.78	.	.	.
TRU-01	<i>Lauraceae</i>	<i>Persea</i>	<i>ferruginea</i>	.	.	.	7.9	22.0	51.7	.	0.7	23.3	.	.	.	.
TRU-01	<i>Melastomataceae</i>	<i>Miconia</i>	<i>sp.</i>	128	.	.	3.9	15.0	48.0	95.6	0.9	22.0	.	.	.	.
TRU-01	<i>Brunelliaceae</i>	* <i>Brunellia</i>	<i>inermis</i>	122	.	.	4.3	14.1	26.8	.	1.1	21.8	0.68	.	.	.

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

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

\*\* Correlation is significant at  $p < 0.01$

\* Correlation is significant at  $p < 0.05$

**Table S3: Standardized major axis regression slopes and their confidence intervals for log-log transformed relationships comparing leaf traits of lowland (~173 species) and upland (~120 species) species, depicted in Figures 2, 4 and 5 in the main text.** Analysis undertaken using individual replicates. Coefficients of determination ( $r^2$ ) and significance values ( $p$ ) of each bivariate relationship are shown. Significantly different  $p$  values are shown in bold. 95% confidence intervals (CI) of SMA slopes and  $y$ -axis intercepts are shown in parentheses. Where SMA tests for common slopes revealed no significant differences between the two groups (i.e.  $p > 0.05$ ), common slopes were used (with CI of the common slopes provided). Where there was a significant difference in the elevation (i.e.  $y$ -axis intercept) of the common-slope SMA regressions, values for the  $y$ -axis intercept are provided. Where appropriate, significant shifts along a common slope are indicated.

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

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

Abbreviations:  $A_{400,a}$  light-saturated net photosynthesis measured under 400  $\mu\text{mol mol}^{-1}$  atmospheric  $[\text{CO}_2]$ ;  $C_{i400}$ , intercellular  $\text{CO}_2$  partial pressure at 400  $\mu\text{mol mol}^{-1}$  atmospheric  $[\text{CO}_2]$ ;  $C_{a400}$ , atmospheric  $\text{CO}_2$  partial pressure at 400  $\mu\text{mol mol}^{-1}$  atmospheric  $[\text{CO}_2]$ ;  $C_{i400} : C_{a400}$ , ratio of intercellular to atmospheric  $\text{CO}_2$  at 400  $\mu\text{mol mol}^{-1}$   $[\text{CO}_2]$ ;  $A_{400:N}$ , ratio of light-saturated net photosynthesis measured under 400  $\mu\text{mol mol}^{-1}$  atmospheric  $[\text{CO}_2]$  over leaf N;  $A_{2000,a}$ , light-saturated net photosynthesis measured under 2000  $\mu\text{mol mol}^{-1}$  atmospheric  $[\text{CO}_2]$ ;  $C_{i2000}$ , intercellular  $\text{CO}_2$  at 2000  $\mu\text{mol mol}^{-1}$  atmospheric  $[\text{CO}_2]$ ;  $A_{2000:N}$ , ratio of light-saturated net photosynthesis measured under 2000  $\mu\text{mol mol}^{-1}$  atmospheric  $[\text{CO}_2]$  over leaf N;  $R_d$ , leaf dark respiration measured at 400  $\mu\text{mol mol}^{-1}$  atmospheric  $[\text{CO}_2]$ ; Leaf  $T$ , leaf temperature inside gas exchange cuvette; Chl, chlorophyll a and b content.

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

**Table S5: Standardized major axis regression slopes and their confidence intervals for relationships comparing leaf traits of lowland (~126 species) and upland (~40 species) species, depicted in Figures 7 and S2 in the main text.** Analysis undertaken using individual replicates. Coefficients of determination ( $r^2$ ) and significance values ( $p$ ) of each bivariate relationship are shown. Significantly different  $p$  values are shown in bold. 95% confidence intervals (CI) of SMA slopes and  $y$ -axis intercepts are shown in parentheses. Where SMA tests for common slopes revealed no significant differences between the two groups (i.e.  $p > 0.05$ ), common slopes were used (with CI of the common slopes provided). Where there was a significant difference in the elevation (i.e.  $y$ -axis intercept) of the common-slope SMA regressions, values for the  $y$ -axis intercept are provided. Where appropriate, significant shifts along a common slope are indicated.

