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Thaise Emilio, Carlos A. Quesada, Flávia R.C. Costa, Hans ter Steege [and others]

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Plant Ecology & Diversity, 2014
Vol. 7, Issues 1–2, 215–229, http://dx.doi.org/10.1080/17550874.2013.772257

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Soil physical conditions limit palm and tree basal area in Amazonian forests

Thaise Emilio[a]*, Carlos A. Quesada[b], Flávia R.C. Costa[c], William E. Magnusson[c], Juliana Schietti[a], Ted R. Feldpausch[d], Roel J.W. Brienen[d], Timothy R. Baker[d], Jerome Chave[e], Estebán Álvarez[f], Alejandro Araújo[g], Olaf Bánki[h], Carolina V. Castilho[i], Eurídice N. Honorio C.[d,j], Timothy J. Killeen[k], Yadvinder Malhi[l], Erick M. Oblitas Mendoza[m], Abel Monteagudo[n], David Neill[o], Germaine Alexander Parada[f], Antonio Peña-Cruz[n], Hirma Ramirez-Angulo[p], Michael Schwarz[q], Marcos Silveira[r], Hans ter Steege[s], John W. Terborgh[t], Raquel Thomas[u], Armando Torres-Lezama[p], Emilio Vilanova[p] and Oliver L. Phillips[d]

[a]Programa de Pós-Graduação em Ecologia, Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brasil; [b]Coordenação de Pesquisa em Dinâmica Ambiental, INPA, Manaus, Brasil; [c]Coordenação de Pesquisa em Biodiversidade, INPA, Manaus, Brasil; [d]School of Geography, University of Leeds, Leeds, UK; [e]Laboratoire Evolution et Diversité Biologique, CNRS and Université Paul Sabatier, Toulouse, France; [f]Medellín Botanical Garden, Medellín, Colombia; [g]Museo de Historia Natural Noel Kempff Mercado, Santa Cruz, Bolivia; [h]Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Amsterdam, Nederlands; [i]EMBRAPA, Centro de Pesquisa Agroflorestal de Roraima, Boa Vista, Roraima, Brasil; [j]Instituto de Investigaciones de la Amazonía Peruana, Iquitos, Peru; [k]Conservation International, Arlington, USA; [l]Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford, UK; [m]Programa de Capacitação Institucional, INPA, Manaus, Brasil; [n]Jardín Botánico de Missouri, Oxapampa, Perú; [o]Universidad Estatal Amazónica, Facultad de Ingeniería Ambiental, Puyo, Pastaza, Ecuador; [p]Instituto de Investigaciones para el Desarrollo Forestal (INDEFOR,) Universidad de Los Andes, Mérida, Venezuela; [q]University of Applied Sciences Eberswalde, Eberswalde, Germany; [r]Centro de Ciências Biológicas e da Natureza, Universidade Federal do Acre, Rio Branco, Brasil; [s]Naturalis Biodiversity Center, Leiden, Netherlands; [t]Nicholas School of the Environment and Earth Sciences, Duke University, Durham, USA; [u]Iwokrama International Centre for Rain Forest Conservation and Development, Iwokrama, Guyana

(*Received 7 March 2012; final version received 18 May 2012*)

Background: Trees and arborescent palms adopt different rooting strategies and responses to physical limitations imposed by soil structure, depth and anoxia. However, the implications of these differences for understanding variation in the relative abundance of these groups have not been explored.
Aims: We analysed the relationship between soil physical constraints and tree and palm basal area to understand how the physical properties of soil are directly or indirectly related to the structure and physiognomy of lowland Amazonian forests.
Methods: We analysed inventory data from 74 forest plots across Amazonia, from the RAINFOR and PPBio networks for which basal area, stand turnover rates and soil data were available. We related patterns of basal area to environmental variables in ordinary least squares and quantile regression models.
Results: Soil physical properties predicted the upper limit for basal area of both trees and palms. This relationship was direct for palms but mediated by forest turnover rates for trees. Soil physical constraints alone explained up to 24% of palm basal area and, together with rainfall, up to 18% of tree basal area. Tree basal area was greatest in forests with lower turnover rates on well-structured soils, while palm basal area was high in weakly structured soils.
Conclusions: Our results show that palms and trees are associated with different soil physical conditions. We suggest that adaptations of these life-forms drive their responses to soil structure, and thus shape the overall forest physiognomy of Amazonian forest vegetation.

Keywords: ecological limiting factors; life-forms; palm-dominated forests; quantile regression; soil structure; tropical forest; vegetation types

Introduction

Amazonian forests play an important role in the global carbon cycle but how much carbon is stored in these ecosystems is still uncertain. Variation in biomass is directly related to variation in stand basal area and stand-level wood density. Mean stand-level wood density is dependent both on species composition (Baker et al. 2004) and environmental factors (Patiño et al. 2009), such as soil fertility and climate. The environmental correlates of basal area are less clear. There is important site-to-site variability (Malhi et al. 2006) that appears to be less correlated with broad-scale regional predictors than with local predictors such as disturbance or the presence (or absence) of limiting soil properties.

Soil and climate have been widely investigated to understand forest structure and composition in Amazonia (Laurance et al. 1999; Roggy et al. 1999; Malhi et al. 2006; ter Steege et al. 2006; Quesada et al. 2012) and elsewhere (Paoli et al. 2007; Slik et al. 2010). Soil physical conditions in particular, such as water-holding capacity, drainage, and physical structure, are important factors that affect tree growth, mortality and floristic composition in the tropical forests worldwide (Dietrich et al. 1996; Ferry et al. 2010; Gourlet-Fleury et al. 2011; Quesada et al. 2012). However,

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*Corresponding author. Email: thaise.emilio@gmail.com their influence in determining large-scale patterns of forest structure and composition in the tropics is poorly known.

Structural dominance by palms (and other life-forms, such as lianas and bamboos) has been used in the Brazilian forest classification system (IBGE 2012) to distinguish forest types (see Appendix 1, Emilio et al. 2010), and to develop improved allometric equations for biomass calculation in the Brazilian Amazon (Nogueira et al. 2008). Palm-dominated forests cover 20% of Brazilian Amazonia (IBGE 1998) and large extensions of other Amazonian countries. Given this widespread occupation of forest by palms, understanding how palms vary in abundance could help to better understand basal area and biomass variation across Amazonian forests. At a single site in the Amazon, Castilho et al. (2006) reported that tree biomass was higher in well-drained clay soils while arborescent palm biomass was higher in poorly drained, sand-rich soils. This suggests that soil physical conditions may have different effects on these two plant life-forms. The aim of this study was to investigate the relationships between soil physical properties and the basal area of both trees and palms across Amazonia.

In addition to the direct effect that soil physical properties may exert on plant roots, soil physical constraints can also indirectly affect forest basal area by increasing turnover. Quesada et al. (2012) showed that Amazonian forests have greater turnover rates where soil properties constrain root development (e.g. shallow impediment layers, high bulk density, anoxic horizon). At local scales, the proportion of stems that die uprooted or snapped off by other falling trees is generally greater in sandy and waterlogged soils (Toledo et al. 2011). The dominant modes of mortality may also vary depending on whether the plant is a tree or a palm. In Ecuador, dicotyledonous trees mostly died uprooted and snapped while arborescent palms mostly died standing and snapped (Gale and Barfod 1999).

The differences in the response of plant life-forms, such as palms and trees, to soil physical properties and disturbance are likely to be related to differences in their physiological and morphological adaptations, particularly growth strategies and the root system. Palms lack vascular cambium and do not show secondary growth. To compensate, primary tissues continually increase in their mechanical strength with gradual lignification of fibrous and parenchymatous tissue, resulting in stronger stems as palm height increases (Tomlinson 2006). The absence of secondary growth in palms may be advantageous against wind damage, but prevents dormancy, implying that they must have special adaptations (e.g. aerenchyma, pneumatophores) to deal with seasonally stressful conditions (Tomlinson 2006). In contrast, cambial dormancy is a common strategy in many tree species (Zuidema et al. 2012) and allows them to occupy seasonally unfavourable environments, such as seasonally dry or waterlogged forests, with or without morphological adaptations to such conditions.

