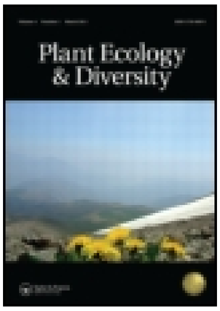

Plant Ecology & Diversity
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/tped20

Vertical distance from drainage drives floristic composition changes in an Amazonian rainforest

Juliana Schietti [a], Thaise Emilio [a], Camilo D. Rennó [b], Debora P. Drucker [c], Flávia R.C. Costa [d], Anselmo Nogueira [e], Fabricio B. Baccaro [a], Fernando Figueiredo [d], Carolina V. Castilho [f], Valdely Kinupp [g], Jean-Louis Guillaumet [h], Ana Raquel M. Garcia [a], Albertina P. Lima [d] & William E. Magnusson [d]

[a] Programa de Pós-Graduação em Ecologia, Instituto Nacional de Pesquisas da Amazônia - INPA, Manaus, Brazil

[b] Divisão de Processamento de Imagens/OBT, Instituto Nacional de Pesquisas Espaciais - INPE, São José dos Campos, Brazil

[c] EMBRAPA - Monitoramento por Satélite, Campinas, Brazil

[d] Coordenação de Pesquisa em Biodiversidade, Instituto Nacional de Pesquisas da Amazônia - INPA, Manaus, Brazil

[e] Departamento de Botânica, Universidade de São Paulo, São Paulo, Brazil

[f] EMBRAPA - Centro de Pesquisa Agroflorestal de Roraima, Boa Vista, Brazil

[g] Herbário EAFM, Ciência e Tecnologia do Amazonas, Manaus, Brazil

[h] Laboratoire de Phanérogamie - Muséum National d'Histoire Naturelle, Paris, France
Accepted author version posted online: 12 Mar 2013.Published online: 24 Apr 2013.

Plant Ecology & Diversity, 2013
http://dx.doi.org/10.1080/17550874.2013.783642

Taylor & Francis
Taylor & Francis Group

Vertical distance from drainage drives floristic composition changes in an Amazonian rainforest

Juliana Schietti[a]*, Thaise Emilio[a], Camilo D. Rennó[b], Debora P. Drucker[c], Flávia R.C. Costa[d], Anselmo Nogueira[e], Fabricio B. Baccaro[a], Fernando Figueiredo[d], Carolina V. Castilho[f], Valdely Kinupp[g], Jean-Louis Guillaumet[h], Ana Raquel M. Garcia[a], Albertina P. Lima[d] and William E. Magnusson[d]

[a]*Programa de Pós-Graduação em Ecologia, Instituto Nacional de Pesquisas da Amazônia – INPA, Manaus, Brazil;* [b]*Divisão de Processamento de Imagens/OBT, Instituto Nacional de Pesquisas Espaciais – INPE, São José dos Campos, Brazil;* [c]*EMBRAPA – Monitoramento por Satélite, Campinas, Brazil;* [d]*Coordenação de Pesquisa em Biodiversidade, Instituto Nacional de Pesquisas da Amazônia – INPA, Manaus, Brazil;* [e]*Departamento de Botânica, Universidade de São Paulo, São Paulo, Brazil;* [f]*EMBRAPA – Centro de Pesquisa Agroflorestal de Roraima, Boa Vista, Brazil;* [g]*Herbário EAFM, Ciência e Tecnologia do Amazonas, Manaus, Brazil;* [h]*Laboratoire de Phanérogamie – Muséum National d'Histoire Naturelle, Paris, France*

(*Received 28 January 2012; final version received 5 March 2013*)

Background: Plant composition changes with topography and edaphic gradients that correlate with soil-water and nutrient availability. Data on soil water for the Amazon Basin are scarce, limiting the possibility of distinguishing between soil and soil-water influences on plant composition.
Aim: We tested a new proxy for water table depth, the terrain height above nearest drainage (HAND), as a predictor of composition in trees, lianas, palms, shrubs, and herbs and compared HAND to conventional measures of height above sea level (HASL) and horizontal distances from nearest drainage (HDND).
Methods: Plant-species composition in 72 plots distributed across 64 km^2 of lowland evergreen terra firme forest was summarised using non-metric multidimensional scaling (NMDS). NMDS scores were regressed against estimates of HAND, HASL and HDND.
Results: Plant composition was highly correlated with the vertical distance from water table, capturing up to 82% of variation. All life forms showed highest turnover rates in the zone with seasonally water-saturated soils, which can extend 350 m from stream margins.
Conclusions: Floristic composition is closely related to water table depth, and HAND appears to be the most robust available topographical metric of soil-water gradients. Brazilian conservation laws protecting 30-m-wide riparian buffers are likely to be too narrow to encompass the full zone of highest floristic turnover and may be ineffective in safeguarding riparian plant diversity.

