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► To cite this version:

Cécile Auréle Julie Girardin, Yadvinder Malhi, Luiz Aragao, Marlene Mamani, Walter Huaraca Huasco, et al.. Net primary productivity allocation and cycling of carbon along a tropical forest elevational transect in the Peruvian Andes.. *Global Change Biology*, Wiley, 2010, A (A), pp.3176. 10.1111/j.1365-2486.2010.02235.x . hal-00552620

HAL Id: hal-00552620

<https://hal.archives-ouvertes.fr/hal-00552620>

Submitted on 6 Jan 2011

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**Net primary productivity allocation and cycling of carbon
along a tropical forest elevational transect in the Peruvian
Andes.**

Journal:	<i>Global Change Biology</i>
Manuscript ID:	GCB-09-0936.R1
Wiley - Manuscript type:	Primary Research Articles
Date Submitted by the Author:	11-Feb-2010
Complete List of Authors:	Girardin, Cécile; Oxford University, School of Geography and the Environment; Oxford University, Wolfson College Malhi, Yadvinder; Oxford University, Environmental Change Institute Aragao, Luiz; University of Exeter, School of Geography Mamani, Marlene; Universidad San Antonio Abad, Department of Biology Huaraca Huasco, Walter; Universidad San Antonio Abad, Department of Biology Durand, Liliana; Universidad San Antonio Abad, Department of Biology
Keywords:	carbon, tropical montane forests, ecophysiology, net primary productivity, carbon stocks, residence time, soil water content , temperature
Abstract:	The net primary productivity, carbon stocks and turnover rates (i.e. carbon dynamics) of tropical forests are an important aspect of the global carbon cycle. These variables have been investigated in lowland tropical forests, but they have rarely been studied in tropical montane forests. This study examines spatial patterns of above- and below-ground carbon dynamics along a transect ranging from lowland Amazonia to the high Andes in S.E. Peru. Fine root biomass values increased from 1.50 Mg C ha ⁻¹ at 194m to 4.95±0.62 Mg C ha ⁻¹ at 3020 m, reaching a maximum of 6.83±1.13 Mg C ha ⁻¹ at the 2020 m elevation site. Above-ground biomass values decreased from 123.50 Mg C ha ⁻¹ at 194 m to 47.03 Mg C ha ⁻¹ at 3020 m. Mean annual below-ground productivity was highest in the most fertile lowland plots (7.40±1.00 Mg C ha ⁻¹ yr ⁻¹) and ranged between 3.43±0.73 Mg C ha ⁻¹ yr ⁻¹ and 1.48±0.40 Mg C ha ⁻¹ yr ⁻¹ in the pre-montane and montane plots. Mean annual above-ground productivity was estimated to vary between 9.50±1.08 Mg C ha ⁻¹ yr ⁻¹ (210 m) and

	<p>2.59±0.40 Mg C ha⁻¹ yr⁻¹ (2020 m), with consistently lower values observed in the cloud immersion zone of the montane forest. Fine root carbon residence time increased from 0.31 years in lowland Amazonia to 3.78±0.81 years at 3020 m and stem carbon residence time remained constant along the elevational transect, with a mean of 54±4 years. The ratio of fine root biomass to stem biomass increased significantly with increasing elevation, whereas the allocation of net primary productivity above- and below-ground remained approximately constant at all elevations. Although net primary productivity declined in the tropical montane forest, the partitioning of productivity between the ecosystem sub-components remained the same in lowland, pre-montane and montane forests.</p>



For Review Only

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1 **Title:** Net primary productivity allocation and cycling of carbon along a tropical
2 forest elevational transect in the Peruvian Andes.

3 **Running title:** Net primary productivity from Andes to Amazon.

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16 **Keywords:** Carbon, tropical montane forests, ecophysiology, net primary
17 productivity, carbon stocks, residence time, soil water content, temperature,
18 elevational gradient, Andes, Amazon basin.

19 20 **Abstract**

21 The net primary productivity, carbon stocks and turnover rates (*i.e.* carbon dynamics)
22 of tropical forests are an important aspect of the global carbon cycle. These variables
23 have been investigated in lowland tropical forests, but they have rarely been studied in

¹ **Author contribution statement:** Experimental design: C.A.J.G., Y.M., L.E.O.C.A., N.S., M.S., data gathering: C.A.J.G., W.H.H., M.M., L.D., J.R., J.E.S., analysis: C.A.J.G., K.F., J.R., interpretation of results: C.A.J.G., Y.M., D.J.M., L.E.O.C.A; paper writing: C.A.J.G.

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3 24 tropical montane forests. This study examines spatial patterns of above- and below-
4
5 25 ground carbon dynamics along a transect ranging from lowland Amazonia to the high
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8 26 Andes in S.E. Peru. Fine root biomass values increased from 1.50 Mg C ha⁻¹ at 194m
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10 27 to 4.95±0.62 Mg C ha⁻¹ at 3020 m, reaching a maximum of 6.83±1.13 Mg C ha⁻¹ at
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12 28 the 2020 m elevation site. Above-ground biomass values decreased from 123.50 Mg
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17 30 productivity was highest in the most fertile lowland plots (7.40±1.00 Mg C ha⁻¹ yr⁻¹)
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19 31 and ranged between 3.43±0.73 Mg C ha⁻¹ yr⁻¹ and 1.48±0.40 Mg C ha⁻¹ yr⁻¹ in the pre-
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21 32 montane and montane plots. Mean annual above-ground productivity was estimated to
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23 33 vary between 9.50±1.08 Mg C ha⁻¹ yr⁻¹ (210 m) and 2.59±0.40 Mg C ha⁻¹ yr⁻¹ (2020
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25 34 m), with consistently lower values observed in the cloud immersion zone of the
26
27 35 montane forest. Fine root carbon residence time increased from 0.31 years in lowland
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29 36 Amazonia to 3.78±0.81 years at 3020 m and stem carbon residence time remained
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31 37 constant along the elevational transect, with a mean of 54±4 years. The ratio of fine
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33 38 root biomass to stem biomass increased significantly with increasing elevation,
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35 39 whereas the allocation of net primary productivity above- and below-ground remained
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37 40 approximately constant at all elevations. Although net primary productivity declined
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39 41 in the tropical montane forest, the partitioning of productivity between the ecosystem
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41 42 sub-components remained the same in lowland, pre-montane and montane forests.
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52 44 Introduction

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55 45 The important role of the Amazonian lowland forest in global biogeochemical cycles,
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57 46 and in particular the global carbon cycle, is widely recognised (IPCC, 2007).
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59 47 However, the carbon cycle of tropical montane forests (TMFs) is only starting to be
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3 48 explored. In the Amazon basin, the montane forests of the Andes extend from the
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5 49 lowlands up to 3000 – 4000 m a.s.l. In addition to their intrinsic interest, studies of the
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8 50 ecosystem functioning of montane forests provide an opportunity to explore how
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10 51 environmental variables (particularly temperature and soil moisture) affect ecosystem
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12 52 functions, whilst keeping seasonal factors constant. In particular, there is no dormant
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15 53 winter or drought season that complicates interpretation of latitudinal gradients. In
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17 54 this paper, we explore the production, allocation, and turnover of carbon along an
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20 55 elevation gradient in the Peruvian Amazon and Andes.
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22 56
23
24 57 A number of studies have reported on variation of above-ground biomass with
25
26 58 elevation in TMFs in Borneo, Ecuador, Puerto Rico, Venezuela, New Guinea, Panama
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28 59 and Hawaii (Kitayama *et al.*, 1994, Delaney *et al.*, 1997, Leuschner *et al.*, 2007).
29
30 60 These consistently report a decline in above-ground biomass with increasing elevation
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32 61 as a key characteristic of TMFs. There have been far fewer studies of below-ground
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34 62 biomass. Observations of fine root carbon stocks in Southern Ecuador and in Borneo
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36 63 show an increase in fine root carbon stocks with increasing elevation (Kitayama *et al.*,
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38 64 2002, Leuschner *et al.*, 2007). Based on these previous findings, we would expect to
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40 65 observe a shift in the partitioning of carbon standing stocks from above- to below-
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42 66 ground as elevation increases.
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50 68 Net primary productivity (NPP) is defined as the amount of carbon incorporated into
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52 69 new organic matter produced by a plant of ecosystem in a specified time interval. The
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54 70 components of NPP include the production of stems, branches, leaves, flowers, fruit,
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56 71 coarse and fine roots, volatile organic compounds, and root exudates. Although there
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58 72 is a long record of tropical forest above-ground net primary productivity (NPP_{AG})
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3 73 measurement studies in the ecological literature, only a handful of studies focus on
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5 74 TMFs (reviewed in Clark *et al.*, 2001). Studies in the Jamaican Blue Mountain, the
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8 75 Luquillo Mountains in Puerto Rico, Mount Kinabalu in Borneo, and the Ecuadorian
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10 76 Andes consistently reported a decline in NPP_{AG} with increasing elevation. Whereas its
11
12 77 cause is still poorly understood, this is reported as one of the most fundamental
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14 78 features of tropical montane forests. The quantification of below ground net primary
15
16 79 productivity (NPP_{BG}) is still in its early years and our understanding of total
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18 80 ecosystem-level productivity is very limited. To date, only one study in South
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20 81 Ecuadorian montane forests published NPP_{BG} estimates along an elevational transect
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22 82 (Roderstein *et al.*, 2005) but did not report parallel measurements of NPP_{AG} (see,
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24 83 however, new results reported by Moser *et al.*, this volume). The study found that fine
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26 84 root production, $NPP_{FineRoot}$, increases with increasing elevation.
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34 86 The mean residence time of carbon in biomass can be estimated by dividing each
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36 87 carbon pool's standing stocks by the NPP of that pool. Only a few studies have
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38 88 estimated stem carbon turnover rates or residence times in tropical forests (Malhi *et*
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40 89 *al.*, 1999, 2006); none of these were carried out on TMFs. Similarly, very few studies
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42 90 have been conducted on carbon turnover rates of fine roots in tropical forests (Cuevas
43
44 91 *et al.*, 1988, Herbert *et al.*, 1999, Ostertag, 2001), with only one study of an
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46 92 elevational transect (Graefe *et al.*, 2008).
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51 93
52
53 94 Raich *et al.* (1997) measured above-ground productivity and soil respiration in three
54
55 95 Hawaiian rainforests, but to date there have been no complete analyses of NPP and its
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57 96 allocation along a tropical elevation transect. Here, we present the first reported
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59 97 analysis of total directly measured NPP and its allocation along a large vertical
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3 98 gradient in the tropics. We also describe changes in total biomass and its distribution
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5 99 between above-ground and below-ground components in nine tropical forests sites
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8 100 along an elevational transect in the Peruvian Andes. In addition, we provide an
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10 101 examination of overall changes in ecosystem carbon dynamics across the elevational
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12 102 transect. To this end, we analyse standing stocks, production rates, and residence
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14 103 time of above-ground (stems, canopy) and below-ground (roots) vegetation
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16 104 components. Specifically, we test the following hypotheses:

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20 105 (1) There is no change in total C stocks with elevation, but there is a shift in relative
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22 106 stock of carbon from above- to below-ground (Leuschner *et al.*, 2007).

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25 107 (2) Total NPP declines with elevation, but the proportion of NPP allocated to above-
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27 108 and below-ground components stays fixed along the elevation gradient.

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30 109 (3) The NPP allocation patterns on the elevation transect are the same as those
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32 110 observed for lowland Amazonian forests (Aragão *et al.*, 2009, Malhi *et al.*, 2009).

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34 111 (4) NPP decline can largely be explained by decreasing temperature as elevation
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36 112 increases.

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40 41 114 **Materials and Methods**

42 43 44 45 115 ***Site characteristics***

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48 116 The study region is the focus of the interdisciplinary Andes Biodiversity and
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50 117 Ecosystem Research Group (ABERG, darwin.winston.wfu.edu/andes/). Nine
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52 118 permanent tree sampling plots of 1 ha each were established along an elevational
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54 119 gradient ranging from 194 m to 3025 m elevation, extending from lowland forest (<
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56 120 800 m), through pre-montane (800 - 1200 m), lower montane (1200 - 2200 m) and
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59 121 upper montane forest (2200 - 3400 m). Of these, six experimental sites were

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3 122 established at elevations from 3020 m to 1500 m on the eastern slope of the Andes, in
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5 123 the Kosñipata valley, Province of Paucartambo, Department of Cusco, Southern
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8 124 Peruvian Andes. One site was established at 1000 m in an adjacent valley (Tono
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10 125 valley). A further two lowland Amazonian sites were established and monitored
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12 126 according to the same protocol in the Tambopata reserve, Tambopata Province,
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14 127 Department of Madre de Dios, Peru, approximately 244 km east of the main transect.
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16 128 Data from these two lowland sites were published in Aragão *et al.* (2009). Site
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18 129 descriptions are provided in Table 1. The transect ranging from the high Andes to
19
20 130 lowland Amazonian sites (nine plots in total) is hereafter referred to as the Kosñipata
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22 131 transect. Plots established from 1855 m to 3020 m are located on a ridge adjacent to
23
24 132 an ancient Inca path referred to as the Trocha Union. As the path is fairly inaccessible
25
26 133 and carved on difficult terrain, it is rarely used. As the geological substrate and
27
28 134 topographic position can have a significant bearing on montane forest dynamics
29
30 135 (Takyu *et al.*, 2002), all the montane plots along the Trocha Union were established
31
32 136 along a ridge-top with the same substrate (Palaeozoic shales-slates), with the
33
34 137 exception of the 1855 m plot (situated on a granite batholith). Plots at 1000 m and
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36 138 below are situated on clay rich sediments formed from alluvial deposition (though all
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38 139 are now above river flood levels). All plots along the elevational transect were
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40 140 selected in areas with relatively homogeneous stand structure, geological substrate
41
42 141 and topography, and with no sign of significant recent human influence. All have
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44 142 closed canopies without any large gaps. Soil C, nitrogen and phosphorus stocks in the
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46 143 top 50 cm are highest in the 2000 - 3025 m band, where there is a build-up of a thick
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48 144 layer of humic material (typically 20 - 30 cm thick) above carbon- rich topsoil (C.A.J.
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50 145 Girardin, submitted). The base of the cloud zone is located at 1500 - 1800 m, and the
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3 146 cloud forest zone extends to the tree line at approximately 3400 m, above which *puna*
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5 147 grasslands dominate.
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9 148 *Weather*