Palms and dicotyledonous trees also differ in their root systems. Trees develop roots that can reach depths of up to 10 m to access water (Nepstad et al. 1994). The development of deep roots provides mechanical stability and helps trees to prevent water deficit where soils are deep and well structured. Palms do not have extensive root systems, but they compensate this disadvantage by developing high root water pressures (Davis 1961). This may confer a competitive advantage in shallow or compacted soils. In soils that limit root development, trees may be more susceptible to anchorage problems, especially if associated with steep topography (Gale and Barfod 1999; Toledo et al. 2011). In contrast, palms are more stable than trees due to their stem anatomy (Tomlinson 1990) that allows them to remain strongly anchored to the ground, even without deep roots. In addition, palms have smaller canopies and large leaves instead of woody branches. Palm leaves are less carbon expensive to rebuild than tree branches, so their loss if hit by a falling branch or tree may be expected to have relatively minor impact on the structure and stability of the plant, and its carbon balance. Hence, palms appear to be better adapted to grow in highly dynamic forests.

In summary, we would expect that trees are at an advantage in deep, well-drained soils where their extensive root systems provide good anchorage and are able to extensively exploit soil resources. On the other hand, palms may outcompete trees in shallow, poorly drained soils, since they may be able to cope better with water-saturated soil and limited rooting space. Therefore, one could expect that the responses of palms and trees to soil physical properties shows opposite patterns, and this could result in a significant shift in the relative contribution of trees and palms to forest structure across Amazonia as a function of soil properties. So far, no attempt has been made to understand what could explain the relative contribution of arborescent palms and trees to forest structure and physiognomy across Amazonia.

Here, we use a unique set of permanent study plots across Amazonia to analyse the relationship between soil physical constraints and basal area of trees and palms in order to better understand how soil physical limitations affect the structure and physiognomy of Amazonian forests. We also explore the relationship among precipitation, soil fertility and forest turnover and basal area variation in trees and palms.

Methods

Vegetation data

We compiled forest-structure data from the RAINFOR Forest Plots database (Lopez-Gonzalez et al. 2011, downloaded from http://www.forestplots.net (Lopez-Gonzalez et al. 2012)) and the PPBio database (Pezzini et al. 2012, downloaded from http://ppbio.inpa.gov.br (PPBio 2012)). We used data from 74 Amazonian plots that have both plant and soil data. Most plots are 1 ha in area (see Table 1 for plot dimensions and data sources). In each of these plots, all stems (trees and palms) with a diameter at breast height (DBH) $\geq$ 10 cm were measured and identified to at least family level. The basal areas of trees and arborescent palms were calculated and used as response variables in regression analyses.

Table 1. Basal area (BA) and environmental data from 74 Amazonian forest plots used in this study.

									Soil physical constraint scores							
Plot code	Latitude	Longitude	Altitude (m a.s.l.)	Plot area (ha)	Palm BA (m^2 ha^{-1})	Palm BA (%)	Tree BA (m^2 ha^{-1})	Tree BA (%)	Soil anoxia	Topography	Soil depth*	Soil structure*	Precipitation (m^m $year^{-1}$)	IE	Forest class**	Turnover rates (%)
ALF-01^R	−9.59830	−55.93690	269	1.00	0.18	2.42	7.27	97.58	0	0	4	1	2356	2.04		1.73
ALF-02^R	−9.57840	−55.91760	277	1.00	3.79	14.15	22.99	85.85	0	0	4	2	2356	2.23		
ALM-01^R	−11.80000	−71.47000	400	2.00	4.04	13.41	26.08	86.59	2	2	4	1	2395	6.57		2.33
ALP-11^R	−3.95000	−73.43000	114	0.44	2.31	8.07	26.32	91.93	0	3	3	1	2784	3.62	TF-3	3.09
ALP-12^R	−3.95000	−73.44000	125	0.4	0.34	1.32	25.37	98.68	3	0	1	1	2784	2.46	TF-2	2.05
ALP-21^R	−3.95000	−73.44000	114	0.48	1.15	4.49	24.48	95.51	3	3	4	3	2784	0.4	TF-3	2.58
ALP-22^R	−3.95000	−73.44000	125	0.44	2.04	7.49	25.18	92.51	0	3	4	1	2784	5.13	TF-2	2.12
ALP-30^R	−3.95000	−73.43000	130	1.00	0.21	0.94	22.1	99.06	0	0	4	3	2784	0.49	TF-1	1.27
BOG-01^R	−0.70000	−76.48000	257	1.00	1.32	4.39	28.78	95.61	0	3	1	2	3133	12.47		2.65
BOG-02^R	−0.70000	−76.47000	284	1.00	1.94	7.74	23.12	92.26	0	4	1	2	3133	8.48		3.80
CAX-01^R	−1.74000	−51.46000	15	1.00	0.01	0.03	33	99.97	0	0	4	4	2206	1.81	TF-11	0.86
CAX-02^R	−1.74000	−51.46000	15	1.00	0.02	0.07	28.47	99.93	0	0	4	4	2206	1.56	TF-11	1.74
CAX-06^R	−1.72000	−51.46000	20	1.00	0.02	0.05	36.79	99.95	0	0	4	4	2206	2.28	TF-12	1.27
CRP-01^R	−14.54000	−61.50000	350	1.00	0	0.00	19.05	100.00	0	3	3	3	1364	7.66		3.03
CRP-02^R	−14.54000	−61.50000	350	1.00	0.18	0.76	23.62	99.24	0	2	3	3	1364	5.22		3.13
CUZ-01^R	−12.50000	−68.97000	190	1.00	1.75	7.44	21.77	92.56	2	0	3	0	2098	8.69	FAT-2	2.53
CUZ-02^R	−12.50000	−68.97000	190	1.00	4.01	14.10	24.42	85.90	2	0	3	0	2098	8.07	FAT-2	2.43
CUZ-03^R	−12.50000	−68.96000	190	1.00	3.22	12.62	22.29	87.38	3	0	3	0	2098	6.82	FAT-1	2.68
CUZ-04^R	−12.50000	−68.96000	190	1.00	3.96	14.27	23.8	85.73	2	0	3	0	2098	8.12	FAT-1	2.90
DKE-02^P	−2.95000	−59.94000	85	1.00	0.11	0.54	20.41	99.46	0	0	4	4	2197	1.75		
DKE-03^P	−2.95000	−59.93000	100	1.00	0.04	0.17	23.39	99.83	0	0	4	3	2197	1.13		
DOI-01^R	−10.57000	−68.31000	203	1.00	1.26	4.95	24.18	95.05	1	0	3	0	1902	2.92		2.00
DOI-02^R	−10.55000	−68.31000	203	1.00	0.06	0.38	15.54	99.62	3	0	2	0	1902	5.62		4.32
ELD-01^R	6.11484	−61.41159	210	0.25	0	0.00	31.82	100.00	0	2	4	4	2522	1.11		0.91

(*Continued*)

Table 1. (Continued)