Bivariate relationship (y- vs. x-axis)	Group	$r^2$	$p$	Slope	Slope CI	Intercept	$p$	Common slope	Common slope CI	$p$	Common slope y-axis intercept	Shift along a common slope?
$n_P$ vs. $M_a$	Lowland	0.012	0.258	-0.2421	(-0.292, -0.201)	57.02	0.072	-0.2172	(-0.187, -0.253)	0.698	53.600	No, $p = 0.185$
	Upland	0.002	0.719	-0.1797	(-0.231, -0.134)	47.64					52.945	
$n_R$ vs. $M_a$	Lowland	0.042	<b>0.011</b>	-0.1217	(-0.143, -0.104)	24.841	0.482	-0.1176	(-0.104, -0.133)	<0.001	24.303	No, $p = 0.794$
	Upland	0.001	0.809	0.1110	(0.090, 0.137)	-5.861					27.171	
$n_E$ vs. $M_a$	Lowland	0.023	0.087	-0.0279	(-0.033, -0.023)	6.362	0.249	-0.0296	(-0.026, -0.034)	<0.001	6.579	No, $p = 0.227$
	Upland	0.001	0.870	-0.0339	(-0.045, -0.026)	8.240					7.605	
$n_P$ vs. $N_a$	Lowland	0.358	<b>&lt;0.001</b>	-16.52	(-19.23, -14.18)	55.21	0.711	-16.76	(-14.73, -19.08)	0.017	55.676	Yes, $p < 0.001$
	Upland	0.001	0.773	-17.43	(-22.36, -13.59)	60.53					59.063	
$n_R$ vs. $N_a$	Lowland	0.171	<b>&lt;0.001</b>	-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	<b>0.003</b>	-9.725	(-11.842, -7.987)	32.64					29.802	
$n_E$ vs. $N_a$	Lowland	0.382	<b>&lt;0.001</b>	-1.732	(-1.992, -1.506)	6.156	0.001					
	Upland	0.165	<b>0.002</b>	-3.039	(-3.889, -2.374)	10.278						
$n_P$ vs. $P_a$	Lowland	0.154	<b>&lt;0.001</b>	-225.4	(-268.6, -189.2)	42.22	0.002					
	Upland	0.028	0.186	-129.5	(-165.9, -101.1)	43.04						
$n_R$ vs. $P_a$	Lowland	0.013	0.175	-90.48	(-106.4, -76.96)	17.23	0.167	-84.48	(-74.36, -96.08)	<0.001	16.677	Yes, $p < 0.001$
	Upland	0.030	0.106	-75.48	(92.97, -61.28)	23.26					24.851	
$n_E$ vs. $P_a$	Lowland	0.050	<b>0.013</b>	-19.99	(-23.79, -16.80)	4.635	0.568	-20.60	-17.84 -23.75	<0.001	4.692	Yes, $p = 0.001$
	Upland	0.155	<b>0.003</b>	-21.89	(-28.19, -16.99)	7.047					6.824	
$n_A$ vs. $M_a$ (log-transformed)	Lowland	0.070	<b>0.003</b>	-1.2405	(-1.471, -1.046)	2.143	0.085	-1.152	(-0.992, -1.345)	0.025	1.958	No, $p = 0.742$
	Upland	0.002	0.794	-0.8934	(-1.233, -0.647)	1.475					2.026	
$n_A$ vs. $N_a$ (log-transformed)	Lowland	0.445	<b>&lt;0.001</b>	-1.078	(-1.231, -0.945)	-0.159	0.099	-1.129	(-0.999, -1.273)	<0.001	-0.145	No, $p = 0.189$
	Upland	0.156	<b>0.011</b>	-1.403	(-1.881, -1.046)	0.037					-0.054	
$n_A$ vs. $P_a$ (log-transformed)	Lowland	0.056	<b>0.008</b>	-0.556	(-0.661, -0.468)	-1.065	0.446	-0.576	(-0.495, -0.670)	<0.001	-1.086	Yes, $p < 0.001$
	Upland	0.100	<b>0.047</b>	-0.640	(-0.869, -0.471)	-0.957					-0.904	