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11 149 Weather patterns along the elevational gradient are described in a companion paper in
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13 150 this issue (C.A.J. Girardin *et al.*, submitted). Mean annual air temperatures over the
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15 151 study period ranged from 26.4 °C (194 m) to 11.8 °C (3000 m). There was a close
16
17 152 association between elevation and temperature ($r^2=0.99$, $P<10^{-4}$), implying a vertical
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19 153 lapse rate of soil temperature of 4.79 °C km⁻¹, and a lapse rate of air temperature of
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21 154 4.94 °C km⁻¹. Over the measurement period (Aug 2007 – Aug 2008), precipitation
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23 155 showed a humped relationship with elevation, with our recorded highest values (3086
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25 156 - 2746 mm yr⁻¹) near the base of the mountain range (1000 - 1500 m). Light incidence
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27 157 and soil water content (SWC) showed no clear relationships with elevation. There
28
29 158 may be microsite effects along the elevational gradient, which reflect the
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31 159 geomorphological situation rather than the influence of elevation per se (Moser *et al.*,
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33 160 2008). This is illustrated by the variation of rainfall patterns between the two forest
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35 161 sites under investigation at 3000 m: the plot located on a slope (3025 m) was, on
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37 162 average, drier and received higher annual light incidence than that located on the
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39 163 Trocha Union ridge (3020 m). Nonetheless, within the cloud immersion zone, SWC is
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41 164 typically above 25% throughout the year, because of limited evapotranspiration and
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43 165 fog deposition
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55 167 *Above-ground carbon stocks and fluxes*

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58 168 We determined wood productivity using multiple censuses of the forest plots. Tree
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60 169 censuses were carried out in our plots in 2003 and 2007 to determine the growth rate

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3 170 of existing surviving trees and the rate of recruitment of new trees. Mortality was
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5 171 estimated for each site by calculating the biomass of trees that were measured in 2003
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8 172 and dead in 2007. Only trees >10cm diameter at breast height (dbh) were included in
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10 173 the census. These measurements were subsequently converted into estimates of coarse
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12 174 wood productivity using allometric equations for moist forest stands that relate tree
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14 175 diameter to biomass (Chave *et al.*, 2005). Two equations were explored in order to
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16 176 determine the importance of including tree height in biomass estimates of montane
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18 177 forest trees:
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24 179 $AGB=0.0776*(\rho * (DBH^2) * H)^{0.94}$ (1)
25
26

27 180 $AGB=\rho * \exp(-1.499+2.1481*\ln(DBH) +0.207*(\ln(DBH))^2 -0.0281*(\ln(DBH))^3)$ (2)
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30 181
31 182 Where AGB is above-ground biomass in kg m⁻², ρ is density of the wood obtained
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33 183 from (Chave *et al.*, 2006), DBH is diameter at breast height in cm, and H is height in
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35 184 m. Both were derived from the same pan-tropical dataset, however (2) only
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37 185 incorporates diameter information and so is applicable for data sets where height
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39 186 information is not available. As we had some height data from each plot, equation (1)
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41 187 was used for the subsequent analysis. It includes census data on diameter at breast
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43 188 height, a single measurement of tree height and species specific values for wood
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45 189 density. Tree height was available for approximately 125 trees in each plot. Where
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47 190 tree height was not available for particular trees, it was estimated by fitting an
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49 191 exponential model to existing height and diameter at breast height data for trees at that
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51 192 elevation. To convert biomass values into carbon, we assumed that dry stem biomass
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53 193 is 50% C (Chave *et al.*, 2005).
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4 195 We calculated annual above-ground woody biomass productivity, NPP_{Stem} , from full
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6 196 plot census data from 2003 and 2007. This was calculated using the allometric
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8 197 equations of Chave et al (2005), including estimates for height, as described above.

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10 198 The biomass of new recruits measured at the second census was then added.

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13 199
14 200 To determine seasonal variation in NPP_{Stem} , we employed three-monthly dendrometer
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16 201 band measurements on approximately 200 randomly selected trees per plot from
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18 202 August 2007 to January 2009. Dendrometer measurements were converted into three-
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20 203 month biomass increments for each tree. To scale from the dendrometer trees to the
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22 204 full plot, we grouped the tree species by genus. From the full census data we
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24 205 determined the annual NPP of each genus g , and what fraction of the annual NPP of
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26 206 each genus was captured by dendrometers, f_g . The three-monthly whole-plot NPP of
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28 207 each genus was then estimated by dividing the dendrometer-measured three-month
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30 208 NPP of that genus by f_g . These whole plot estimates of NPP for each genus were then
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32 209 summed over genus to obtain a total plot NPP.
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40 211 Given that some species of tree ferns and palms can grow vertically without
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42 212 increasing in girth, hence measuring their increase in diameter at breast height over
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44 213 time is futile, we included tree ferns and palms as recruits in our NPP estimates and in
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46 214 our stem biomass estimates, as described in Malhi *et al.* (2004), but did not estimate
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48 215 growth rates over time. The proportion of tree ferns in the plots ranged from 2.5%
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50 216 (1000 m and 3020 m) to 21% (2020 m), peaking between 1855 m and 2720 m. Palm
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52 217 proportion varied from 0% (3100 m) up to 27% one plot in the Tambopata lowlands.
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55 218 There were no tree ferns at the lowland sites, and no palms above 1500 m elevation
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3 220 Canopy productivity was estimated by collecting litterfall in 0.25 m² litter traps (PVC
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5 221 tubes and 1 mm mesh nylon screen, 25 per hectare) set up 1 m above the ground.
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7 222 Litterfall was collected bi-weekly to minimise loss by decomposition, split into
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9 223 different components, oven dried at 80 °C and weighed. Components of litterfall
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11 224 include leaves; reproductive organs (fruits and flowers); twigs (up to 2 cm girth,
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13 225 including bark); epiphytes and bromeliads (all parts combined); and fine debris
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15 226 (unidentifiable particles that pass through 2 mm mesh). In the present analysis, we
16
17 227 refer to the sum of leaves, twigs, reproductive organs, epiphytes, bromeliads and
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19 228 unidentified material as canopy productivity.
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28 230 *Below ground carbon stocks and fluxes*

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31 231 Soil and root C stocks were estimated using soil cores only (these soil cores were
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33 232 sampled during the installation of ingrowth cores), while root production was
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35 233 estimated using two independent approaches, rhizotrons and soil ingrowth cores. The
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37 234 comparison of these two approaches gives us some metric of confidence in these
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39 235 results. A detailed description of the methodologies described here is presented in
40
41 236 Metcalfe *et al.* (2008a). For an in depth review and critique of these methods refer to
42
43 237 Vogt *et al.* (1998) and Hendricks *et al.* (2006).
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49 239 *Rhizotrons*

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52 240 NPP_{BG} was determined using rhizotron root observation chambers (Burke *et al.*,
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54 241 1994). These observation chambers were framed on three sides using lumber or metal.
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56 242 The fourth side was a 6 mm thick pane of Perspex 40 cm deep, 0 cm being the surface
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58 243 of the organic top layer, and 35 cm wide. Lowland sites with thin organic layers had
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60 244 their observation chambers mostly in mineral soils, while at highland sites with thick

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3 245 organic layers, the chambers mostly observed root growth in the organic layers and
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5 246 not in the mineral soil (Table 1). The rhizotron measurements began two months after
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8 247 installation, once we could observe the roots growing rapidly against the observation
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10 248 chamber, to let the roots recover from the initial disturbance resulting from severing
11
12 249 the roots during the installation of rhizotrons. Three rhizotrons were installed at sites
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15 250 chosen to encompass the topographic variation in each plot, in November 2006, at the
16
17 251 end of the dry season. Monthly root growth was recorded from the rhizotrons over 23
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19 252 months. Each month, root increments were recorded at each session by tracing over
20
21 253 visible roots with permanent markers on transparent A4 acetate sheets placed over the
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23 254 glass face. Information on root diameter class was recorded through colour coding (<1
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25 255 mm = black, 1 - 2 mm = blue, 2 - 3 mm = red, <4 mm = green) and the dates of root
26
27 256 appearance and disappearance were recorded by numbering each root increment
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29 257 traced. Root intersections with the rhizotron screens were counted on each sheet and
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31 258 converted to biomass production per unit ground area using the method described in
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33 259 Bernier & Robitaille (2004). In this method, the number of roots contacting the
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35 260 rhizotron screen at each time-step, together with root diameter, is used to calculate the
36
37 261 total cross-sectional surface area of intersecting roots using the equations presented by
38
39 262 Bernier & Robitaille (2004). As roots can only intersect with the rhizotron screen
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41 263 from one side, the resulting value was doubled, assuming that if there was not an
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43 264 empty space behind the rhizotron screen, an equal amount of roots would contact the
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45 265 rhizotron screen from the other side.
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54 267 *Root ingrowth cores*

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57 268 NPP_{BG} was also quantified in all plots using the ingrowth core technique (Vogt *et al.*,
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59 269 1998, Steingrobe *et al.*, 2000, Hendricks *et al.*, 2006), following the methodology

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3 270 described in Metcalfe *et al.* (2008b). These are cores of root-free soil surrounded by
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5 271 mesh bags in which roots were allowed to grow over a set period of time (three
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8 272 months), providing estimates of root production per unit area and time ($\text{Mg ha}^{-1} \text{ yr}^{-1}$).
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10 273 Nine ingrowth cores were installed in the plots in May 2007, three of which were in
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12 274 close proximity to rhizotrons. Soil cores were extracted and soil layers were separated
13
14 275 into O-horizon organic layer (OL) and A- and B-horizon mineral layer (ML). Fine
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16 276 roots were manually removed every three months using a method which corrects for
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18 277 underestimation of fine root biomass. Roots were manually extracted from soil cores
19
20 278 during 10 min time intervals, over a period of 40 min. The curve of cumulative
21
22 279 extraction over time was used to predict root extraction beyond 40 min (Metcalfe *et*
23
24 280 *al.*, 2007). This method only accounts for live fine roots, as the three-monthly sample
25
26 281 period was much lower than the turnover time of the roots. Root-free soil was then
27
28 282 replaced in each ingrowth core, maintaining the horizon layering of the undisturbed
29
30 283 soil. Sampled roots were rinsed in water to remove soil particles, oven dried at 70°C
31
32 284 in the lab until constant mass, weighed and scanned as greyscale images at 600 dpi
33
34 285 resolution. Fine root biomass and mass of the soil OL were measured using the first
35
36 286 soil cores sampled in May 2007. NPP_{BG} was estimated from the quantity of root mass
37
38 287 produced in the three month interval since the last collection. Fine and coarse roots
39
40 288 were defined as <2 mm and >2 mm in diameter, respectively. The scanned images
41
42 289 were analyzed using commercially available software (WinRHIZO Pro version 2003
43
44 290 b, Regent Instruments, Canada), to calculate root length and surface area, according to
45
46 291 the methodology described by Metcalfe *et al.* (2008). Finally, OL depth and root mass
47
48 292 within the OL were also measured using soil cores in August 2008 at 25 points for
49
50 293 each elevation (only five at 2000 m). As it is very difficult to discern between biomass
51
52 294 and necromass of fine roots, fine root biomass are likely to be overestimated.
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4 295 ***Net Primary Productivity calculations***
5

6 296 Net primary productivity (NPP) of an ecosystem can be defined as the total biomass
7
8 297 of autotrophs produced in a specified time interval (Roy *et al.*, 2001). Total
9
10 298 productivity (NPP_{Total}) can be divided into below-ground (NPP_{BG}) and above-ground
11
12 299 (NPP_{AG}) production of carbon per unit time. Above-ground NPP consists of stem
13
14 300 production (NPP_{Stem}), canopy production (NPP_{Canopy}), branch turnover (NPP_{Branch}) and
15
16 301 volatile organic compound production (NPP_{VOC}).
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21 302
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23 303
$$NPP_{AG} = NPP_{Stem} + NPP_{Canopy} + NPP_{Branch} + NPP_{VOC} \quad (3)$$

24
25 304

26
27 305 We obtained stem (NPP_{Stem}) and leaf (NPP_{Canopy}) production values through direct
28
29 306 measurement. NPP_{Canopy} consist of leaves, small branches, flowers and fruit. As we
30
31 307 did not directly measure branch production in this study, it is scaled from NPP_{Stem}
32
33 308 using the ratio (0.4) of NPP_{Branch}:NPP_{Stem} estimated from published values in lowland
34
35 309 Amazonian plots (Aragão *et al.*, 2009). NPP_{VOC} is the emission of volatile organic
36
37 310 carbon from the vegetation. VOC flux appears to be a very small component of the
38
39 311 carbon cycle of tropical forests (Malhi *et al.*, 2009) and is not quantified in this study.
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44 312

45
46 313 NPP_{BG} consists of fine (NPP_{FineRoot}) and coarse root (NPP_{CoarseRoot}) production (Clark
47
48 314 *et al.*, 2001a), and exudate production.
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53 316
$$NPP_{BG} = NPP_{FineRoot} + NPP_{CoarseRoot} + NPP_{Exudate} \quad (4)$$