Plot code	Latitude	Longitude	Altitude (m a.s.l.)	Plot area (ha)	Palm BA (m^2 ha^{-1})	Palm BA (%)	Tree BA (m^2 ha^{-1})	Tree BA (%)	Soil physical constraint scores: Soil anoxia	Topography	Soil depth*	Soil structure*	Precipitation (m^m $year^{-1}$)	IE	Forest class**	Turnover rates (%)
HCC-22^{R}	−14.53000	−60.73000	747	1.00	2.22	8.79	23.04	91.21	0	0	3	3	1479	4.74		2.60
ELD-02^{R}	6.11470	−61.41155	180	0.25	0	0.00	37.57	100.00	0	2	4	4	2522	0.76		0.54
ELD-03^{R}	6.40059	−61.08833	380	0.25	0	0.00	16.64	100.00	0	2	0	1	2522	2.07		1.81
ELD-04^{R}	6.08836	−61.40058	350	0.25	0	0.00	27.16	100.00	0	2	0	1	2522	3.27		1.36
FMH-01^{R}	5.17000	−58.69000	98	1.00	0	0.00	42.35	100.00	0	0	4	3	2822	1.09		0.49
FMH-02^{R}	5.17000	−58.69000	122	1.00	0	0.00	36.26	100.00	0	0	4	3	2822	1.00		1.28
FMH-03^{R}	5.18000	−58.70000	115	1.00	0	0.00	31.92	100.00	0	0	4	3	2822	0.34		0.89
HCC-21^{R}	−14.53000	−60.74000	729	1.00	1.66	6.73	23.01	93.27	0	0	2	1	1479	7.68		3.76
IPM-82^{P}	−5.63000	−62.19000	67	1.00	1.71	8.00	19.66	92.00	1	0	3	2	2574	2.44		
IPM-83^{P}	−5.64000	−62.18000	67	1.00	1.11	4.46	23.79	95.54	1	1	4	2	2574	3.29		
IWO-03^{R}	4.53000	−58.78000	100	1.00	0.04	0.11	35.28	99.89	0	0	4	3	2248	0.78		0.40
IWO-12^{R}	4.73000	−58.72000	61	1.00	0.1	0.40	24.72	99.60	1	0	4	1	2405	1.80		2.91
JAS-02^{R}	−1.06981	−77.61631	452	1.00	2.18	8.31	24.05	91.69	0	3	2	2	3645	3.05		2.89
JAS-03^{R}	−1.07713	−77.60966	384	1.00	1.06	3.75	27.19	96.25	0	2	3	2	3645	2.66		2.11
JAS-04^{R}	−1.07323	−77.61223	430	1.00	2.39	6.55	34.11	93.45	0	3	2	2	3645	3.24		1.95
JEN-11^{R}	−4.88000	−73.63000	151	1.00	0.2	0.77	25.66	99.23	0	1	4	4	2642	1.98	TF-1	1.77
JEN-12^{R}	−4.90000	−73.63000	122	1.00	1.17	4.76	23.43	95.24	2	0	2	3	2642	1.45	TF-1	1.04
JEN-13^{R}	−4.92000	−73.53000	145	1.00	4.58	19.69	18.68	80.31	3	0	3	2	2642	1.78		2.06
LFB-01^{R}	−14.58000	−60.83000	245	1.00	0.95	3.56	25.72	96.44	0	0	4	4	1479	1.25		2.70
LFB-02^{R}	−14.58000	−60.83000	227	1.00	1.14	3.93	27.89	96.07	0	0	4	4	1479	1.52		2.73
LSL-01^{R}	−14.40000	−61.14000	189	1.00	0.4	2.21	17.68	97.79	4	0	2	3	1460	2.08		2.51
LSL-02^{R}	−14.40000	−61.14000	190	1.00	0.48	1.89	24.93	98.11	3	0	3	3	1460	2.55		1.39
MNU-03^{R}	−11.90000	−71.40000	312	2.00	4.08	14.63	23.8	85.37	0	0	2	0	2477	1.53		3.74
MNU-04^{R}	−11.91000	−71.40000	312	2.00	3.8	14.50	22.41	85.50	1	2	3	1	2477	3.63		2.52
MNU-05^{R}	−11.88000	−71.41000	312	2.00	2.09	6.24	31.42	93.76	3	0	4	1	2477	8.52		1.91

(*Continued*)

Table 1. (Continued)

									Soil physical constraint scores							
Plot code	Latitude	Longitude	Altitude (m a.s.l.)	Plot area (ha)	Palm BA (m^2 ha^{-1})	Palm BA (%)	Tree BA (m^2 ha^{-1})	Tree BA (%)	Soil anoxia	Topography	Soil depth*	Soil structure*	Precipitation (m^m year^{-1})	IE	Forest class**	Turnover rates (%)
MNU-06^R	−11.89000	−71.40000	312	2.25	5.04	16.34	25.81	83.66	3	0	4	1	2477	8.59		2.40
MTH-01^R	−8.88000	−72.79000	246	1.00	2.92	14.96	16.6	85.04	0	4	3	2	1655	8.04		2.93
NOU-02^R	4.08000	−52.67000	110	1.00	0.04	0.12	33.14	99.88	0	0	4	4	3280	1.57		1.27
NOU-10^R	4.08000	−52.67000	110	1.00	0	0.00	23.23	100.00	0	0	4	4	3280	1.74		2.01
NOU-12^R	4.08000	−52.67000	110	1.00	0.6	1.97	29.84	98.03	0	2	4	4	3280	2.13		1.85
NOU-17^R	4.08000	−52.67000	110	1.00	0.47	1.31	35.33	98.69	0	2	3	2	3280	2.40		1.02
NOU-21^R	4.08000	−52.67000	110	1.00	0.24	0.77	31.03	99.23	0	2	4	3	3280	1.32		1.27
POR-01^R	−10.82000	−68.78000	268	1.00	1.26	4.11	29.39	95.89	0	2	3	1	1720	1.41		2.01
POR-02^R	−10.80000	−68.77000	268	1.00	1.94	8.78	20.15	91.22	0	2	1	2	1720	1.32		2.61
SUC-01^R	−3.25000	−72.91000	107	1.00	1.09	3.92	26.75	96.08	1	3	4	2	2813	3.77	TF-1	2.12
SUC-02^R	−3.25000	−72.90000	98	1.00	0.7	2.53	26.93	97.47	0	4	4	1	2813	3.71	TF-1	2.64
SUC-03^R	−3.25000	−72.92000	118	1.00	0.03	0.11	26.62	99.89	3	0	3	1	2813	6.23	TF-1	2.31
TAM-01^R	−12.84000	−69.29000	205	1.00	6.66	23.58	21.58	76.42	0	1	4	1	2523	2.96	FAT-3	2.64
TAM-02^R	−12.83000	−69.29000	210	1.00	6.1	20.90	23.09	79.10	0	0	2	0	2391	3.56	FAT-3	2.01
TAM-04^R	−12.84000	−69.28000	210	0.42	2.18	7.13	28.41	92.87	3	0	3	1	2523	4.14	SW	2.67
TAM-05^R	−12.83000	−69.27000	220	1.00	0.5	1.90	25.78	98.10	1	0	3	1	2391	4.47	TF-2	2.61
TAM-06^R	−12.84000	−69.30000	200	1.00	7.5	22.45	25.91	77.55	1	3	3	0	2523	5.67	FAT-3	2.39
TAM-07^R	−12.83000	−69.26000	225	1.00	0.49	2.02	23.74	97.98	0	1	4	2	2391	3.38	TF-2	2.67
TIP-03^R	−0.64000	−76.15000	221	1.00	0.44	1.67	25.95	98.33	3	0	3	0	2987	7.83		3.30
YAN-01^R	−3.44000	−72.85000	132	1.00	0.64	2.18	28.77	97.82	1	3	4	1	2786	9.21		3.12
YAN-02^R	−3.43000	−72.84000	109	1.00	0.42	1.36	30.53	98.64	1	2	4	3	2786	5.72		1.65
ZAR-01^R	−4.01000	−69.91000	126	1.00	0.71	4.22	16.1	95.78	1	0	3	3	2837	0.71		1.14
ZAR-02^R	−4.00000	−69.90000	126	1.00	1.7	8.79	17.64	91.21	0	0	3	2	2837	3.51		1.10
ZAR-03^R	−3.99000	−69.90000	130	1.00	0.4	1.82	21.58	98.18	0	1	3	2	2762	1.93		1.41
ZAR-04^R	−3.99000	−69.91000	146	1.04	0.63	2.43	25.3	97.57	0	1	3	2	2762	2.60		1.22

*Soil depth and structure scores inverted from Quesada et al. (2010).