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

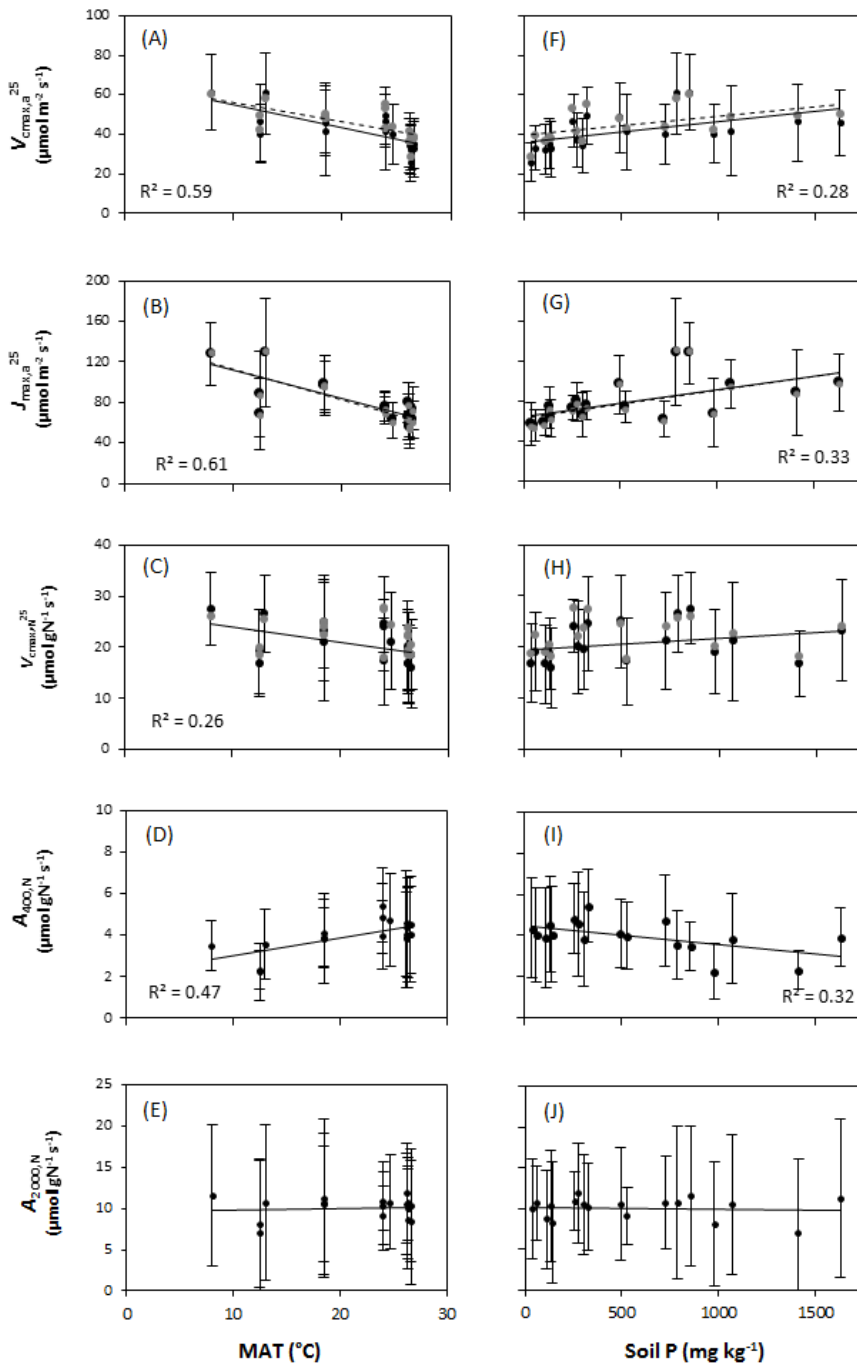
Model	Fixed component	DF	AIC	BIC	-2LL
<b><math>V_{\text{cmax},a}^{25}</math></b>					
1	log10(Soil P) + $N_a$ + Site. $N_a$ + $P_a$ + Site. $P_a$ + $N_a.P_a$	9	1663.5	1693.1	-822.7
2	log10(Soil P) + $N_a$ + Site. $N_a$ + $P_a$ + Site. $P_a$ + log10(Soil P). $N_a$	9	1664.0	1693.7	-823.0
3	log10(Soil P)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