54
55 317

56
57 318 Whereas we estimated NPP_{FineRoot} directly, NPP_{CoarseRoot} presents a methodological
58
59 319 challenge and is very difficult to estimate directly. Hence NPP_{CoarseRoot} was estimated
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2
3 320 as a fraction of NPP_{Stem} , following the method proposed by Malhi *et al.* (2009):
4
5 321 $NPP_{CoarseRoot}=0.21(\pm 0.03)*NPP_{Stem}$ where 0.21 ± 0.03 is the mean ratio of below-
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7
8 322 ground stocks to above-ground stocks reported across lowland tropical forests. This
9
10 323 may result in underestimation of production, as the NPP of smaller roots is likely to
11
12 324 exceed that of large structural roots. For the TMFs, we chose to use the same ratio
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14
15 325 with a higher uncertainty (0.21 ± 0.10); on wind or erosion prone sites it is likely that
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17 326 trees invest more in coarse root anchoring, but on the other hand on shallow montane
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19 327 soils they are not able to have a large root core or deep roots.
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24 329 Exudates and export to mycorrhizae are not measured in this study, resulting in an
25
26 330 underestimation of the NPP_{BG} values presented in this study to our knowledge. This
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28 331 component has never been explicitly measured in any tropical forest, it has been
29
30 332 found to account for 3-15% of NPP in temperate forests (Vogt *et al.*, 1982, Bekku *et*
31
32 333 *al.*, 1997, Clark *et al.*, 2001 b).
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36 334

37 38 39 335 ***Analytical techniques***

40
41 336 We used these data to describe the spatial variations of above- and below-ground C
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43 337 stocks, NPP and turnover rates along the Kosñipata transect. All uncertainty estimates
44
45 338 are given as the standard error of the mean. The statistical significance of correlation
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47 339 coefficients was based on a two tailed approach, d.f. = n-2, $P < 0.05$. Linear
48
49 340 regression analyses were conducted to identify significant elevational trends in
50
51 341 ecosystem allocation to different NPP components and the relationships between
52
53 342 components. All statistical analyses were performed with the R version 2.9.0
54
55 343 statistical package (Chambers, 2009).
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344

345 Results

346 *Carbon stocks*

347 Estimates of carbon stocks are presented in Table 2. We calculated stem biomass
348 using two of the moist forest stand equations presented by Chave *et al.* (2005), as
349 described above. Equation (1) requires measurements of tree height, H . Equation (2)
350 does not account for height, and we employ it here to explore the importance of
351 directly accounting for height. Equation (2) assumes a fixed polynomial relationship
352 between $\ln(H)$ and $\ln(DBH)$ derived for lowland tropical forests. It would only be
353 valid if the tree form, as expressed by the relationship between diameter and height,
354 did not vary with elevation. Hence the comparison of these two equations gives us
355 some indication of the importance of variation in tree form with elevation in
356 determining forest biomass. Our data show that the allometric form of trees in our
357 sites varies with elevation: trees at high elevation have less stature for the same dbh,
358 *i.e.* tree form becomes gradually more squat and stunted with increasing elevation.
359 Hence, using equation (2) would result in a systematic overestimation of biomass by
360 $52\pm 10\%$ at higher elevations. Fig. 1a demonstrates the importance of including height
361 estimates into stem carbon stocks calculations in TMFs, as height is the dominant
362 factor dictating a decline in above-ground carbon stocks with increasing elevation.
363 Fig. 1a includes published data from nine plots in lowland Amazonia (two of which
364 are the lowland plots from this transect), for which biomass was estimated using the
365 same methodology and equation (2). We observed a significant decrease in stem
366 biomass with increasing elevation with equation (1) ($r^2=0.80$, $P<0.0005$, $n=17$).

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3 368 Fig. 1b indicates a step change in fine root biomass in the soil organic layer at the
4
5 369 base of the cloud immersion zone. Fine root carbon stocks increased from 1.50 Mg C
6
7 370 ha^{-1} at 194 m to $6.54 \pm 0.54 \text{ Mg C ha}^{-1}$ at 1855 m, and thereafter no significant changes
8
9 371 in root carbon stocks were observed within the cloud immersion zone. Coarse root
10
11 372 biomass was calculated as a fixed fraction of stem biomass, and thus we presumed
12
13 373 coarse root biomass to follow a similar pattern to stem biomass and decrease with
14
15 374 elevation. Fine root to stem biomass ratio increased with elevation, from 0.02 at 194
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17 375 m to 0.11 at 3020 m.
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26 377 ***Net Primary Productivity***

27
28 378 The patterns of NPP components along the elevational gradient are shown in Fig. 2
29
30 379 and 3. $\text{NPP}_{\text{Total}}$ estimated in nine plots along the elevational transect did not decline
31
32 380 monotonically with increasing elevation. However, we observed a change in regime
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34 381 in the pre-montane and montane forests: lowland values ($16.9 \pm 1.48 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ at
35
36 382 210 m and $13.6 \pm 1.25 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ at 194 m, Aragão *et al.* 2009) were significantly
37
38 383 higher than values recorded in the Andes ($7.07 \pm 0.98 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ at 1000 m to
39
40 384 $4.11 \pm 0.26 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ at 3020 m). This relationship is particularly apparent in Fig.
41
42 385 2, in which values from central Amazonia reported by Malhi *et al.* (2009) and Aragão
43
44 386 *et al.* (2009) are also included. Here, TMF values of $\text{NPP}_{\text{Total}}$ are significantly lower
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46 387 than $\text{NPP}_{\text{Total}}$ from even the least fertile soils in central Amazonia.
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53
54 389 NPP_{Stem} ranged between 0.79 ± 0.08 (1855 - 2020 m) and $2.80 \pm 0.24 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$
55
56 390 (210 m), with a change in regime between lowland Amazonian forests and pre-
57
58 391 montane to montane forests. Likewise, we recorded a significant decline in $\text{NPP}_{\text{Canopy}}$
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60 392 with increasing elevation (slope=-0.001, $r^2=0.74$, $P=0.002$, $n=9$) (Fig. 3a). Hence,

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3 393 NPP_{AG} decreased with elevation (slope = -0.001, $r^2=0.69$, $P=0.005$, $n=9$). These linear
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5 394 relationships provide indications on the overall tendency of the trends we observed,
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7
8 395 however, rather than a steady linear decline, there appears to be a fairly rapid decline
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10 396 in NPP_{AG} with elevation until the base of the cloud immersion zone (around 1500 m),
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12 397 and then no trend in NPP_{AG} with elevation within the cloud zone all the way up to the
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14 398 tree line. There appears to be two distinct regimes, one below the clouds where NPP
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16 399 declines with elevation, and one within the cloud zone where NPP does not change
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18 400 with elevation. Average NPP_{AG} was estimated at 3.53 ± 0.38 Mg C ha⁻¹ yr⁻¹ ($n=7$) in
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20 401 the TMF and 8.87 ± 0.63 Mg C ha⁻¹ yr⁻¹ ($n=2$) in the lowland Amazonian plots.
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27 403 A change in regime of NPP_{BG} was observed around 1000 m, with a decrease in
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29 404 production and with the lowest values recorded within the cloud immersion zone,
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31 405 between 1.96 ± 0.18 and 1.48 ± 0.40 Mg C ha⁻¹ yr⁻¹. NPP_{FineRoot} followed a similar
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33 406 pattern, with values decreasing from 6.80 ± 1.0 Mg C ha⁻¹ yr⁻¹ in the lowlands (210 m)
34
35 407 to 1.23 ± 0.40 Mg C ha⁻¹ yr⁻¹ in the upper TMF (Fig. 3c). NPP_{FineRoot} represented the
36
37 408 largest proportion of below-ground productivity, ranging between 83% and 92% of
38
39 409 NPP_{BG}. NPP_{CoarseRoot} (Fig. 2) was estimated as a fixed fraction of above-ground
40
41 410 production stem biomass ($21\pm 10\%$). As a result, we estimated a decrease in
42
43 411 NPP_{CoarseRoot} in the TMF, from 0.60 ± 0.09 (194 m) to 0.21 ± 0.04 (3020 m) Mg C ha⁻¹
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45 412 yr⁻¹.
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52 414 Measurements of NPP and respiration fluxes are presented in Table 3. An analysis of
53
54 415 the patterns of NPP_{Total} partitioning into above- and below-ground components
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56 416 demonstrated that the ratio of NPP_{BG} to NPP_{AG} (Fig. 4) shows high site-to-site
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58 417 variation (between 0.2 and 1.2) but no evidence of any overall trend with elevation.
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3 418 The mean value of the ratio is 0.69 ± 0.44 . A significant exception was the forest at
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5 419 1855 m, where we observed a high NPP_{BG} driven by high fine root productivity. To
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7
8 420 a small extent, this lack of trend in above- and below-ground partitioning is forced by
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10 421 the fact we set $NPP_{CoarseRoot}$ as a fixed fraction of NPP_{Stem} . However, this effect is
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12 422 relatively small, because $NPP_{CoarseRoot}$ is a relatively small component of NPP_{BG} (5-
13
14 423 17%), and NPP_{Stem} is a relatively small component of NPP_{AG} (~34%).
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19
20 425 The ratio of each NPP component to NPP_{Total} showed no significant trends with
21
22 426 elevation (Fig. 5). On average, below the cloud base, 18 ± 5 % of NPP_{Total} is allocated
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24 427 to stems, 34 ± 29 % to canopy and 37 ± 15 % to fine roots ($n=3$). Above the cloud base,
25
26 428 21 ± 7 % of NPP_{Total} is allocated to above-ground woody biomass, 32 ± 7 % to canopy
27
28 429 and 37 ± 15 % to fine roots ($n=6$). Fig. 6 shows the relationships between NPP_{AG}
29
30 430 ($y=0.58 \pm 0.05 * x$, $n=9$) and NPP_{BG} ($y=0.39 \pm 0.05 * x$, $n=9$) with NPP_{Total} in the
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32 431 Kosñipata transect, with regressions forced through the origin. These variables are not
33
34 432 independent and thus the correlation statistics are not meaningful, but the regression
35
36 433 slopes are meaningful. Across the elevational transect, the regression suggests that
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38 434 NPP_{AG} and NPP_{BG} are 58 ± 5 % and 39 ± 5 % of NPP_{Total} . The slopes of the relationships
39
40 435 were remarkably similar for (i) the nine plots from the Kosñipata transect only, (ii) the
41
42 436 lowland Amazonian plots from Aragão *et al.* (2009) only, and (iii) both data sets
43
44 437 combined. We found a significant relationship between NPP_{Canopy} and NPP_{Stem} (Fig. 7)
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46 438 when we included all plots of the Kosñipata transect as well as when we included
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48 439 montane forests.
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54 441 Regressions of the components of NPP against environmental parameters are
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56 442 presented in Table 4. There are particularly strong correlations between annual mean
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3 443 air temperature and NPP_{Canopy} and NPP_{FineRoot} , and weaker correlations with stem
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5 444 productivity. Overall 78% ($P < 0.005$) of the variance in NPP_{Total} correlated with
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7
8 445 temperature. Rainfall directly is a weak predictor of NPP, though it may explain some
9
10 446 of the residuals once temperature correlation is factored out.
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13 447

16 448 *Residence Time*

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19 449 A significant decrease in stem biomass with elevation coupled with a decrease in
20
21 450 NPP_{Stem} resulted in no significant change in stem carbon residence time with
22
23 451 increasing elevation (Table 5, Fig. 8a). In the Kosñipata transect, the mean stem C
24
25 452 residence time was 54 ± 4 years ($n=9$). However, as fine root biomass increased with
26
27 453 elevation and NPP_{FineRoot} was lower in TMFs than in most lowland forest plots, fine
28
29 454 root carbon residence time (Table 5, Fig. 8b) increased significantly with increasing
30
31 455 elevation ($r^2=0.80$, $P=0.006$, $n=7$) from 0.31 ± 0.61 years (194 m) to 3.78 ± 0.81 years
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33 456 (3020 m).
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41 458 **Discussion**

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45 459 We have presented data on C stocks, productivity, allocation and residence time of
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47 460 seven Andean montane and pre-montane forests and two lowland Amazonian
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49 461 rainforest sites. In addition, we reviewed published data from nine lowland plots, two
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51 462 of which were the lowland plots of our elevation transect (Aragão *et al.*, 2009, Malhi
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53 463 *et al.*, 2009). Our results confirmed that above-ground biomass and productivity are
54
55 464 the main contributors of total C stocks and NPP at all elevations. Overall, NPP_{Total}
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57 465 was lower in the pre-montane and montane forests than in lowland Amazonia. This
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3 466 pattern was driven by a decline in above- and below-ground NPP in pre-montane and
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5 467 montane forests, with lower values recorded within the cloud immersion zone.
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10 11 469 ***No change in total carbon stocks with elevation*** 12

13 470 A decline in above-ground biomass with increasing elevation in altitudinal transects is
14
15 471 a common feature of TMFs. Our results corroborate previous findings by showing a
16
17 472 significant decline in above-ground woody biomass with increasing altitude (Fig. 1).
18
19 473 Further, Fig. 1 demonstrates that calculated stem biomass shows no significant trend
20
21 474 with elevation when we do not include the decline in tree height in our allometric
22
23 475 equation (Chave *et al.*, 2005). Hence, we can attribute this decline solely to a decrease
24
25 476 in tree stature with increasing elevation, confirming the importance of measuring tree
26
27 477 height when estimating above-ground carbon stocks in TMF ecosystems. In terms of
28
29 478 below-ground carbon allocation, we observed a step change in fine root biomass at the
30
31 479 base of the cloud immersion zone, with consistently higher fine root biomass in the
32
33 480 TMF than in the pre-montane and lowland plots. Further, the soil organic matter C
34
35 481 stocks increase significantly with elevation. Hence, if we include increases in the soil
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37 482 carbon stock pool and fine root carbon stocks in our estimates of below-ground
38
39 483 carbon stocks, *these results are consistent with our first hypothesis: there is no*
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41 484 *significant change in total C stock with elevation, but there is a shift in relative stock*
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43 485 *of carbon from above- to below-ground.*
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53 54 487 ***Net primary productivity*** 55