**Modified from Anderson *et al.* 2009 (available for 23 plots).

^{P}Data downloaded from http://ppbio.inpa.gov.br; ^{R} data downloaded from http://www.forestplots.net

Soil sampling and determination of chemical and physical properties

Soil sampling and analysis were undertaken by the PPBio/HIDROVEG and RAINFOR projects (Malhi et al. 2002), using equivalent protocols (PPBio/HIDROVEG: http://ppbio.inpa.gov.br/manuais; RAINFOR: www.geog.leeds.ac.uk/projects/rainfor/projdocs.html). One soil pit was dug in the dominant soil type, where soil descriptions were made. In addition, samples were taken at 5–10 complementary points with a hand-held auger adapted to collect undisturbed soil samples (Eijkelkamp Agrisearch Equipment BV, Giesbeek, The Netherlands). Sampling points followed a random stratified distribution so as to obtain representative soil collections of each area. The soils were sampled up to 2 m deep, but chemical data reported here are for surface samples only (0–30 cm), while the entire profile was considered for soil physical properties. For a detailed description of the methods see Quesada et al. (2010).

Effective cation exchange capacity (I_E) is used here as a proxy for general soil fertility since there are strong relationships between I_E (hereafter called fertility), soil P and total elemental composition (Quesada et al. 2010). Samples were analysed for exchangeable cations by the silver-thiourea method (Pleysier and Juo 1980), and the sum of concentrations for exchangeable Ca, Mg, K, Na and Al are reported.

Soil descriptions followed a standard protocol (Jahn et al. 2006), with special attention to the measurement of effective soil depth, depth to C horizon (where possible), horizon distribution (i.e. identification and depth of visible soil diagnostic horizons), colour, distribution of rocks, concretions (i.e. presence of coarse, hard material in the soil as petroplinthite, gravel, or other hardened material), ironstone layers or other hardpans, redox features, root distribution, drainage capacity, soil hardness, soil structure (i.e. aggregate distribution, type and stability), organic matter content and topographic position of the pit. Three bulk density samples were collected from the pit walls at the same depths as for the soil samples (0–5, 5–10, 10–20, 20–30, 30–50, 50–100, 100–150, 150–200 cm).

For quantifying the magnitude of root-limiting soil physical properties (hereafter soil physical constraints), we used the same approach as in Quesada et al. (2010, 2012), assigning sequential scores to different levels of physical limitations. This was done by reading the field descriptions of soil and assigning to each category a score (Table 2; see details in Quesada et al. 2010). These scored categories provide information on topography, soil depth, soil structure and anoxic conditions in a semi-quantitative form. To aid interpretation, here we inverted Quesada's original scale for soil depth and structure, so that shallower, poorly structured soils had lower scores, while deeper, well-structured soils had higher scores (Table 2). We used each

Table 2. Soil physical constraint scores modified from Quesada et al. (2010).

Soil physical constraint rating categories	Score[1]
(1) *Effective soil depth* (soil depth, hardpans)	
Shallow soils (< 20 cm)	0
Less shallow (20–50 cm)	1
Hardpan or rock that allows vertical root growth; other soils between 50 and 100 cm deep.	2
Hardpan, rocks or C horizon ≥ 100 cm deep	3
Deep soils ≥ 150 cm	4
(2) *Soil structure*	
Very dense, very hard, very compact, without aggregation, root restrictive	0
Dense, compact, little aggregation, lower root restriction	1
Hard, medium to high density and/or with weak or block-like structure	2
Loose sand, slightly dense; well aggregated in sub-angular blocks, discontinuous pans	3
Good aggregation, friable, low density	4
(3) *Topography*	
Flat 0°	0
Gently sloping 1–8°	1
Gently undulating 8–19°	2
Steep 20–44°	3
Very steep > 45°	4
(4) *Anoxic conditions*	
Unsaturated conditions	0
Deep saturated zone (maximum of high saturation > 100 cm deep); deep redox features	1
Deep saturated zone (maximum of high saturation 50 cm deep); redox features	2
Seasonally flooded; soils with high clay content and very low porosity and/or dominated by plinthite	3
Constantly flooded; patches of stagnated water	4

[1] Soil depth and structure scores inverted from Quesada et al. (2010).

soil physical constraint characteristic as an independent explanatory variable in regression analyses.

Forest turnover

Forest turnover was calculated as the proportion of stems (trees and palms combined) entering and leaving the plot per year. Annual mortality and recruitment rates were estimated separately using standard procedures, based on logarithmic models. These models assume a constant probability of mortality and recruitment through each inventory period (Swaine et al. 1987; Phillips et al. 2004), and they were corrected for census interval following the recommendations by Lewis et al. (2004). We then considered the mean value of mortality and recruitment over the entire period as the forest turnover rate for each plot, which we present as a percentage of all stems present.

Data analysis

We used ordinary least square regressions (OLS) to examine the relationships between tree basal area, palm basal area, environmental predictor variables, and turnover rates. Environmental variables included the soil chemical and physical properties described above, and annual precipitation obtained from the interpolated WorldClim dataset (Hijmans et al. 2005), which varied from 1333–4113 mm year^{-1} across our study area. The interpolations of WorldClim dataset for Amazonia are based on the few meteorological stations that are available for this region (Hijmans et al. 2005). However, as the stations are well spaced, the interpolation could well represent the large-scale precipitation trends that we analysed.

To select the model that best explained tree and palm basal area variation, we carried out an exhaustive search including all predictor variable combinations, using additive linear models. Interactions between soil physical constraints, rainfall and soil fertility, were also tested. Akaike's Information Criterion (AIC) was adopted as a measure of goodness of fit. AIC penalises parameter-rich models to prevent over-fitting. This procedure is preferable to sequential searching protocols in avoiding Type-I error because the models are not explicitly compared through statistical tests (MacNally 2000). We then ranked our 74 models from best (i.e. lowest) to worst (i.e. highest) AIC value. The ΔAIC of a model is the difference between the AIC of a model to that of the best model. Models with ΔAIC <2 were considered as informative as the best model and the importance of explanatory variables in these models was determined according to their frequency of occurrence in the subset of the best models (Richards 2005). After the best models were chosen, path analysis was used to determine the direct and indirect effects of the environmental variables on palm and tree basal area.

Given that soil physical constraints are highly related to forest turnover, some authors have assumed a causal relationship between them (Quesada et al. 2012). Nevertheless, to untangle the complex relationships between soil properties, stem turnover and forest basal area, simple direct relationships may not adequately describe the system, as both direct and indirect effects may occur. Therefore, we also built a path model that included the best environmental predictors selected by the ΔAIC criteria, combined with the turnover rate to better understand the direct and indirect effects of soil physical properties on palm and tree basal area.

We performed quantile regressions (QR) in addition to OLS, as basal area variation was not homogeneous in relation to the environmental variables in some cases. QR (Koenker and Bassett 1978) is a method for estimating relationships between variables for all portions of a probability distribution without ignoring any part of the data. This method is robust to outliers and skewed distributions (Cade et al. 1999). In addition, fitting higher percentiles of response variables as a function of the independent variable should estimate the upper limit set by the measured independent factors. This approach was undertaken mainly because, if an independent variable can be considered a limiting factor, the models estimated for the upper quantiles should have better predictive values than OLS models (Cade and Noon 2003). To evaluate for which cases QR should be a better predictive model than OLS, we carried out the joint test of equality of slopes described by Koenker and Bassett (1982). This test evaluates if the slopes of QR and OLS differ from each other. If so, the distribution is heteroscedastic and the QR model should be considered instead of the OLS model. We used the QR fitted for each independent variable separately and the quantiles with tau $= 0.25$, tau $= 0.50$ and tau $= 0.90$, for this test.