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

**Table S7: Comparison of mean values of  $V_{\text{cmax}}$  and  $J_{\text{max}}$  at 25°C values ( $V_{\text{cmax}25}$  and  $J_{\text{max}25}$ , respectively) in upland and lowland plants calculated using different activation energies ( $E_a$ ) for each parameter (i.e.  $V_{\text{cmax}}$  and  $J_{\text{max}}$ ), and  $K_c$  and  $K_o$  constants when calculating  $V_{\text{cmax}}$ .** Here, we compare values calculated using  $E_a$  values reported by Farquhar *et al.* (1980) and Bernacchi *et al.* (2002). For Farquhar *et al.* (1980),  $E_a$  values of  $K_c$  and  $K_o$  used were 59.4 and 36.0 kJ mol<sup>-1</sup>, respectively. For Bernacchi *et al.* (2002), the  $E_a$  values of  $K_c$  and  $K_o$  were 80.99 and 23.72 kJ mol<sup>-1</sup>. For calculations made using Farquhar *et al.* (1980), we used  $E_a$  values for  $V_{\text{cmax}}$  and  $J_{\text{max}}$  of 64.8 and 37.0 kJ mol<sup>-1</sup>, respectively; for Bernacchi *et al.* (2002), the  $E_a$  values for  $V_{\text{cmax}}$  and  $J_{\text{max}}$  were 65.3 and 43.9 kJ mol<sup>-1</sup>, 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 constants		$V_{\text{cmax},a}^{25}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	$J_{\text{max},a}^{25}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )
Farquhar et al. (1980)	Lowland species	35.9 $\pm$ 14.6 <sup>a</sup>	66.7 $\pm$ 18.6 <sup>a</sup>
	Upland species	48.8 $\pm$ 20.0 <sup>b</sup>	96.9 $\pm$ 36.9 <sup>b</sup>
Bernacchi et al. (2002)	Lowland species	39.7 $\pm$ 15.6 <sup>a</sup>	64.7 $\pm$ 18.6 <sup>a</sup>
	Upland species	50.5 $\pm$ 18.5 <sup>b</sup>	96.6 $\pm$ 37.3 <sup>b</sup>