56 57 488 *Total NPP declines with elevation*

58 489 NPP_{Total} was lower in the pre-montane and montane forests than in lowland
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60 490 Amazonia. In a study on nine lowland Amazonian forest plots, Aragão *et al.* (2009)

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3
4 491 estimated an average NPP_{Total} of $12.6 \pm 2.5 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$. The present study estimated
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6 492 a significantly lower average NPP_{Total} of $5.68 \pm 0.44 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ ($n=7$) in the TMFs.
7
8 493 All components of NPP_{Total} measured for this study (NPP_{Canopy} , NPP_{Stem} and
9
10 494 $NPP_{FineRoots}$) were significantly lower in TMF plots compared to the two lowland
11
12 495 Amazonian plots of this transect. Further, we found evidence of a change in regime of
13
14 496 NPP_{AG} rates in the cloud forest zone, where NPP_{AG} rates are lower than in most
15
16 497 lowland Amazonian plots (Fig. 2). This decline is driven by above- and below-ground
17
18 498 NPP allocation. Stem and canopy productivity are both significantly lower in the pre-
19
20 499 montane and montane forests than in lowland Amazonia, confirming previous
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22 500 published observations of NPP_{AG} along elevational transects from Hawaii (Raich *et*
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24 501 *al.*, 1997, Herbert *et al.*, 1999, Schuur *et al.*, 2001) and Borneo (Kitayama *et al.*,
25
26 502 2002) and of NPP_{Canopy} from Jamaica (Tanner *et al.*, 1999), Puerto Rico (Waide *et al.*,
27
28 503 1998), and Ecuador (Roderstein *et al.*, 2005). These authors used NPP_{Canopy} as a proxy
29
30 504 of NPP_{AG} . Similarly, Malhi *et al.* (2009) and Aragão *et al.* (2009) found that in
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32 505 lowland Amazonian forests, canopy productivity appears to be a good proxy for
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34 506 NPP_{AG} . Our results confirm that this relationship holds in montane forests (Fig. 7).
35
36 507 Further, the number of plots we established along the transect allowed us to observe a
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38 508 change in regime in NPP_{AG} between lowland forest and montane forest for the first
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40 509 time in an elevational transect.
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42 510
43
44 511 Studies that attempt to quantify NPP_{BG} in tropical montane forests are more limited in
45
46 512 number. To date, only one study determined NPP_{BG} , in South Ecuador (Roderstein *et*
47
48 513 *al.*, 2005), and a second is being proposed for this site in (C.A.J. Girardin, in prep).
49
50 514 Roderstein *et al.* (2005) found that, along a transect of three plots in the Ecuadorian
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52 515 Andes (1050 - 3060 m), NPP_{Canopy} declined, whereas $NPP_{FineRoot}$ increased threefold,

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2
3 516 revealing a clear belowground shift in carbon allocation with increasing elevation. We
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5 517 found that, along seven plots ranging from the high Andes to lower montane forests,
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7 518 NPP_{FineRoot} remained constant within the cloud immersion zone (1855 m to 3025 m),
8
9 519 with values below those reported in the least fertile soils of lowland Amazonia (Fig.
10
11 520 3c). Whereas we observed a decline in NPP_{Canopy} in TMFs compared to pre-montane
12
13 521 and lowland sites, our results showed no evidence of a shift in allocation to
14
15 522 $NPP_{\text{FineRoots}}$ as elevation increases. Instead, at our site, we found that productivity
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17 523 decreases proportionately above- and below-ground in TMFs, *supporting our*
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19 524 *hypothesis (2): total NPP declines with elevation, but the proportion of NPP allocated*
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21 525 *to above- and below-ground stays fixed.*
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29 527 ***Net primary productivity allocation patterns on the elevation transect are the same***
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31 528 ***as those observed in lowland Amazonia.***
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34 529
35 530 Aragão *et al.* (2009) found several significant relationships between the components
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37 531 of NPP. Here, we tested these relationships to determine if the patterns observed in
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39 532 lowland Amazonian forests hold in the Kosñipata montane forests. We found that the
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41 533 ratio of NPP_{BG} to NPP_{AG} did not change significantly along the elevational gradient
42
43 534 (Fig 4). The allocation of NPP to stems, canopy and fine roots did not change with
44
45 535 elevation. Further, we established that the relationship found by Aragão *et al.* (2009)
46
47 536 between NPP_{AG} , NPP_{BG} and NPP_{Total} (i.e. a significant increase in both NPP_{AG} and
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49 537 NPP_{BG} with increasing NPP_{Total}) also applies to our TMF transect. Both studies found
50
51 538 a similar sensitivity of above- and below-ground productivity to changes in NPP_{Total}
52
53 539 (Fig. 6). These relationships confirm that, although the total productivity of forests is
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55 540 reduced in the mountains, the allocation patterns of NPP do not change with elevation
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57 541 in our elevation transect. However, Moser *et al.* (submitted; this volume) reported a
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3 542 very different pattern of NPP allocation along an Ecuadorian elevational gradient,
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5 543 hence, generalising about the relationships between NPP components in tropical
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8 544 montane forests may still be premature.
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11
12 546 Nonetheless, in a review of above-ground NPP in 104 Neotropical forest plots, Malhi
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14
15 547 *et al.* (2004) observed a constant partitioning between NPP_{Stem} and NPP_{Canopy}
16
17 548 ($NPP_{\text{Stem}}=1.73(\pm 0.09)\times NPP_{\text{Canopy}}$) when they combined their data with published
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19 549 results from (Clark *et al.*, 2001b). In a subsequent study, Aragão *et al.* (2009) found a
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21
22 550 significant relation between stem and canopy productivity
23
24 551 ($NPP_{\text{Canopy}}=1.61(\pm 0.07)\times NPP_{\text{Stem}}$, $r^2=0.58$, $P<0.001$) when they combined their results
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26
27 552 to those presented in Malhi *et al.* (2004). The evidence from the Kosñipata elevational
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29 553 transect confirmed that this relationship holds in our TMF plots, providing further
30
31 554 support that NPP_{Canopy} is a good proxy for NPP_{Total} in moist tropical forests (Fig. 7).
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33 555 *These findings are consistent with hypothesis (3): the TMF of the Kosñipata*
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35 556 *elevational gradient displays the same NPP allocation patterns as those observed in*
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37 557 *lowland Amazonian forests by Aragão et al. (2009) and Malhi et al. (2004).*
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44 559 *Factors controlling net primary productivity*

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47 561 In one of the most thorough appraisals of tropical forest NPP quantification of recent
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49 562 years, Clark *et al.* (2001) compiled data from 39 tropical forest sites and estimated
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51 563 total tropical forest NPP. Their estimates ranged between 3.1 and 21.7 Mg C ha⁻¹ yr⁻¹,
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53 564 confirming that our estimates of 4.11 (3020 m) to 7.07 (1000 m) Mg C ha⁻¹ yr⁻¹ in
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55 565 TMFs are situated in the lower range of lowland forest estimates. Tropical forest NPP
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57 566 was found to be poorly correlated with mean annual temperature and with annual
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59 567 rainfall (Clark *et al.*, 2001b, Del Grosso *et al.*, 2008). Some authors found that NPP
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3 568 decreases at extremely high precipitation ($>3000 \text{ mm yr}^{-1}$), due to the indirect effects
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5 569 of excess moisture, such as low soil oxygen resulting in slow mineralisation rates and
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7
8 570 the loss of nutrients through leaching (Clark *et al.*, 2001b, Schuur, 2001). More
9
10 571 recently, Malhi *et al.* (2004) concurred with these observations, and also reported that
11
12 572 NPP_{Stem} varied substantially at the regional scale, and that a large part of this regional
13
14 573 variation was due to soil type. Subsequently, Aragão *et al.* (2009) investigated the
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16 574 relationship between soil fertility and NPP in ten Amazonian forests on contrasting
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18 575 soil types, confirming the relationship between soil fertility (particularly phosphorus
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20 576 status) and productivity.
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27 578 Palm litter was not accounted for in the lowland plots, implying a further
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29 579 underestimation of $\text{NPP}_{\text{Canopy}}$ at 210 m and 194 m. Nonetheless, $\text{NPP}_{\text{Canopy}}$ was
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31 580 significantly lower in the cloud forest than in the pre-montane and lowland forests,
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33 581 showing evidence of a change of regime at the cloud base (Fig. 3a). Within the cloud
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35 582 immersion zone, $\text{NPP}_{\text{Canopy}}$ did not change significantly. The decrease in canopy
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37 583 production with increasing elevation may be largely explained by temperature
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39 584 ($r^2=0.76$, $P<0.005$, $n=9$), however, as temperature decreases linearly with elevation
40
41 585 and $\text{NPP}_{\text{Canopy}}$ does not, this relationship may be a result of the indirect effects of
42
43 586 temperature rather than the direct effects of temperature on plant physiology. Several
44
45 587 authors have suggested that plants adjust their carbon allocation patterns in response
46
47 588 to imbalances in resource availability (nutrients or water) (Bloom *et al.*, 1985, Litton
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49 589 *et al.*, 2007). Since SWC is typically above 25% in our plots, water shortage should
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51 590 not be limiting plant growth in any of our study sites. Nevertheless, water saturation
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53 591 in the soil may have prevented mineralization, reducing nutrient supply to the roots,
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55 592 as suggested by Leuschner *et al.* (2007).
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5 594 Our results indicate a strong correlation ($r^2=0.78$, $P<0.005$, $n=9$) between NPP_{Total} and
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8 595 mean annual temperature, particularly so in the case of fine root ($r^2=0.77$, $P<0.005$,
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10 596 $n=9$) and canopy productivity ($r^2=0.76$, $P<0.005$, $n=9$). Of course, correlation does not
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12 597 necessarily indicate causation; further, linear regressions are not valid if there is a
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14 598 sudden regime change at cloud base, as observed in this elevational gradient (Fig. 3).

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17 599 The results of linear regressions are provided here to provide a summary statistic of
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19
20 600 the overall trend observed along the elevational gradient, although we are cautious not
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22 601 to over interpret them. Thus, over this extreme elevation gradient it is likely that
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24 602 temperature plays an important role in influencing ecosystem function. This could be
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26 603 through direct effects of temperature on plant physiology, or indirect effects via slow
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28 604 decay and mineralization rates, which affect nutrient supply and canopy nitrogen and
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30 605 leaf area index. Physiological studies at the 3025 m site in Wayquecha indicate no
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32 606 decline in plant physiological capacity, but a decline in canopy leaf area and overall
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34 607 canopy leaf nitrogen and N: P ratio (Fisher *et al.*, this issue). Hence the decline in
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36 608 NPP components could be related to the observed decline in leaf nitrogen supply.
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38 609 Finally, we observed a high rate of $NPP_{FineRoot}$ at 1855 m compared to other montane
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40 610 forest sites, with values comparable to that of some lowland sites. Although this site is
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42 611 located at the base of the cloud immersion zone, soil water content is lower at this site
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44 612 than in other montane forest sites, as the soils are very steep and well drained in that
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46 613 plot. It is also possible that the anomaly at 1855 m is driven secular trends, if long-
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48 614 term warming is causing cloud base height to rise and the previous cloud base region
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50 615 to dry. Although light incidence and rainfall patterns do not change significantly
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52 616 within the cloud immersion zone, soil water content is uniformly high within the
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3 617 cloud immersion zone (probably a consequence of droplet deposition and low
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5 618 transpiration rates) and decreases significantly below 1855 m.
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10 620 There appears to be a temperature dependency of NPP in non-saturated soils, but no
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12 621 temperature sensitivity in the saturated soils. This may imply that the controlling
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14 622 factor is soil mineralisation rates, which are strongly influenced by temperature in the
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16 623 lower sites, but are restricted by soil saturation within the cloud zone. Hence our
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18 624 results only partly confirm our hypothesis (4): *NPP decline can largely be explained*
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20 625 *by decreasing temperature as elevation increases, albeit this relationship is likely to*
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22 626 *be an indirect one, via decay and mineralization rates.*
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30 31 629 ***Carbon residence time***

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34 630 The discrepancy between above- versus below-ground allocation between biomass
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36 631 and NPP may be explained by differences in residence time of the carbon in above-
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38 632 and below-ground components. The stock of carbon in a particular carbon pool
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40 633 depends both on the rate of production of that pool and the mean residence time (or
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42 634 decomposition rate) of that pool. Carbon residence time differs for different pools of
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44 635 carbon in the ecosystem (Malhi *et al.*, 2009). Coarse wood has the longest residence
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46 636 time. Above-ground, stems have a carbon residence time of 42 to 71 years with
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48 637 insignificant lower residence times occurring at higher elevations as a result of high
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50 638 disturbance caused by high wind exposure and steep slopes in the high elevation sites.
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52 639 In Amazonian forests, coarse wood (stems and branches) represent about 30% of
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54 640 NPP_{AG}, with a mean residence time of 50 to 100 years (Malhi *et al.*, 2006).
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3 642 In contrast, the carbon residence times in below-ground components increase with
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5 643 elevation from 4 months in the lowlands to almost 4 years at high elevations (Fig. 8).
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8 644 Root residence time should be partly determined by the cost of root tissue
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10 645 construction and maintenance, which is related to root C and N content (Gill &
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12 646 Jackson 2000). There is evidence that low root tissue N content is linked with longer
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15 647 residence time (Hendricks *et al.*, 1993; Gordon & Jackson 2000). Hence, water-
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17 648 logged soils would contribute to longer residence time by slowing root mineral
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19 649 uptake. Increasing soil acidity, as that found in the high elevation soils of the
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22 650 Kosñipata transect, was also found to increase fine root residence time in temperate
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24 651 forests (Jentschke *et al.*, 2001). In our study, decreasing temperatures explained 78%
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26 652 of the variance in fine root residence time (slope=-0.24, $r^2=0.78$, $P<0.05$, $n=6$). This
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28 653 long residence time explains the shift in C stocks from above- to below-ground as
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30 654 elevation increases, despite the consistently slower productivity rates observed below-
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32 655 ground.
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39 ***Concluding remarks***