We also attempted to understand the variation in forest physiognomy in response to soil physical constraints. We adopted the forest classification of Anderson et al. (2009), who used a region-growing technique and non-supervised classification algorithm to classify forest plots from Landsat 7/ETM+ and SRTM images and determine forest physiognomy at a local-scale resolution, and a vegetation map provided by IBGE (1998) for the palm-dominated forests map presented in Figure 4. The local-scale forest classification was used only for small windows surrounding the ALP, CAX, CUZ, JEN and TAM study areas (Table 1), as it could not be generalised to other areas. As far as we know, there is no vegetation map available for the entire Amazon with an appropriate resolution to allow us to distinguish palm-dominated from other *terra-firme* forests across all study areas. The Brazilian RADAMBRASIL vegetation map (Brasil 1978) is not useful to distinguish vegetation types at the local scale because only the dominant vegetation classes at a scale of 1:250,000 were mapped (Emilio et al. 2010). For other Amazonian countries, available vegetation maps are not comparable or the vegetation-class resolution is too coarse. Anderson et al. (2009) distinguished seven forest types in the RAINFOR sites, including one-third of the plots included here. For this study, we grouped Anderson's vegetation units into four classes: *terra-firme* forests where large palms do not contribute greatly to the forest canopy (TF), *terra-firme* forests where large palms do contribute greatly to the forest canopy (TFP), *Mauritia* swamps (SW), and forests over alluvial terraces (FAT). There are few examples of the SW and FAT categories and it is difficult to formally test the relationship between soil conditions and forest structure. Therefore, we only explored these relationships graphically without use of formal statistical methods.

Statistical analyses were carried out by using the R statistical platform (R Development Core Team 2011) and the quantreg package (Koenker 2011). Maps were prepared with ArcGis 9.0.

Results

In our dataset, trees accounted for most of the basal area in *terra-firme* Amazonian forests (94 ± 6%). However, palms contributed up to 23% of basal area in some areas in the western Amazon (Table 1) with *Iriartea deltoidea* being the dominant arborescent palm species; *Oenocarpus bataua* dominated in the central Amazon and Guiana Shield.

Simple OLS regressions showed that palm and tree basal area exhibited different responses to the same environmental variables (Figure 1). Tree basal area was significantly positively related to soil depth and annual precipitation, while palm basal area showed no relationship to these variables. Palm basal area was related to soil fertility ($r^2 = 0.10$, $P = 0.004$) while tree basal area did not show a significant relationship with soil fertility. Soil structure was the only environmental variable significantly related to both tree and palm basal area, and it defined the upper boundary of palm and tree basal area in opposite ways. Palms attained greater total basal area in less-structured soils while tree basal area was greater in well-structured soils. Soil structure alone explained up to 26% of the variance in palm basal area and up to 10% of the variance in tree basal area in simple OLS regressions.

Multiple linear models showed essentially the same relationships as the simple OLS models (Table 3). For palms, models including topography, soil depth and fertility were as informative (ΔAIC <2) as the simple soil-structure model. The inclusion of other environmental variables in the model for palm basal area only very weakly increased and, in some cases, even decreased explanatory power. For trees, best models included soil structure, with the *P*-value for this factor significant in almost all models. Precipitation was the second best variable in the tree basal area model. Models that included both soil structure and precipitation explained up to 23% of tree basal area variance.

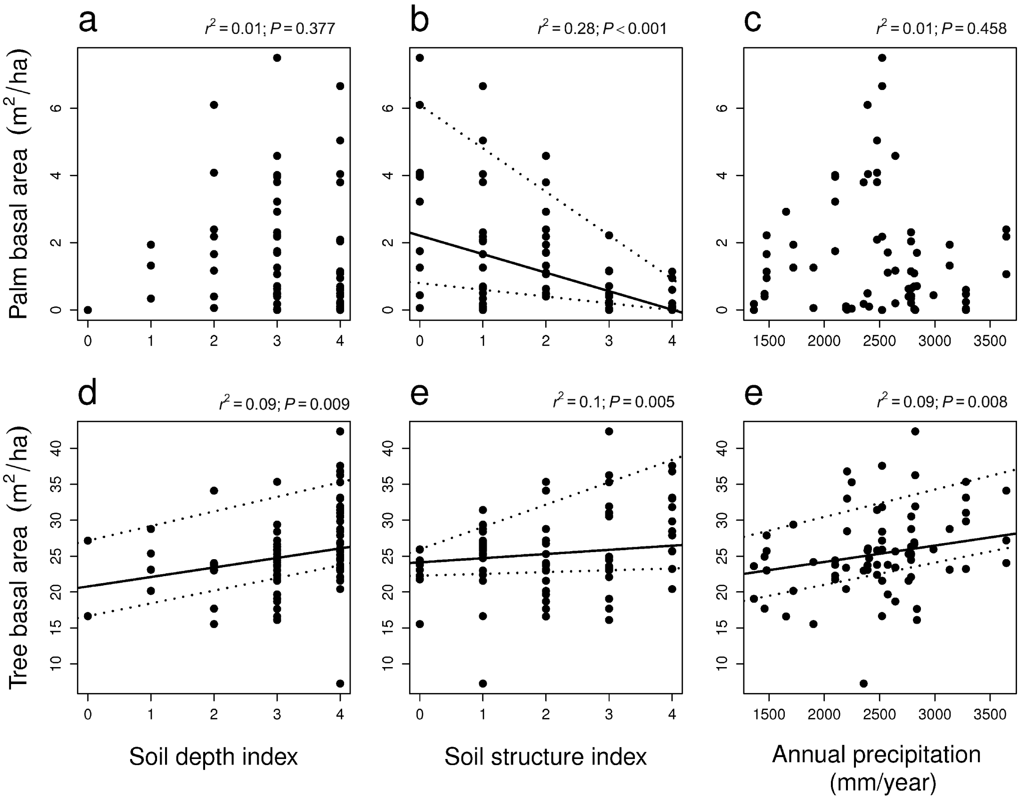

Figure 1. Simple relationships between basal area, soil physical properties and precipitation. Solid lines represent mean values predicted by ordinary linear regression (OLS, which here also coincide with the quantile regression, tau = 0.5). The dotted lines represent the values predicted by the linear quantile regressions, tau = 0.25 and tau = 0.9. The same model (linearised Gaussian in (c), and linear for the others) was adopted for the ordinary linear and quantile regressions. Lines are shown only when the OLS model is significant at the 0.05 level. The r^2- and *P*-values of each OLS are presented at the top of each graph.

Table 3. AIC-ranked linear regression models with ΔAIC < 2. We evaluated 72 models, including simple models of each explanatory variable (soil anoxia, soil depth, soil structure, annual precipitation and fertility), all 57 combinations of the explanatory variables in additive models, and five interaction models with precipitation and each of the other five explanatory variables. All top-rated tree and palm models include soil structure and exclude soil anoxia.

Model	R^2	P	AICc	ΔAICc
palm BA ~ structure***	0.28	<0.0001	190.90	0.00
palm BA ~ depth^{ns}+ structure***	0.29	<0.0001	191.90	1.00
palm BA ~ topography^{ns}+ structure***	0.28	<0.0001	192.80	1.90
palm BA ~ structure*** + fertility^{ns}	0.28	<0.0001	192.81	1.91
tree BA ~ depth^{ns}+ structure*+precipitation**	0.23	0.0003	200.48	0.00
tree BA ~ depth^{ns}+ structure*	0.14	0.0044	201.54	1.06
tree BA ~ depth^{ns}+ structure*+precipitation**+fertility^{ns}	0.23	0.0008	202.32	1.84

***, $P < 0.0001$; **, $P < 0.001$; *, $P < 0.01$; ns, $P > 0.01$.

Topography and soil fertility did not contribute significantly to any model.

Palm basal area variation was heterogeneous along the soil-structure axis (Figure 1). This variation was not reduced significantly in the multiple OLS regressions by the addition of soil anoxia, topography, soil fertility or precipitation as predictor variables (Table 3). Neither the interactions between soil structure and precipitation nor between soil structure and soil fertility was significantly related to palm basal area variation ($P > 0.1$ for interaction term in all models). Tree basal area was related to both soil structure and precipitation in the multiple OLS regressions. Like palms, variation in tree basal area was heterogeneous along the soil-structure axis and variation could not be explained by interactions between explanatory variables in the multiple OLS regressions.