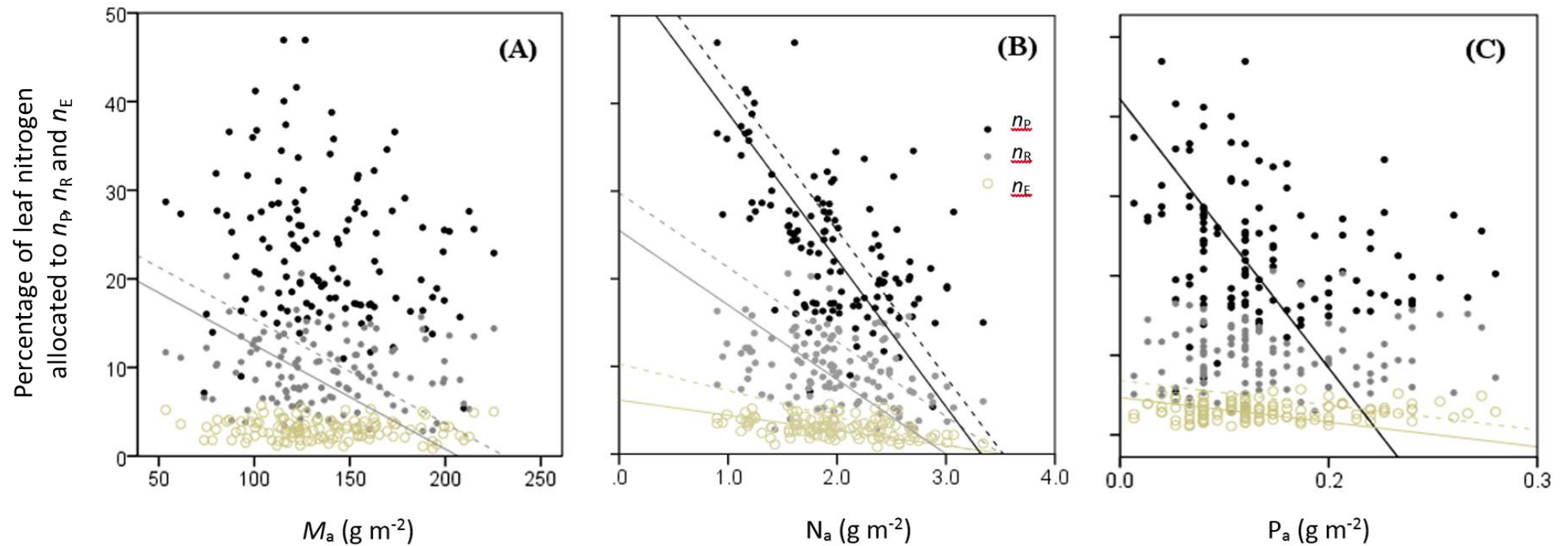
**Figure S1: Plots of maximum carboxylation velocity of Rubisco normalised to 25°C,  $V_{\text{cmax},a}^{25}$  against (A) mean annual temperature (MAT) and (F) soil P concentration; maximum rate of electron transport normalised to 25°C,  $J_{\text{max},a}^{25}$  against (B) MAT and (G) soil P; ratio of  $V_{\text{cmax},a}^{25}$  over leaf N,  $V_{\text{cmax},N}^{25}$  against (C) MAT and (H) soil P; ratio of light-saturated net photosynthesis measured at 400  $\mu\text{mol mol}^{-1}$  atmospheric  $[\text{CO}_2]$  over leaf N,  $A_{400:N}$  against (D) MAT and (I) soil P; and ratio of light-saturated net photosynthesis measured at 2000  $\mu\text{mol mol}^{-1}$  atmospheric  $[\text{CO}_2]$  over leaf N,  $A_{2000:N}$  against (E) MAT and (J) soil P for each site. In (A)-(H), black circles (and solid regression lines) represent photosynthetic parameters calculated using constants of Farquhar *et al.* (1980) and grey circles (and dashed regression lines) represent parameters calculated using Bernacchi *et al.* constants (2002).  $R^2$  values shown are for Farquhar *et al.* (1980) only regressions. Environmental parameters at each site were obtained using site information from Quesada (*et al.* 2010; pers. comm. 2014) and Asner *et al.* (2014a).**