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41 658 In summary, this study describes changes in total biomass and net primary
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43 659 productivity (NPP) and their allocation between above-ground and below-ground
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45 660 components in nine tropical forests sites along an elevational transect in the Peruvian
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47 661 Andes. It found that (i) there is no change in total carbon stock with elevation, but
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49 662 there is a shift in relative stock of carbon from above- to below-ground; (ii) total NPP
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51 663 declines with elevation, but the proportion of NPP allocated to above-ground and
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53 664 below-ground components stays fixed along the elevation gradient; (iii) NPP declines
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55 665 linearly with elevation in lower forests, but is at a fairly constant low level within the
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58 666 cloud forest zone. We conjecture that this pattern is driven by temperature limitation
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3 667 of mineralisation in the in lower forests, and by water-saturation inhibition of
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5 668 mineralisation in the cloud forest zone; and (iv) the NPP allocation patterns on the
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8 669 elevation transect are similar to those observed for lowland Amazonian forests. The
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10 670 discrepancy between above- versus belowground allocation between biomass and
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12 671 NPP is explained by differences in residence time of the carbon in aboveground and
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14 672 belowground components. Aboveground woody biomass components have a carbon
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16 673 residence time of 42 to 71 with lower residence times occurring at higher elevations
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18 674 as a result of high disturbance rates. In contrast, the carbon residence times in
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20 675 belowground components increase with elevation from 4 months in the lowlands to
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22 676 almost 4 years at high elevations.
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29 678 The work presented here and compiled from our other recent publications (Malhi *et*
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31 679 *al.* 2009; Aragão *et al* 2009) probably represents the most comprehensive dataset to
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33 680 date on the carbon allocation of tropical forests (16 study plots in total). We have
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35 681 compiled enough data to propose an approximate “rule of thumb” for the partitioning
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37 682 of NPP in Amazonian and Andean forests (and perhaps in other tropical forests). Our
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39 683 data suggest that approximately $33\pm 30\%$ of NPP_{Total} is allocated to canopy
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41 684 production, $20\pm 8\%$ to above-ground woody production (and $61\pm 21\%$ to above-
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43 685 ground NPP, including coarse root production). Below ground, $35\pm 25\%$ of NPP_{Total} is
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45 686 allocated to fine root production, $4\pm 2\%$ to coarse root production (and hence 39 ± 25
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47 687 $\%$ in total to below-ground NPP). This rule may of course be revised and refined as
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49 688 new data are collected; nevertheless it may be useful as it is for those attempting to
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51 689 model allocation of NPP, and in particular relate NPP to woody biomass construction.
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4 691 Acknowledgements
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7 692 This study is a product of the Andes Biodiversity and Ecosystems Research Group.

8
9 693 This study was financed by an NERC grant, number NE/D014174/1, a grant from the

10
11 694 Andes-Amazon programme of the Gordon and Betty Moore Foundation, and a

12
13 695 scholarship from the Oxford University Environmental Change Institute. We also

14
15 696 thank the Asociación para la Conservación de la Cuenca Amazónica (ACCA) for the

16
17 697 use of the Wayquecha field station, Explorers Inn for the use of Tambopata field

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19 698 station, the Manu National Park and INRENA for permitting us to explore the

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21 699 Peruvian tropical forest.
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835 Tables and Figures

836

837 **Table 1.** Summary of site characteristics

Site Name	Wayqecha	Trocha Union III	Trocha Union IV	Trocha Union VII	Trocha Union VIII	San Pedro	Tono	Tambopata III
Site Code	WAY	TU3	TU4	TU7	TU8	SPD	TON	TAM 3
Latitude	13° 11' 24"	13° 6' 34"	13° 6' 30"	13° 4' 24"	13°4'16"	13°2'56"	12° 57' 33"	12° 50' 11"
Longitude	71° 35' 13"	71° 35' 59"	71° 35' 21"	71° 33' 30"	71°33'18"	71°32'13"	71° 33' 57"	69° 16' 45"
Elevation (m)	3025	3020	2720	2020	1855	1500	1000	210
Aspect	E	W	W	W	W	W	W	-
Mean annual air temp. (°C)	12.5 ± 0.05	11.8 ± 0.01	13.5 ± 0.01	17.4 ± 0.02	18.0 ± 0.01	18.8 ± 0.02	20.7 ± 0.02	26.4
Annual precipitation (mm yr ⁻¹)	1706	1776	2318	1827	2472	2631	3087	2730
Soil organic layer depth (cm)	20.20	42.20	43.63	35.34	26.28	10.55	4.65	1.50
Dominant Families	<i>Weinman- nia; Clusia; Hespero- meles</i>	<i>Clusiaceae; Cunoniceae</i>	<i>Cunoniceae; Lauraceae</i>	<i>Clusiaceae; Alzateaceae</i>	<i>Clethra- ceae; Myrtaceae; Clusiaceae</i>	<i>Euphorbi- aceae; Fabaceae ; Lauraceae</i>	<i>MoraceaeFa baceae; Rubiceae</i>	<i>Bixaceae; Moraceae; Fabaceae</i>

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856 **Table 2** Synthesis of carbon stocks estimates. All values are in Mg C ha⁻¹. Bm, biomass, ML, mineral857 layer, OL, organic layer, BG, below ground. Bm_{CoarseRoots} were estimated as described in the text (Malhi858 *et al.*, 2009). All other values were directly measured as described in the text. Bm_{Stem} were calculated

859 as the sum of all stem stocks of trees >10cm diameter.

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Plot	Elevation (m)	CStock _{Soil} (ML)	CStock _{Soil} (OL)	CStock _{FineRoots}	CStock _{CoarseRoots}	CStock _{BG}	CStock _{Stem}
WAY	3025	2.45	59.6 ± 5.00				64.9
TU3	3020	1.42	68.8 ± 4.47	4.95 ± 0.62	9.88 ± 0.54	14.8 ± 0.82	47.0
TU4	2720	3.97	63.6 ± 4.37	4.05 ± 0.56	13.8 ± 0.78	17.9 ± 0.96	65.9
TU7	2020	8.35	52.1 ± 10.7	6.83 ± 1.13	8.11 ± 1.47	14.9 ± 1.85	38.6
TU8	1855	10.5	58.3 ± 8.45	6.54 ± 0.54	11.7 ± 0.87	18.2 ± 1.03	55.6
SPD	1500	15.7	27.6 ± 1.93		21.6		102.8
TON	1000	5.69	8.45 ± 0.92	2.62 ± 0.29	16.7 ± 0.54	19.3 ± 0.61	79.5
TAM05	210			2.31	31.5	33.8	123.5
TAM06	194	11.9	3.55	1.50	31.5	33.0	118.5

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865 **Table 3** Synthesis of net primary productivity (NPP) estimates. Error estimates are SE of the mean (value \pm SE), SE was not available for NPP_{Stem} as it is the sum of NPP_{Stem}
 866 from each tree in the plot, hence, we assumed a SE of 10%, based on data available from lowland plots (Aragão *et al.*, 2009, Malhi *et al.*, 2009). Elevation is in meters; all
 867 other values are in Mg C ha⁻¹ yr⁻¹. AG, above-ground, BG, below ground. Values in bold were directly measured. NPP_{Branch} data were obtained from Malhi *et al.* (2009).
 868 Other values were estimated as described in the text.

Plot	Elevation (m)	NPP _{FineRoots}	NPP _{CoarseRoots}	NPP _{BG}	NPP _{Stem}	NPP _{FineLitter}	NPP _{Branch}	NPP _{AG}	NPP _{Total}
WAY	3025	1.23 \pm 0.40	0.25 \pm 0.04	1.48 \pm 0.40	1.20 \pm 0.12	1.92 \pm 0.10	0.5 \pm 0.5	3.60 \pm 0.13	5.09 \pm 0.42
TU3	3020	1.31 \pm 0.23	0.21 \pm 0.04	1.52 \pm 0.23	1.00 \pm 0.10	1.19 \pm 0.05	0.4 \pm 0.4	2.59 \pm 0.11	4.11 \pm 0.26
TU4	2720	1.63 \pm 0.34	0.33 \pm 0.04	1.96 \pm 0.35	1.57 \pm 0.16	1.83 \pm 0.06	0.6 \pm 0.6	4.03 \pm 0.17	5.98 \pm 0.39
TU7	2020	1.80 \pm 0.18	0.16 \pm 0.03	1.96 \pm 0.18	0.79 \pm 0.08	1.44 \pm 0.06	0.3 \pm 0.3	2.54 \pm 0.09	4.50 \pm 0.20
TU8	1855	3.26 \pm 0.73	0.17 \pm 0.03	3.43 \pm 0.73	0.79 \pm 0.08	1.44 \pm 0.05	0.3 \pm 0.3	2.55 \pm 0.09	5.97 \pm 0.73
SPD	1500	1.70 \pm 0.40	0.34 \pm 0.05	2.04 \pm 0.41	1.62 \pm 0.16	2.76 \pm 0.13	0.6 \pm 0.6	5.03 \pm 0.18	7.06 \pm 0.44
TON	1000	2.42 \pm 0.81	0.28 \pm 0.04	2.70 \pm 0.81	1.34 \pm 0.13	2.49 \pm 2.02	0.5 \pm 0.5	4.37 \pm 0.55	7.07 \pm 0.98
TAM05	210	6.80 \pm 1.00	0.60 \pm 0.10	7.40 \pm 1.00	2.80 \pm 0.24	5.60 \pm 0.42	1.1 \pm 1.1	9.50 \pm 1.08	16.9 \pm 1.48
TAM06	194	4.80 \pm 0.57	0.60 \pm 0.09	5.40 \pm 0.58	2.60 \pm 0.42	4.60 \pm 0.24	1.0 \pm 1.0	8.24 \pm 1.11	13.6 \pm 1.25

878 **Table 4** Statistical significance of NPP correlations with mean annual values of weather parameters along the Kosñipata elevational transect. Units of slope are in Mg C ha⁻¹
 879 yr⁻¹ °C⁻¹ for temperature correlations and Mg C ha⁻¹ yr⁻¹ mm⁻¹ for rainfall correlations.

Variable	NPP _{Total}		NPP _{Stem}		NPP _{Canopy}		NPP _{AG}		NPP _{FineRoot}		NPP _{BG}		NPP _{BG}	
Constant	Air	Rainfall	Air	Rainfall	Air	Rainfall	Air	Rainfall	Air	Soil	Rainfall	Air	Soil	Rainfall
Slope	0.72	0.005	0.10	0.0008	0.25	0.002	0.35	0.003	0.30	0.29	0.002	0.32	0.31	0.002
P	< 0.005	< 0.5	< 0.05	< 0.5	< 0.005	< 0.5	< 0.005	< 0.5	< 0.005	< 0.05	< 0.5	< 0.005	< 0.05	< 0.5
r ²	0.78	0.33	0.59	0.3	0.77	0.35	0.72	0.34	0.77	0.66	0.28	0.78	0.67	0.29
n	9	9	9	9	9	9	9	9	9	9	9	9	9	9

For Review Only

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3 881 **Table 5** Stem (RT_{Stem}) and fine roots ($RT_{\text{FineRoots}}$) residence time (yrs, \pm SE). As we could not directly estimate SE
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5 882 of stem carbon stocks, we assumed a SE of 3% for RT_{Stem} , based on data available from lowland plots (Aragão *et*
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7 883 *al.*, 2009).
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Elevation (m)	RT_{Stem} (yrs)		$RT_{\text{FineRoots}}$ (yrs)		
3025	39	\pm 1.41			
3020	47	\pm 1.26	3.78	\pm 0.81	
2720	42	\pm 1.48	2.49	\pm 0.63	
2020	49	\pm 2.12	3.80	\pm 0.73	
1855	71	\pm 1.91	2.01	\pm 0.48	
1500	64	\pm 1.77			
1000	59	\pm 1.18	1.09	\pm 0.38	
210	47	\pm 1.31	0.34	\pm 0.61	
194	70	\pm 1.33	0.31	\pm 0.61	

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911 Figure Legends

912 **Figure 1** The variation with elevation of above- and below-ground standing carbon stocks (Mg
913 C ha⁻¹): (a) stem biomass and (b) fine root biomass. Biomass estimated using a height and
914 diameter based allometric equation (a, closed squares) showed a clear decrease in above-
915 ground biomass with increasing elevation, both when data points from this study were
916 combined with data presented in Aragao *et al.* (2009) (dotted line, $y=-0.042x+161.3$, $r^2=0.76$,
917 $P<10^{-4}$, $n=17$) and when we included the data points from the Kosñipata transect only (solid
918 line, $y=-0.023x+116.5$, $r^2=0.65$, $P=0.008$, $n=9$). Biomass estimated without including height
919 data (a, open triangles) showed no change in above-ground biomass with elevation ($y=-$
920 $0.022x+180.3$, $r^2=0.26$, $P=0.24$, $n=7$). Stem biomass values for the lowlands (a, open squares)
921 were obtained from Aragão *et al.* (2009). Root carbon stocks were from the top 30 cm of soil.
922 Root carbon values were obtained from nine soil cores at each elevation (only five at 1000 m).
923 Root carbon content was estimated at 50% as in Malhi *et al.* (2009). Error bars are SE of the
924 mean. The estimated base of the cloud immersion zone is located at 1500 – 1800 m.

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926 **Figure 2** The net primary productivity (NPP) of the seven pre-montane and montane sites from
927 this study compared to values from nine sites in lowland Amazonia. All values to the right of
928 the dotted line, described as published results from lowland Amazonia, are presented in Aragão
929 *et al.* (2009). Bars correspond to NPP_{Total} for each site, they combine NPP_{Canopy} (pale grey),
930 $NPP_{FineRoot}$ (dark grey), NPP_{Stem} (white), and $NPP_{CoarseRoot}$ (black). Error bars are SE of the
931 mean.