Soil structure explained a large fraction of the variation in stand turnover rates ($r^2 = 0.23$, $P < 0.001$). All low-turnover stands (0–2%) had a low proportion of palms and a high proportion of trees (Figure 2). Tree basal area decreased significantly with increasing turnover ($r^2 = 0.21$, $P < 0.001$), while palm basal area was greatest at intermediate levels of turnover (2–3%). The relationship between palm basal area and turnover rates appeared to be non-linear, and a linearised Gaussian model provided a significant fit ($r^2 = 0.24$, $P < 0.001$). However, this non-linear pattern was strongly driven by one plot (DOI-02) with particularly high disturbance rates. When we excluded this plot, the quadratic term of the linearised Gaussian regression became non-significant and linear regression provided a more appropriate fit to our data. The simple OLS regression between palm basal area and stand turnover rate was significant ($r^2 = 0.11$, $P = 0.005$) and suggested that palm basal area increased with increasing turnover rates.

A more complete picture of the relationship between basal area, soil structure and turnover rate was obtained by path analysis (Figure 3). Palm basal area was not directly affected by turnover rate, as the simple regressions above had suggested. When we accounted for the effect of soil structure on turnover rates, the relationship between palm basal area and turnover rate became non-significant. Conversely, tree basal area remained significantly related to turnover rate, but the significant relation to soil structure was lost. Our path analysis showed that the previously observed response of tree basal area to soil structure was indirect and mediated by forest turnover rates which were, in turn, mediated by soil structure. Despite the fact that palm and tree basal area presented opposite response patterns to soil structure and turnover rates, our model showed that palm basal area was not significantly affected by tree basal area.

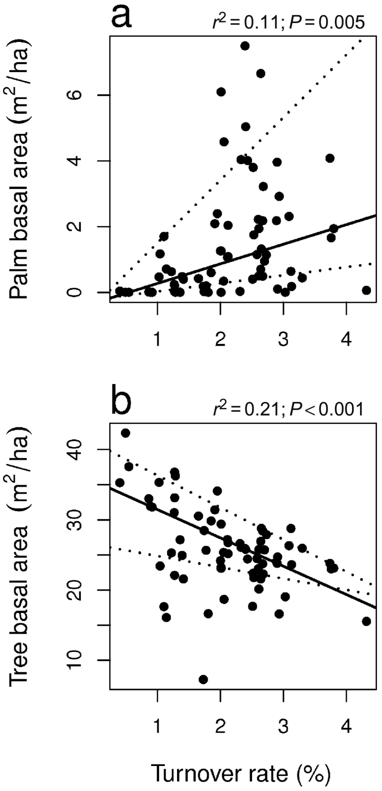

Figure 2. Relationship between forest stand-turnover rates and (a) palm basal area and (b) tree basal area for 60 forest plots for which turnover rate data was available. Dashed lines represent values predicted by quantile regression (tau = 0.9).

At larger scales, the distribution of palm basal area at the plot level was congruent with mapped large-scale

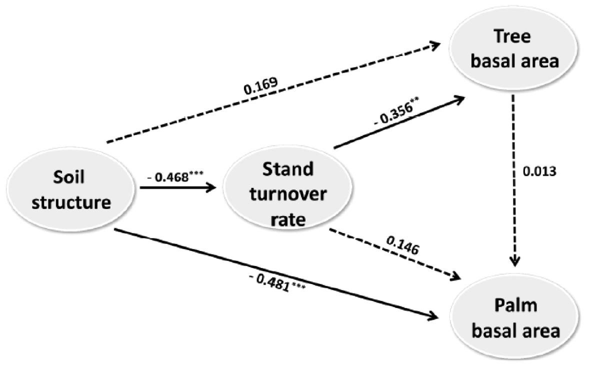

Figure 3. Diagram of direct and indirect effects of soil structure and forest turnover on palm and tree basal area. Arrows point to response variables. Standardised regression coefficients are shown along the lines. Continuous lines indicate significant coefficients and dashed lines non-significant ones.

forest physiognomies: plots with greater palm basal area occurred in and around palm-dominated forests, while plots with lower palm basal area occurred mainly in regions where mapped palm-dominated forests are uncommon (Figure 4(a)). At local scales, physiognomies with high palm dominance occurred mainly over less-structured soils (Figure 4(b)). The soils under alluvial terrace and *Mauritia*-dominated swamps were less structured than those under *terra-firme* sites (Figure 4(b)). Higher soil-structure variation was observed in *terra-firme* forests, where soil structure varied from well-structured friable classes that do not impose much resistance to root penetration to more root-restrictive soils. In agreement with the results suggested by our models, palm-dominated forests (forest over alluvial terraces, *Mauritia*-dominated swamp, palm-dominated *terra-firme*) were mostly found on poorly structured soils (Figure 4(b)). Although our models detected a relationship between tree basal area and soil depth, there were no clear differences in soil depth between forest physiognomies.

Discussion

Basal area partitioning and soil physical constraints

The observed relationship between soil physical constraints and the partitioning of forest basal area between trees and palms suggest that soil-structure conditions establish the upper limit to the basal area of palms and trees in Amazonian *terra-firme* forests. Soil structure was related in opposite ways to the basal area of trees and palms. In addition, the effect of soil structure on basal area was direct for palms but mediated by forest turnover rates for trees. Palm-dominated *terra-firme* forests occurred over less-structured soils, while *terra-firme* forests without canopy-palm dominance occurred more frequently over well-structured soils.

Identifying the specific role of different physical constraints imposed by soils and topography on root development is difficult, as geomorphology and soil conditions are related throughout pedogenesis. For example, in the Amazon region, topography tends to vary regionally, often following local geological history. Where dissected relief occurs, soils tend to be rejuvenated by erosion and thus conditions associated with early pedogenetic development prevail (i.e. limiting physical conditions such as high bulk density and shallow depth), as can be found in the Andes

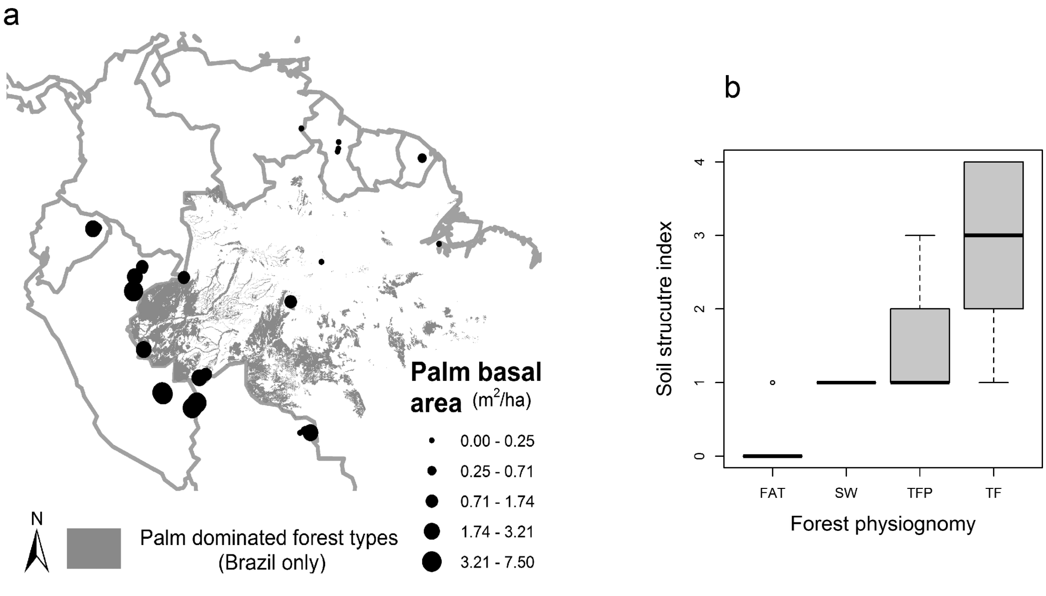

Figure 4. (a) Spatial distribution of palm basal area in 74 forest plots, superimposed on the Brazilian map of palm-dominated forests (modified from IBGE 1998). (b) Soil structure variation between forest physiognomies for ALP, CAX, CUZ, JE and TAM sites ($n = 23$). Soil structure index follows Quesada et al. (2010) and forest classification follows Anderson et al. (2009). Lower values for the soil structure index indicate less structured soils (see Table 1 for a complete description). FAT, forest over alluvial terrace; SW, *Mauritia*-dominated swamp; TFP, palm-dominated *terra-firme* (Anderson's TF 2 and 3); and TF, *terra-firme* forest.

foothills in Peru and Ecuador (BOG plots). Where more stable, flat geomorphology dominates, soil conditions are determined by geological history. If the soils are old and well drained, a highly weathered soil will occur, such as those occurring on the plateaux of the Manaus region in central Amazonia (DKE plots). However, if sediments are young and/or poorly drained, then undeveloped soils occur, as can be found at the Purus–Madeira interfluvial zone (IPM plots). In addition to this general trend, there is large variation in soil physical properties at smaller scales, resulting in a wealth of possible combinations to tease apart the specific causal factors.