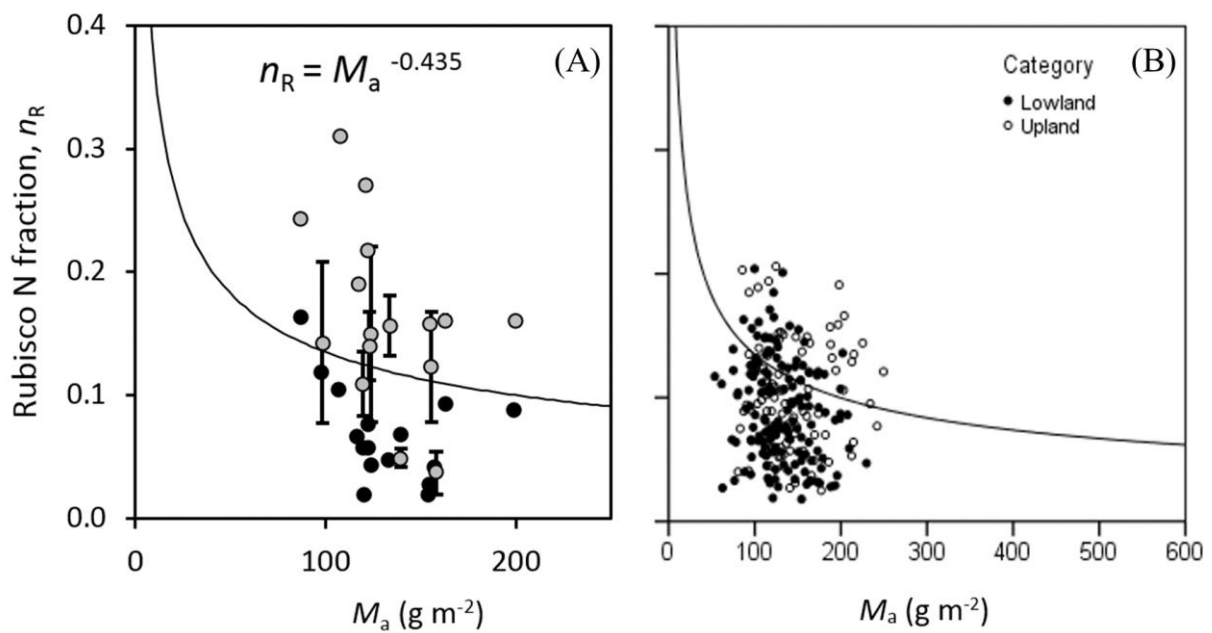


**Figure S2: Plots of % of leaf N to pigment-protein complexes,  $n_P$ , % of leaf N to Rubisco,  $n_R$ , and % of leaf N to electron transport,  $n_E$ , in relation to (A) leaf mass per unit leaf area,  $M_a$ , (B) leaf N-area,  $N_a$ , and (C) leaf P-area,  $P_a$ .** Data points represent individual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

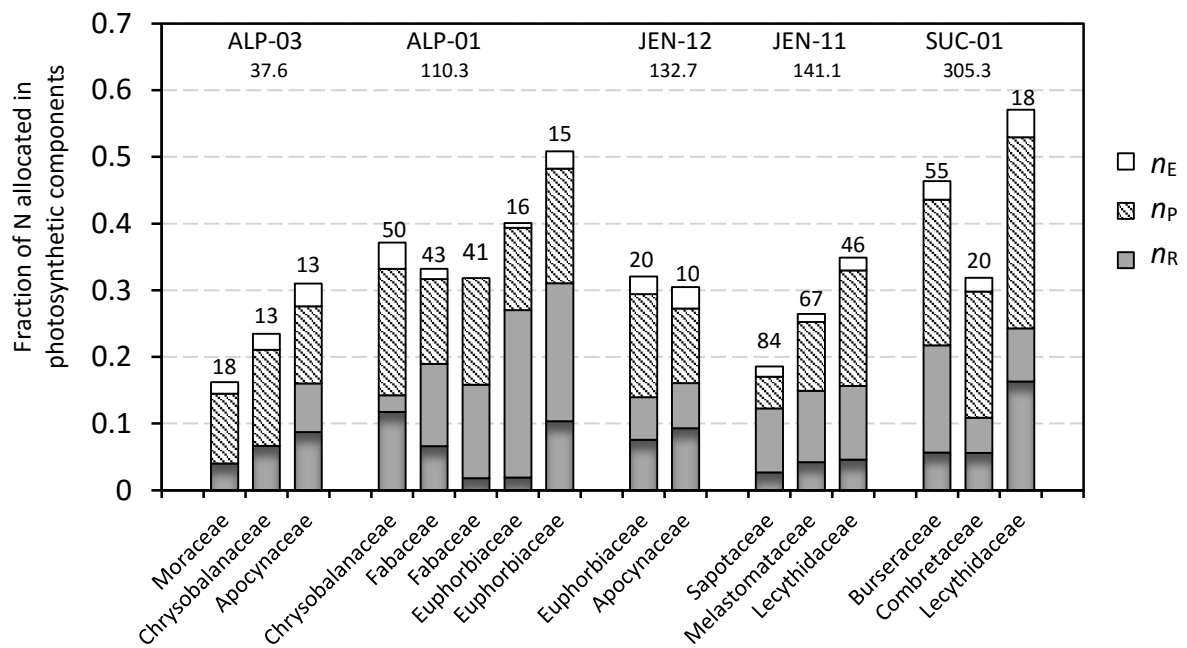
SMA regressions: solid line, lowland species; dashed line, upland species. SMA regressions are given only when the relationships are significant ( $p < 0.05$ ) and when lowland and upland shared similar slopes, refer to Table S5. Analyses were performed on percentage instead of fraction of N to meet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