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933 **Figure 3** Above- and below-ground net primary productivity (Mg C ha⁻¹ yr⁻¹) along the
934 elevational gradient. (a) NPP_{Canopy} (pale grey), (b) $NPP_{FineRoot}$ (dark grey) and (c) NPP_{Stem}

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3 935 (white). All values to the right of the vertical line are presented in Malhi *et al.* (2009) and
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5 936 Aragão *et al.* (2009). Error bars are SE of the mean.
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10 938 **Figure 4** Ratio of below- to above-ground net primary productivity (NPP_{BG}/NPP_{AG}). Results
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12 939 from this study (closed squares) and published results from lowland Amazonia (Aragão *et al.*,
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14 940 2009, Malhi *et al.*, 2009) are represented. Error bars are SE of the mean. The estimated base of
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16 941 the cloud immersion zone is located at 1500 – 1800 m.
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20 943 **Figure 5** Partitioning of net primary productivity (NPP) components along the elevational
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22 944 gradient. (a) NPP_{Stem}/NPP_{Total} , (b) NPP_{Canopy}/NPP_{Total} (c) $NPP_{FineRoot}/NPP_{Total}$ ratios along the
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24 945 elevational gradient. Data from this study (closed squares) is compared to data presented in
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26 946 Aragão *et al.* (2009) (open triangles). Mean value represented by a solid horizontal line. Error
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28 947 bars are SE of the mean. The estimated base of the cloud immersion zone is located at 1500 –
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30 948 1800 m.
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34 950 **Figure 6** Above- (AG) and below-ground (BG) net primary productivity (NPP) relationships
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36 951 with NPP_{Total} . The figure shows NPP_{AG} (closed triangles) and NPP_{BG} (open triangles) data from
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38 952 lowland Amazonian forests published by Aragão *et al.* (2009) as well as NPP_{AG} (closed circles)
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40 953 and NPP_{BG} (open circles) data from the Kosñipata transect. In both forests, a regression
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42 954 analysis with the intercept set to 0 showed a significant positive relationship between NPP_{AG} ,
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44 955 NPP_{BG} and NPP_{Total} . For the Kosñipata transect, NPP_{AG} (solid line, $y = 0.58 \pm 0.025 x$, $r^2 = 0.94$,
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46 956 $P < 10^{-4}$, $n = 9$) and NPP_{BG} (solid line, $y = 0.41 \pm 0.022 x$, $r^2 = 0.89$, $P < 10^{-4}$, $n = 9$). In lowland
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48 957 Amazonian forests, NPP_{AG} (dotted line, $y = 0.61 \pm 0.035 x$, $r^2 = 0.52$, $P < 0.04$, $n = 8$) and NPP_{BG}
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50 958 (dotted line, $y = 0.38 \pm 0.032 x$, $r^2 = 0.40$, $P < 0.08$, $n = 8$). For the combined dataset, NPP_{AG}
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3 959 $(y=0.54\pm 0.026x, r^2=0.89, P<0.0005, n=16)$ and $NPP_{BG} (y=0.44\pm 0.024 x, r^2=0.93, P<0.0005,$
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6 960 $n=16)$. Error bars are SE of the mean.

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10 962 **Figure 7** Relationships between the two above-ground NPP components. We include values
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12 963 from the Kosñipata transect (closed squares, $y=1.73\pm 0.23 x, r^2=0.90, P<0.0005, n=9$) and from
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14 964 lowland sites presented in Aragão *et al.* (2009) and Malhi *et al.* (2009) (open triangles,
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16 965 $y=1.58\pm 0.36 x, r^2=0.44, P<0.05, n=11$). Error bars are SE of the mean.

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22 967 **Figure 8** (a) Stem (b) and fine root carbon residence time (years) along the elevational
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24 968 gradient. Error bars are SE of the mean. The estimated base of the cloud immersion zone is
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26 969 located at 1500 – 1800 m.

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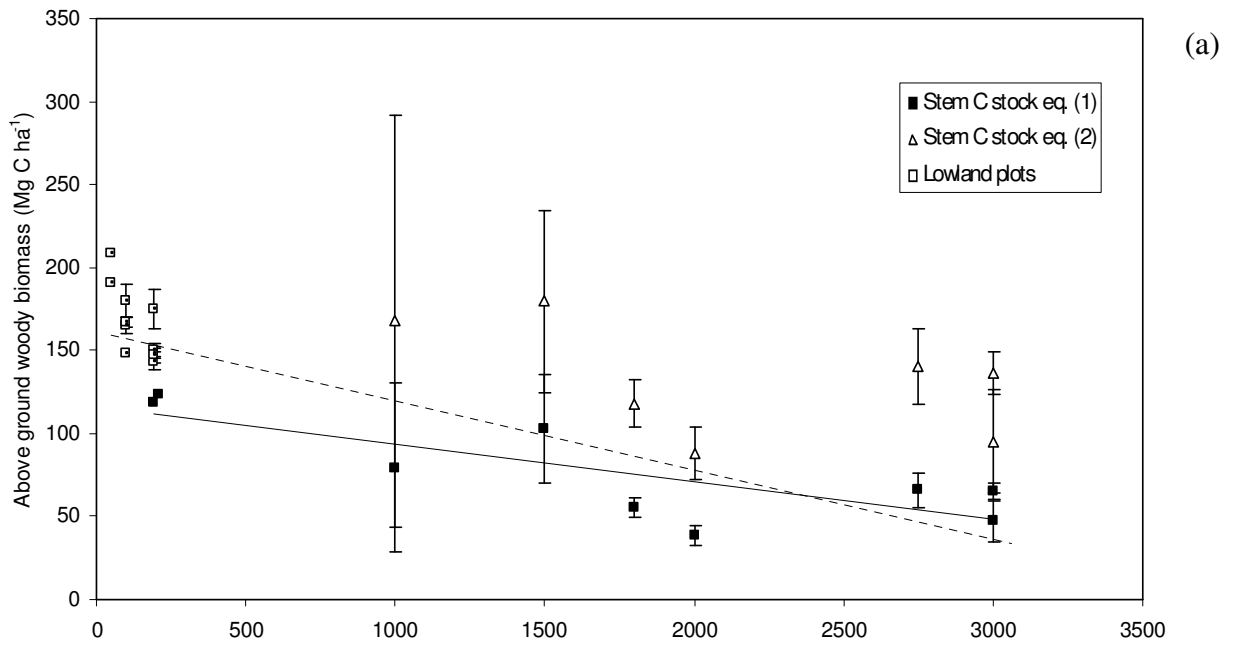
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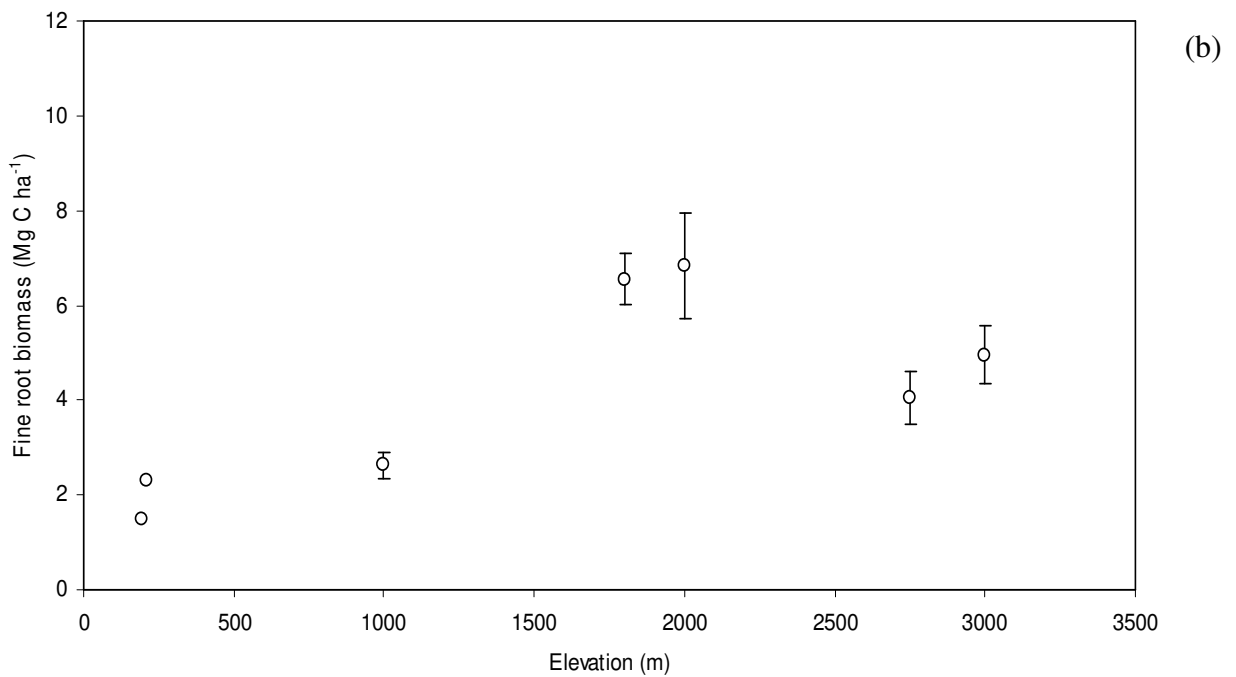
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984 Figures