Mechanisms for basal area partitioning

Our best models consistently selected soil structure as a predictor of basal area, but not the other variables or their interactions. At small scales (i.e. plot level) topography and soil conditions interact and potentially increase the stress caused by limited anchorage and rooting space. Other properties, such as soil structure, depth and hydrological properties also interact to limit water movement and water availability. However, the relative importance of soil structure compared with topography and soil anoxia in our final models suggests that the process underlying the partitioning of basal area distribution between palms and trees may not be directly related to drainage. Our results are more consistent with the hypothesis of self-maintaining forest dynamic feedback mechanisms initiated by edaphic conditions, originally proposed by Quesada et al. (2012). This hypothesis suggests that in forest stands where soils are deep and well structured as a result of millennia of soil weathering, lack of root anchorage will not shorten the lifetime of trees (Quesada et al. 2012). Trees growing in these soil conditions are also on average taller (Feldpausch et al. 2011), which may affect below-canopy light levels and palm abundance. In contrast, in areas where soils are less developed (i.e. western Amazonia, see Quesada et al. 2010), they are usually less weathered and thus more fertile, but they also have physical proprieties, such as shallow impediment layers, high bulk density, and anoxic horizons that restrict root development and anchorage (Quesada et al. 2010). In these sites, mortality rates are higher and disturbances more frequent, resulting in more dynamic forests. Also, trees are on average shorter (Feldpausch et al. 2011), tend to grow faster as a result of the more fertile soils and increased light availability from more open canopies, invest less in wood density, die faster (Phillips et al. 2004), and are more likely to die broken or fallen than standing (Chao et al. 2009). This is in accordance with our data, which show that palm-dominated forests occur more frequently in western and southern Amazonia (Figure 4) where soils show higher levels of soil physical limitation to root development (Quesada et al. 2010) and forests have higher dynamism (Phillips et al. 2004; Quesada et al. 2012). This finding suggests that, in these environments, palm morphological adaptations may be more advantageous than those of trees. This means that soil physical constrains may not only select for different tree growth strategies but also influence life-form partitioning in Amazonian forests.

Plant functional strategies

While soil structure is an important limiting factor for both trees and palms, morphological and physiological differences result in trees and palms reaching maximum basal area at opposite ends of the soil structure gradient. The absence of secondary growth in palms makes them more susceptible to vascular system disruption. Unlike trees, palms cannot build new xylem vessels when embolism damages part of their vascular system (Tomlinson 1990). Therefore, palms must adopt more conservative water-balance strategies, such as rapid stomatal closure when evaporative demand is greater than the soil water content can supply (Sperry 1986; Renninger and Phillips 2010). This strategy may cause palms to grow more slowly than trees. Annual mean adult growth in height varies between 0.08 and 0.8 m in palms (Henderson 2002). We are not aware of studies that registered the growth in height for adult trees in tropical forest, but juvenile tropical trees can grow in height between 0.7–1.5 m per year on average (Clark and Clark 2001). This is equivalent to the mean annual juvenile growth rate of the palm species *Euterpe precatoria* Mart. (Zuidema 2000), a species with one of the highest adult growth rates registered for Amazonian palms (Henderson 2002). This slower growth may result in a competitive disadvantage for palms, so that trees, when not affected by unfavourable soil conditions, can outperform palms. However, the unbranched crown architecture – and hence small canopy volume – associated with high stem mechanical resistance will probably increase the ability of palms to succeed in more dynamic places where soils are also less favourable for trees.

Beyond the differences in life-form, differences among species in functional strategies could also help explain the observed differences in basal area. Some palm species may outperform others in their ability to persist and thrive in areas of high turnover (Montúfar et al. 2011). *Iriartea deltoidea* Ruiz & Pav., *Attalea butyracea* (Mutis ex L.f.) Wess. Boer, *Oenocarpus bataua* Mart., *Euterpe precatoria* Mart., *Socratea exorrhiza* (Mart.) H.Wendl. and *Astrocaryum murumuru* Wallace each contributed at least 10 times more to basal area than any other palm species recorded in our plots. Four of these dominant species (*I. deltoidea*, *O. bataua*, *E. precatoria* and *S. exorrhiza*) develop stilt roots. The sparsely distributed stilt roots of *S. exorrhiza* allow individuals to physically move across the forest floor – changing their original rooting position as the plant grows – likely conferring an advantage to this species in a dynamic environment by avoiding fallen trunks and by acquiring light (Bodley and Benson 1980). In its adult phase, the ability of *S. exorrhiza* to develop a second set of stilt roots may favour this species, allowing it to re-emerge from coarse woody debris commonly present after disturbance (Avalos 2004). The clumped stilt-root architecture of *E. precatoria*, *O. bataua* and *I. deltoidea* does not allow for that kind of disturbance avoidance. However, at least in the case of *E. precatoria*, stilt roots improve trunk stability and may help the stem to develop extreme 'slenderness', with unusually high height–diameter relationships (Avalos and Otárola 2010). As with buttresses in many trees, stilt roots in palms reduce effective bole length and therefore reduce the risk of structural failure due to buckling (Young and Perkocha 1994). In shallow, less-structured and/or hydromorphic soils, the presence of stilt roots and buttresses thus help prevent tree and palm uprooting. Deep roots can also provide anchorage, but shallow or hydromorphic soils restrict the root growth and prevent their development. Stilt roots may therefore confer an advantage to species with this adaptation over those species that rely only on deep roots for anchorage. In addition, the ability of stilt-root palms to generate new adventitious roots at the stem base (Tomlinson 2006) may allow these palms to obtain water and nutrients more efficiently than buttressed trees in these environments.

Geographical patterns of palm dominance

Biogeography may also play an important role in palm-species distribution at large spatial scales (Eiserhardt et al. 2011) and also in overall palm basal area in each region. Biogeographical factors may also interact with soil factors even in the absence of clear biogeographical boundaries for Amazonian palms. The species pool of palms, soil constraints and disturbance regime in each region should interact to define the relative contribution of palms to overall forest basal area. In our study plots, *Iriartea deltoidea* and *Attalea butyracea* were the most abundant arborescent palm species, so it is not surprising that the spatial pattern of palm basal area distribution shown here substantially coincides with the spatial distribution of these two species. These two species were very abundant in our study plots probably because our survey effort was concentrated along the periphery of the Amazon basin. Along the eastern and northern edges of the Amazon basin, oligarchic forests dominated by other palm species occur. *Euterpe oleracea* stands are common over fluvisols in the Amazonian estuaries of Pará and Amapá states in Brazil, *Attalea speciosa* stands occur near to the Amazon borders in the Brazilian states of Maranhão (north), Piauí (north-east), and Goiás (central Brazil) in forest sites subject to intensive disturbance, *Oenocarpus bataua* forms extensive aggregations in seasonal swamp forests on gleyic podzols in central and western Amazonia and dense stands of *Mauritia flexuosa* occur over dystric histosols of the Orinoco, Ucayali and Marañon Rivers (Peters et al. 1989). All these oligarchic forests are associated with young (fluvisols, histosol), low physical quality (gleyic podzol) soils or high-disturbance forests, consistent with our hypothesis that poor soil-structure and more dynamic forests lead to higher palm basal area. Furthermore, our data also show that, within the same region, greater palm basal area is usually attained on the more poorly structured soils (Table 1). Together, these data lead us to suggest that, even though different palm species may be dominant in regions with distinct species pools and biogeographical history, palm dominance is also affected by local soil physical constraints.