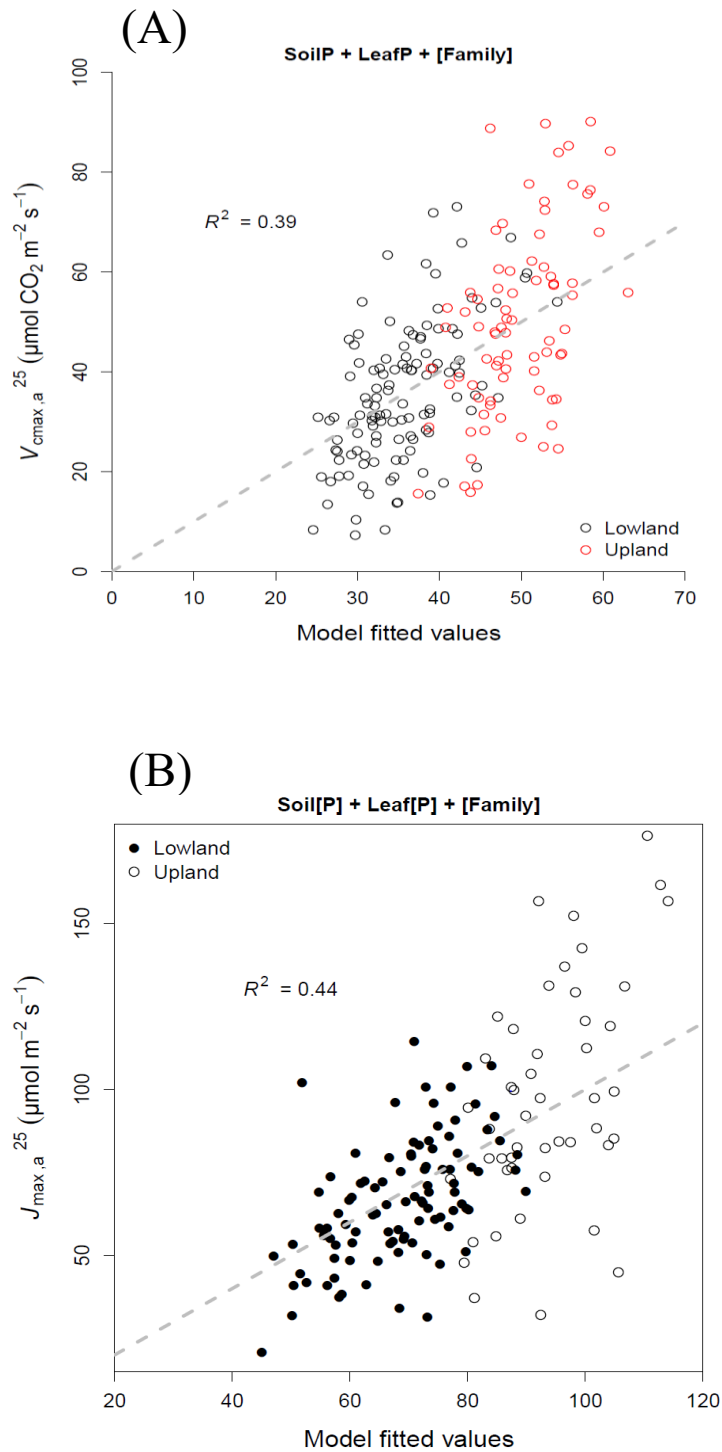
**Figure S3: Plots of fraction of leaf N allocated in Rubisco,  $n_R$  in relation to leaf mass per unit leaf area,  $M_a$ , for (A) 16 lowland species for where both *in vivo* and *in vitro* estimates were available; and (B) 150 lowland and 92 upland species for where *in vivo* data was available. Black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



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



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



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