985 **Figure 1**

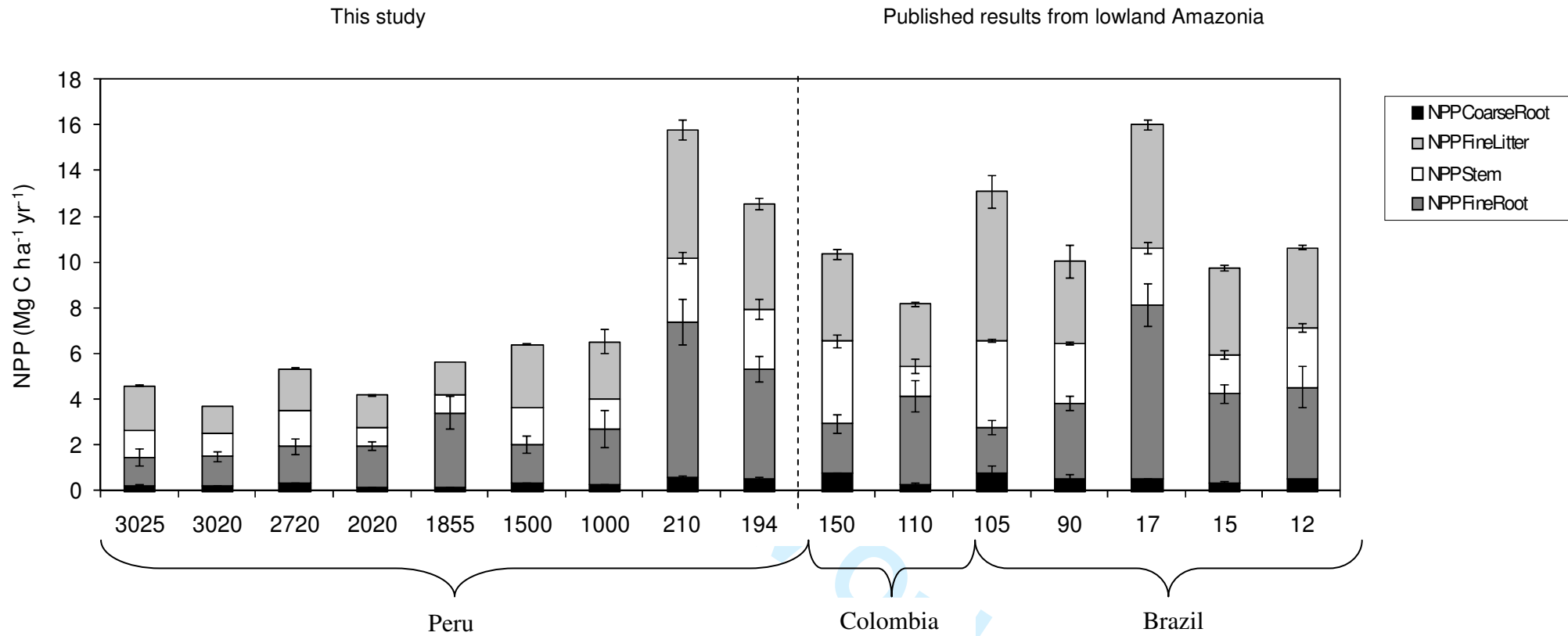


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988 **Figure 2**



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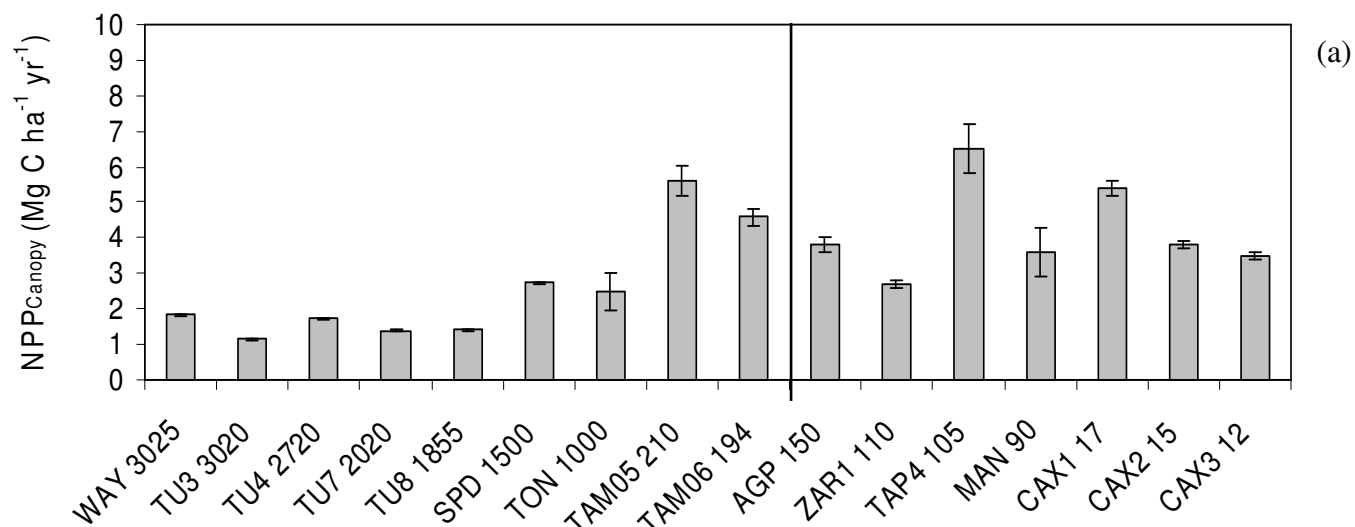
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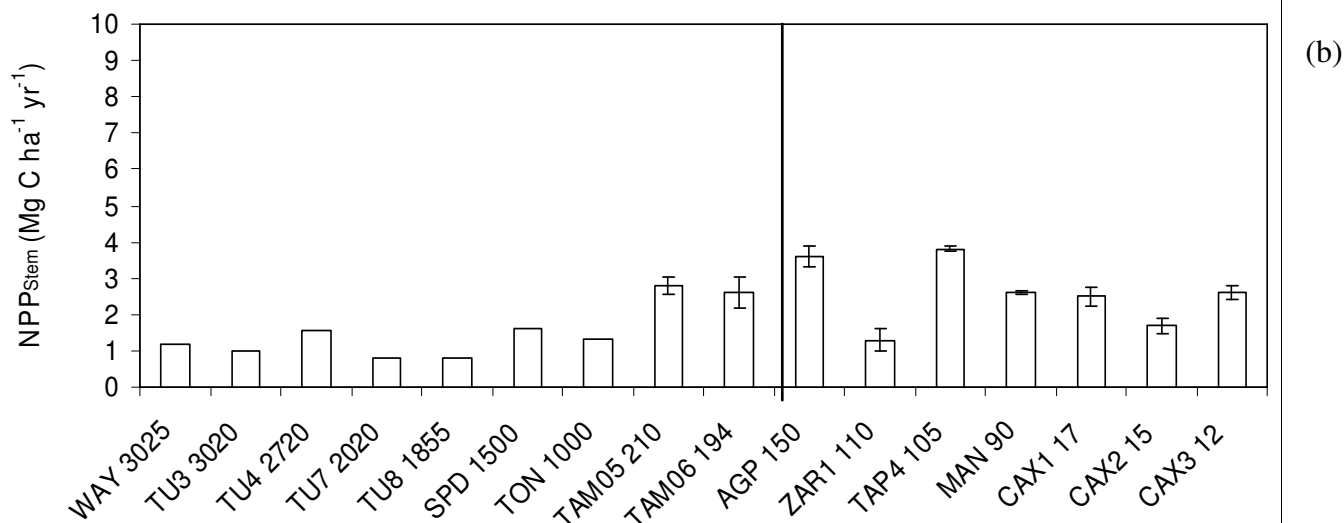
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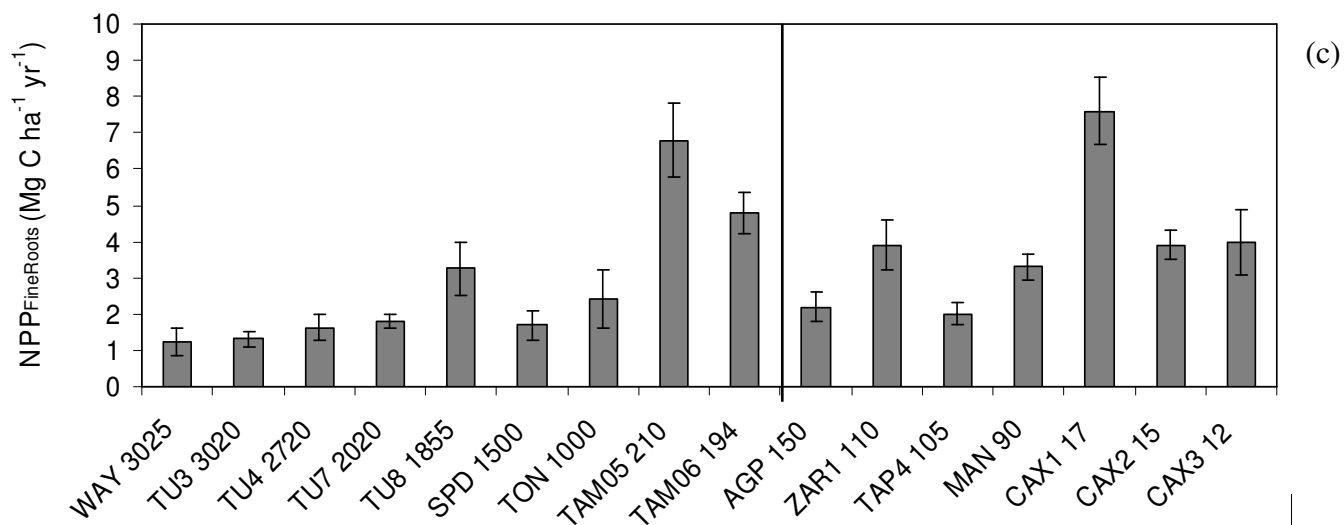
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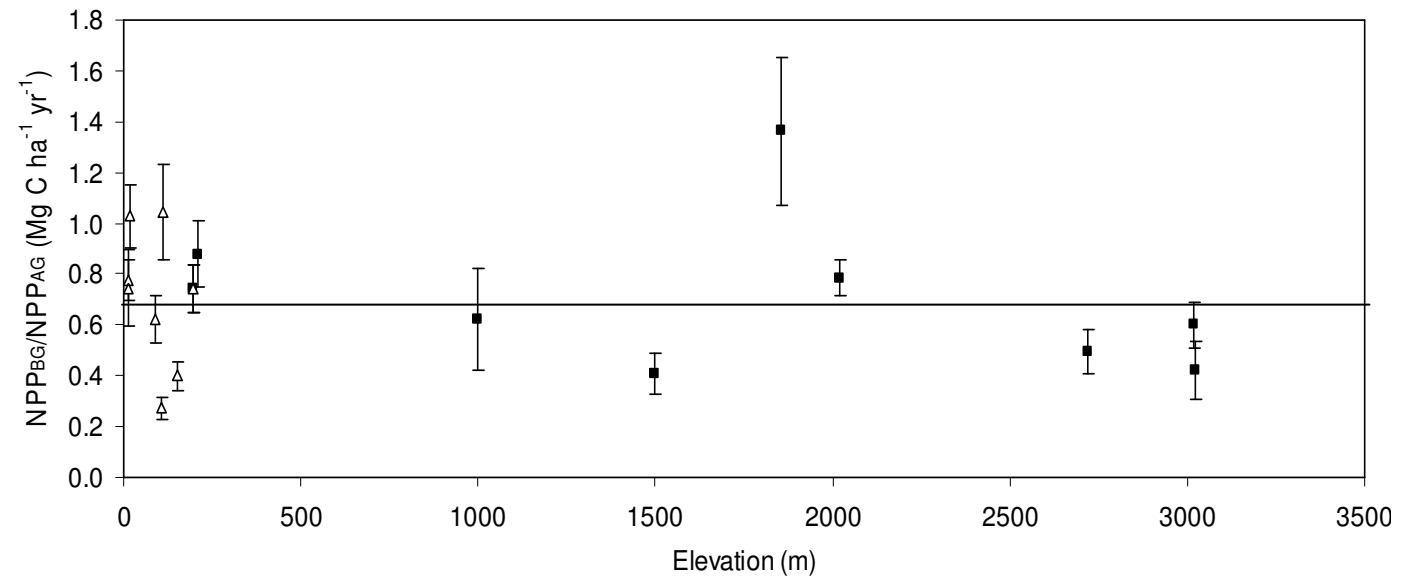


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Figure 4



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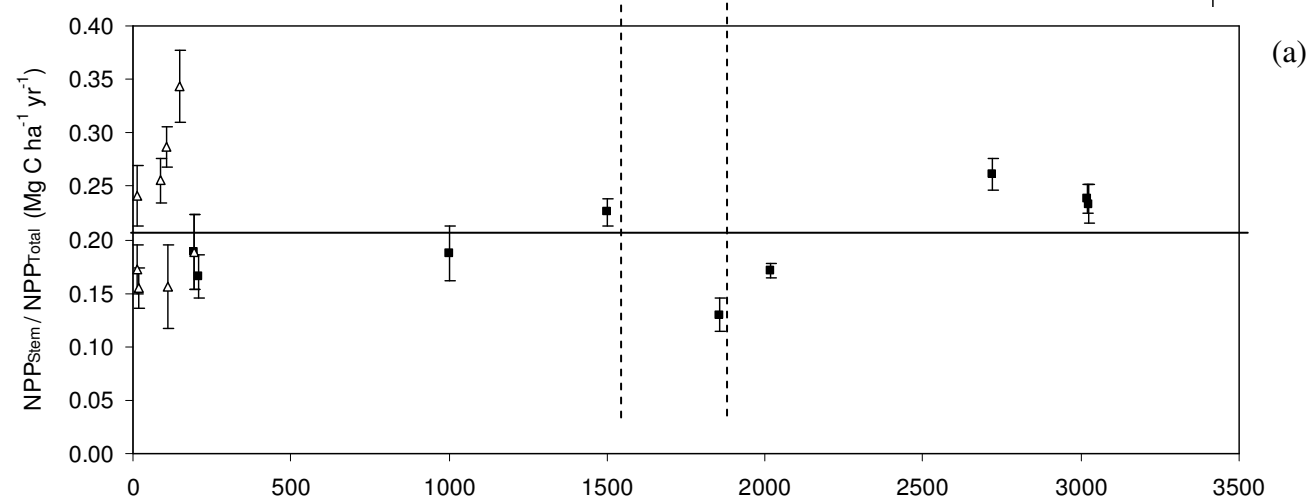


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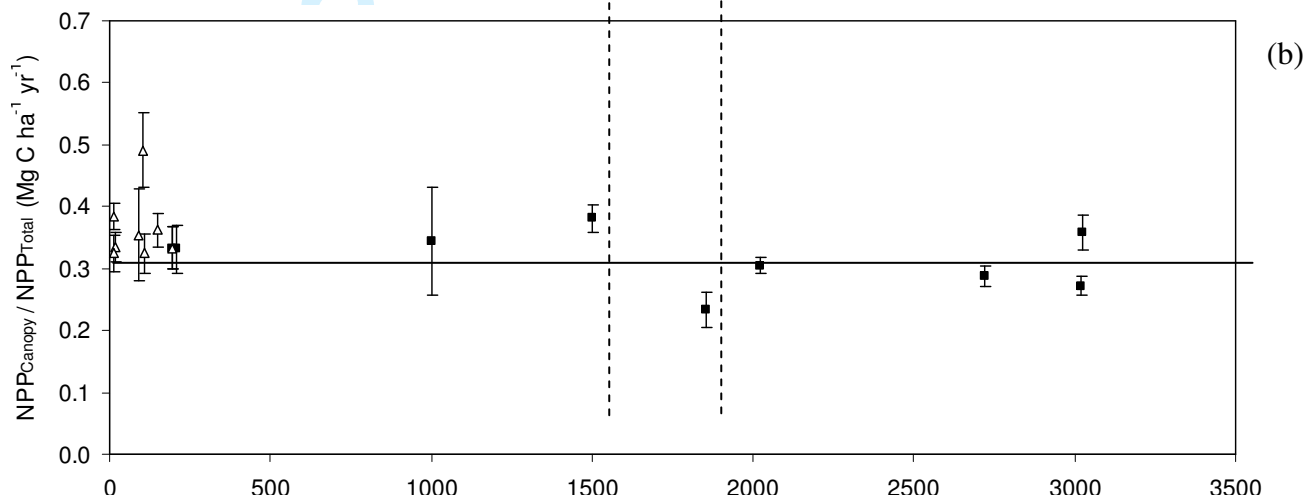
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Figure 5