Conclusions

Trees attained highest basal area in deep, well-structured soils that experienced high rainfall. On the other hand, trees may fail to persist in all available physical space in areas where limiting soil characteristics occur, making space for other life-forms. Our study indicates that palms are an important life-form and they occupy forest space where soils are less developed and less structured. In order to understand the complex puzzle of variation in forest structure across the vast Amazon basin and beyond, we must identify the various potential environmental and historical controls on forest ecosystems. Our study identified one piece of this puzzle by demonstrating that (1) soil physical constraints establish the upper bound for palm and tree basal area, (2) life-forms with contrasting rooting strategies, such as palms and trees, achieve greater basal area at opposite ends of the soil-structure gradient, (3) forest dynamism may be reflected by the differences between palm and tree basal area, and (4) distinct combinations of palm and tree basal areas imposed by soil structure and/or disturbance regimes may be large enough to be observed in forest physiognomy. What remains to be understood is what determines the variation in basal area below the limits imposed by soil physical constraints, and how other life-forms, such as herbs, bamboos and lianas deal with soil–rainfall environmental niche envelopes. A more complete understanding of this will help develop more realistic models of forest response to changing land use and climate that take into account the fact that there are more than just trees and rainfall in Amazonian forests.

Acknowledgements

The National Council for Scientific and Technological Development (CNPq) awarded stipends to TE, and a major grant from the Gordon and Betty Moore Foundation to RAINFOR supported collection of much of the data analysed here. Significant funding for fieldwork was also received from NERC-TROBIT, EU, AMAZONICA, CNPq Universal, CNPq/FAPEAM PRONEX, PPBio Amazônia oriental and CNPq/FAPESP/FAPEAM HIDROVEG project. OP is supported by the European Research Council project 'Tropical Forests in the Changing Earth System'. We thank the many field workers who collected plant and soil data from the 74 RAINFOR and PPBio study sites distributed across eight countries. Data repositories for PPBio sites are maintained by PPBio and CENBAM. Our special thanks to S. Almeida, L. Arroyo, J.G. Barroso, V. Bezard, L. Blanc, P. Castro, W. Castro, F. Cornejo, C. Czimczik, A. Etienne, R. Farias, S. Fauset, G. van der Heijden, F. Kwasie, A. de la Fuente, B. Leudet de la Vallee, J. Lloyd, B. Michel, D. Moura de Freitas, P. Naisoo, O. N'Gwete, E.-A. Nicolini, T. Paine, M.C. Penuela-Mora, A. Roopsind, E. Rutishauser, R. Sante, D. Sasaki, G. da Silva Henicka, G.B. da Silva Oliveira, J. Teran Aguilar and R. Vásquez who participated in data collection in many sites and to G. López-Gonzalez for her work curating and managing the ForestPlots database. We also thank the Flora Program at the Fundação Ecológica Cristalino, Instituto Nacional de Pesquisas da Amazônia, Medellin Botanical Garden, Museu Goeldi, National University of Colombia, and University of Acre for their support of field teams and their activities. This manuscript was partly developed during the 2011 RAINFOR (Gordon and Betty Moore Foundation-UFAC) workshop in Rio Branco, Acre, Brazil. We thank C.L. Bechtoldt for help with English revisions.

Notes on contributors

Thaise Emilio is a Ph.D. student, working with plant species and vegetation distribution across Amazonia. Her research interests include palms and how environmental conditions drive their distribution and abundance.

Carlos A. Quesada is a post-doctoral research associate. His research interests include biogeochemical cycles, Amazonian soils and their interaction with forest structure and dynamics.

Flávia R.C. Costa is a researcher working on the ecological determinants of plant species and community distributions, and anthropogenic influences on plant communities.

William E. Magnusson studies the ecological and evolutionary determinants of Amazonian organisms.

Juliana Schietti is a Ph.D. candidate. Her research interests focus on understanding tropical forest structure and functioning and their relations with soil hydrology and climate.

Ted R. Feldpausch's research interests include the ecology of tropical forests and savannas; effects of global change on forest and savanna composition, structure and carbon accumulation; land-use change, forest disturbance and recovery.

Roel J.W. Brienen is a researcher who is broadly interested in tropical forest dynamics and impacts of global change on tropical forest functioning.

Timothy R. Baker's research focuses on tropical forests and aims to understand past, current, and future patterns of carbon storage and biodiversity in these ecosystems.

Jerome Chave is a senior staff member and is the science coordinator of the Nouragues research station. His field of scientific expertise is spatial patterns of plant diversity in Amazonia and biogeochemical cycles in tropical rain forests.

Estebán Álvarez is a Ph.D. student and is currently working with forest diversity, biomass, and dynamics in complex environmental gradients in Colombia.

Alejandro Araújo Murakami is a researcher focusing on Bolivia's floristic diversity, with a particular interest in ethnobotany and forest ecology. He has worked in Amazonian ecosystems, Chaco-Amazonia transitions (Chiquitanos), and Andean forests.

Olaf Bánki is a conservation biologist and forest ecologist with an interest in drivers of change in forest composition and tree diversity along ecological and geographical gradients in the Guiana Shield.

Carolina V. Castilho is a biologist interested in long-term ecological studies, and uses permanent plots to evaluate changes in biomass, structure, and tree species composition in tropical forests.

Eurídice N. Honorio C. is a Ph.D. student and her research focuses on tropical plant taxonomy in Peru, and she is currently interested in phylogeographic patterns of Amazonian trees.

Timothy J. Killeen is a conservation biologist.

Yadvinder Malhi is a professor. His research interests focus on understanding the ecology and functioning of tropical forests worldwide, and their interactions with climate change.

Erick M. Oblitas Mendoza has been studying the carbon stocks of Amazonian soils. He is currently looking at carbon stocks along an altitudinal gradient from the Andes to the Amazon.

Abel Monteagudo was a M.Sc. student funded by the Amazon Forest Inventory Network (RAINFOR) at the time of the study; currently he is working on a project to understand carbon balance in the Amazon. He is particularly interested in the study of the distribution and diversity of trees in the Amazon.

David Neill's research interests include taxonomic studies of the flora of Ecuador, particularly in the Amazon and Cordillera del Cóndor regions, and quantitative inventories of forest composition and structure in one-hectare inventory plots, with a focus on examining relationships between forest floristic composition, structure and dynamics and geological substrate and soil characteristics.

Germaine Alexander Parada is currently working on floristic inventories of Andean forests in Santa Cruz, Bolivia. He is interested in the ecology of the Amazon rainforest and the Andes in general.

Hirma Ramirez-Angulo's main research interests include the dynamics of tropical forests, with a focus on the application of simulation models to predict forest dynamics.

Michael Schwarz is a M.Sc. student. His research interests include climate change and tropical forests, climate mitigation in developing countries, and climate project finance schemes like REDD and CDM.

Marcos Silveira has been working with plant and forest ecology, with a special interest in factors driving species composition.

Hans ter Steege is a senior researcher and he works on tree alpha- and beta-diversity in the Amazon and Guiana Shield and is interested in how local and regional processes drive diversity.

John W. Terborgh is a research professor. For 36 years, he has operated a research station in the Manu National Park, Peru where Peruvian and international scientists study a wide range of basic and applied problems. His current interests lie in the field of plant–animal interactions and the mechanisms that sustain the high diversity of tropical tree communities.

Armando Torres-Lezama is a forester. His main research interests include sustainable rural development and tropical forest dynamics.

Emilio Vilanova's research interests include tropical forest dynamics, with an emphasis on biomass and carbon estimations, and options for sustainable management of tropical forests.

Oliver L. Phillips co-ordinates the RAINFOR project. His long-term research goal is to understand the dynamics of carbon and biodiversity across the world's tropical forests, how these change with our changing climate, and how they may feed back on the whole planet.

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