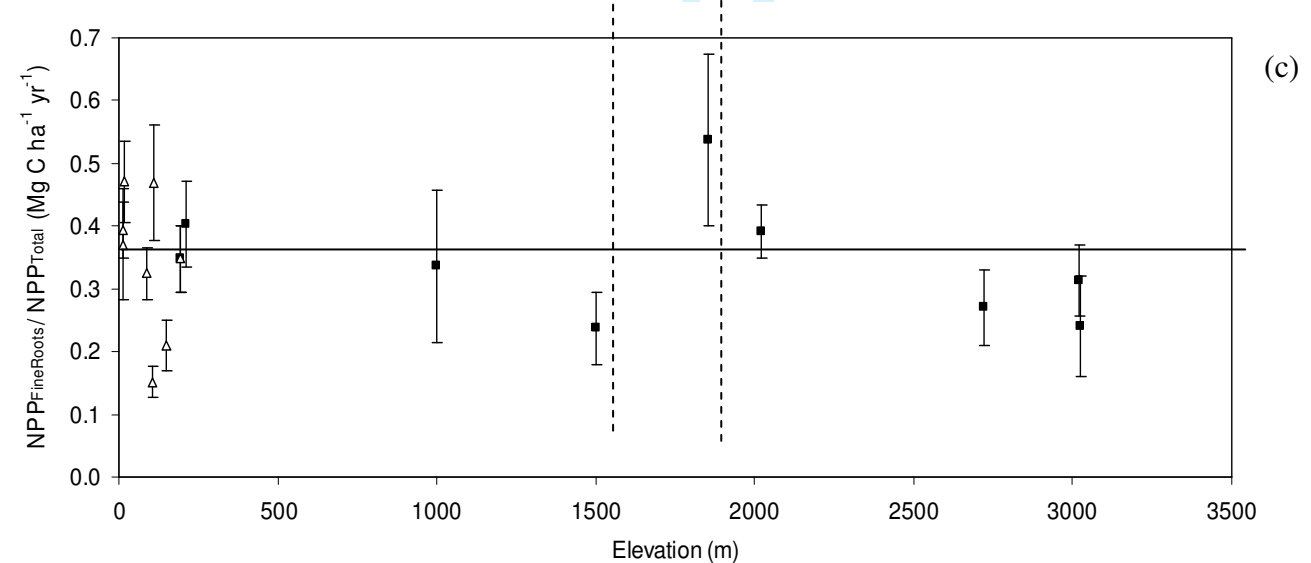
■ This study
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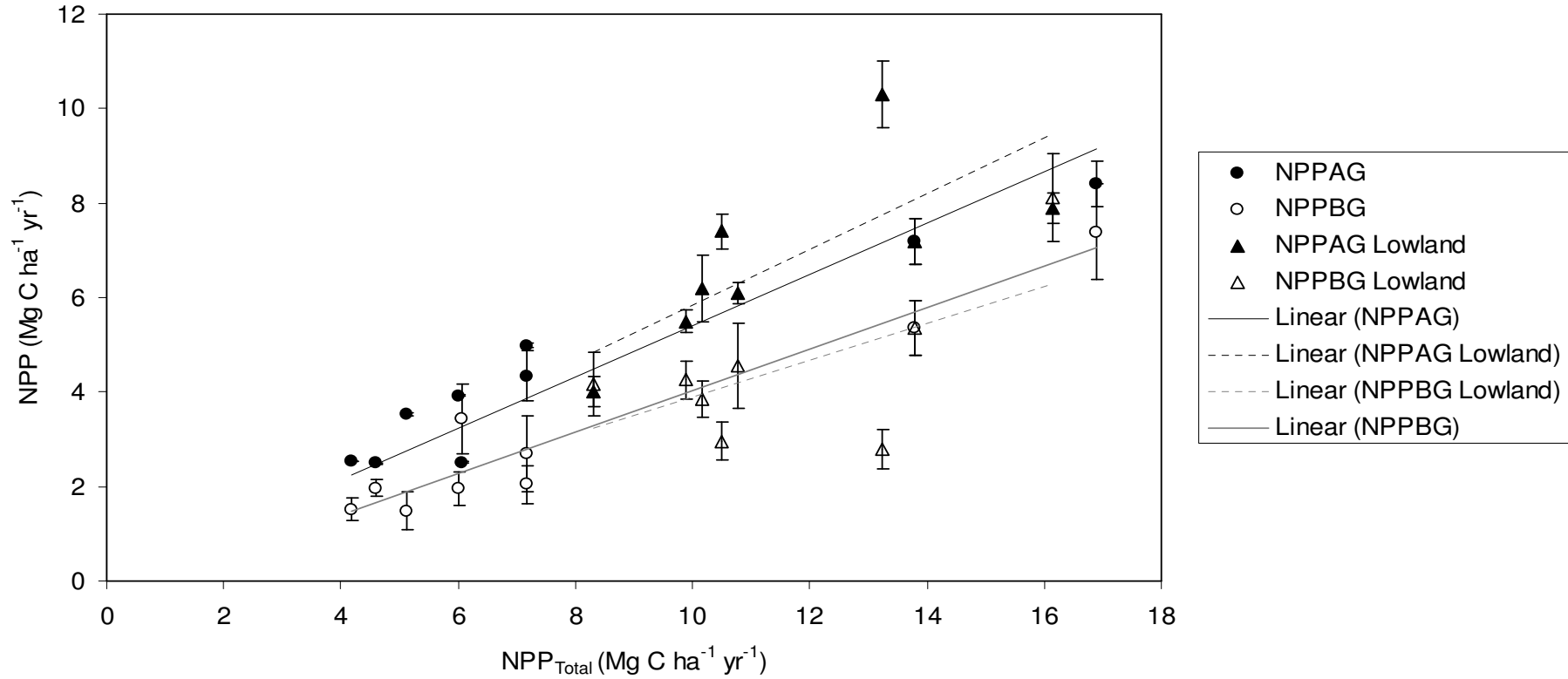
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1014 **Figure 6**

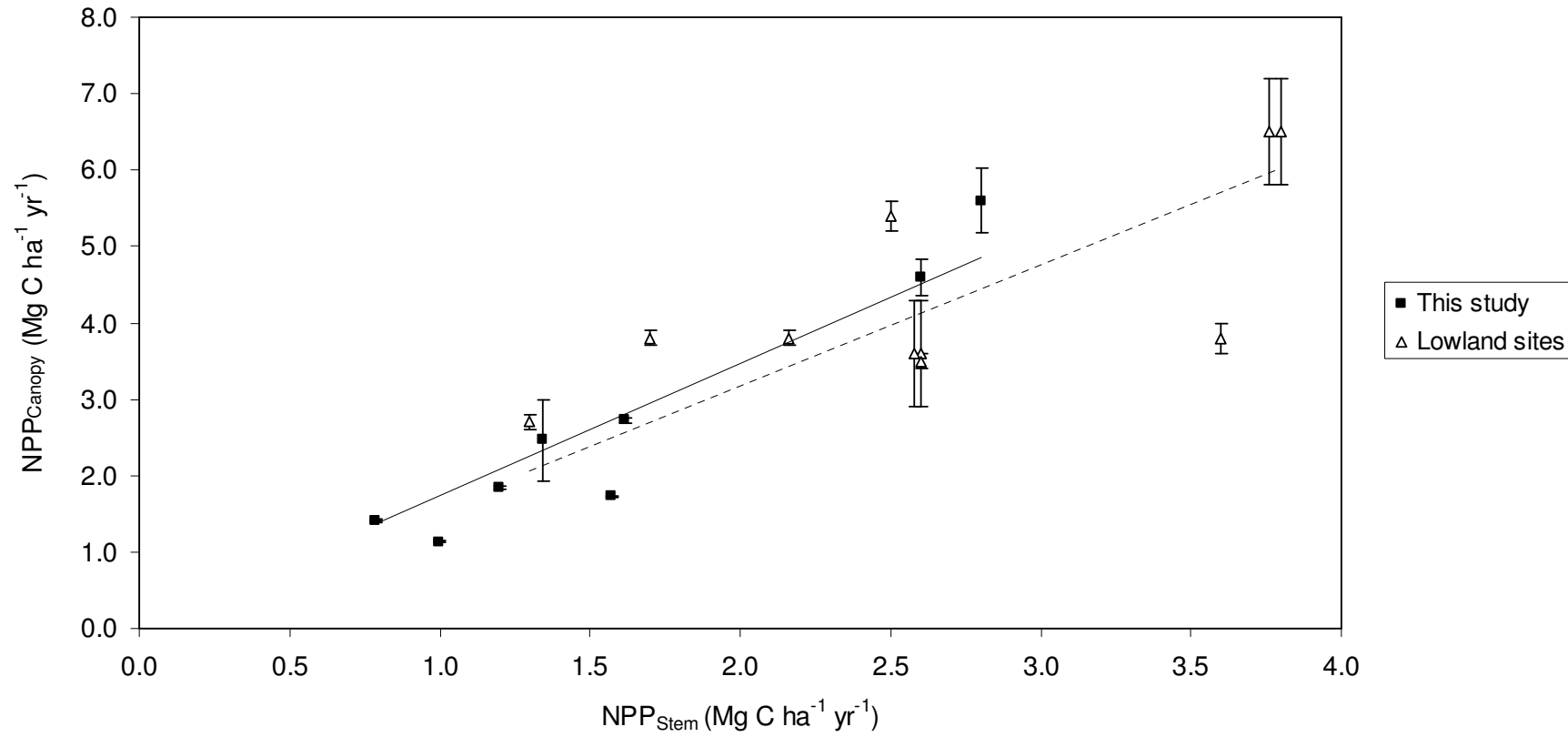


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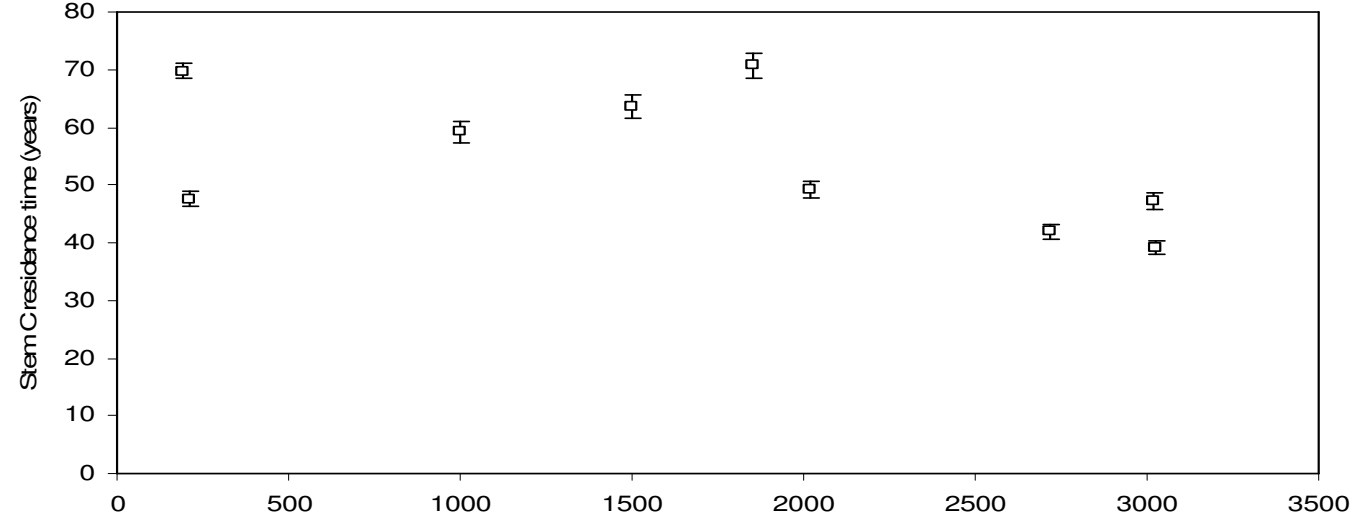
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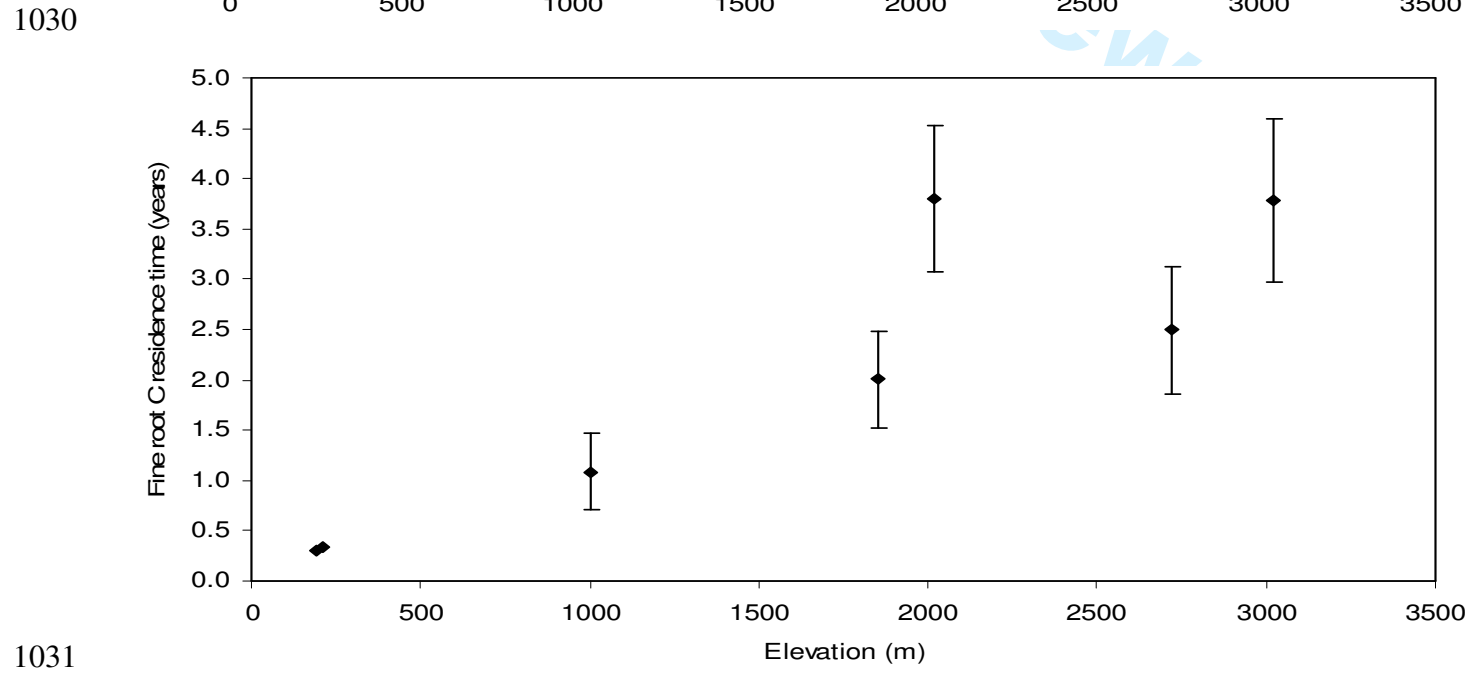
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1029 **Figure 8**



(a)



(b)

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