Keywords: beta diversity; height above nearest drainage; distance from stream; plant species composition; soil hydrology; Shuttle Radar Topography Mission; terra firme forest; topography; tropical rain forest; water table

Introduction

Soil water controls many aspects of forest ecosystem dynamics, including forest structure (Jirka et al. 2007), vegetation-atmosphere interactions (Rodriguez-Iturbe 2000), tree growth and mortality (Phillips et al. 2009), and species distribution and composition (Pyke et al. 2001; Gibbons and Newbery 2002; Groom 2004; Engelbrecht et al. 2007; Jirka et al. 2007; Balvanera et al. 2011). However, few studies have investigated the direct relationship between the variability of soil water and plant species distribution (Engelbrecht et al. 2007; Comita and Engelbrecht 2009), so little is known about how assemblage composition changes along hydrological gradients.

Direct measures of soil water are scarce and unevenly distributed across the Amazon Basin, restricting opportunities to directly relate changes in plant composition to soil-water gradients. It is costly and time-consuming to monitor soil-water variables, such as soil moisture or water table fluctuations, at relevant spatial scales in the field; and remote-sensing data that can be used to infer soil moisture have many restrictions in forested areas (Salas et al. 2002; Smith 2002). This seems to be the main reason that researchers often use topographical variables, such as slope and differences in height above sea level (HASL), to predict plant-composition changes instead of using soil-water variables, even when drainage or soil-water availability is likely to be one of the most important variables that affect species distributions (Tuomisto and Poulsen 2000; Costa et al. 2005, 2009). Therefore, the use of proxies for soil-water availability is a promising strategy to investigate species distribution and soil-water relationships in Amazonian forests (see Balvanera et al. 2011, Kanagaraj et al. 2011).

Topographic position frequently controls soil-water gradients and soil properties (Daws et al. 2002; Brown et al. 2004), with water availability being lower in uplands and higher in valleys, where the water table is vertically closer to the surface. Also, areas horizontally far from streams tend to be more well-drained than areas horizontally close to streams (Campling et al. 2002; Kravchenko

*Corresponding author. Email: jujuschietti@gmail.com

et al. 2002). Both vertical and horizontal distances from streams are useful proxies for plant-available water because soil draining potential is a function of vertical rise and horizontal flow (Marshall et al. 1996). It has been shown that plant composition changes along gradients of horizontal distance from a stream (Naiman et al. 1997; Sabo et al. 2005; Drucker et al. 2008; Costa et al. 2009), and horizontal distances are currently used to define strips along stream margins for riparian-forest protection in Brazil. Horizontal and vertical distances are correlated in micro watershed because the terrain becomes higher with distance from the stream. Nevertheless, horizontal distances from streams may not represent a change in soil-water conditions in large flat areas connected to drainage (Rennó et al. 2008). Such waterlogged areas may extend far from streams but they remain vertically close to the water table. Therefore, vertical distance from a stream should be a better predictor of the hydrological condition experienced by plants, especially in predominantly flat topography. Silvertown et al. (1999) had shown that plant species segregated in water table gradients even in the absence of obvious topographic variation, and argued that many types of plant communities may be structured by soil hydrology gradients. However, until now the potential of vertical distance from the water table in driving plant composition differences has been overlooked in tropical forests since we found only one study addressing plant-composition changes related to water table depth in tropical forests (Jirka et al. 2007).

Species distribution may be shaped by the topography-driven water gradient (Balvanera et al. 2011), based on distinct water requirements (Engelbrecht et al. 2007). It is reasonable to expect that plant functional groups with distinctive morphologies, such as trees, lianas, palms, shrubs and herbs, will also respond differently to the gradient of topography-driven water availability. For many reasons, rooting depth may be a key factor that affects plant growth and survival (Groom 2004). Rooting depth is sensitive to water shortage or excess. Deep-rooting plants, such as trees (Nepstad et al. 1994) and lianas (Restom and Nepstad 2004; Schnitzer 2005) in higher topography, have more access to groundwater throughout the year than shallow-rooted plants such as herbs. If maximum rooting depth plays an important role in plant water access, the distribution of shallow-rooted plants is probably more strongly affected by topography-driven water gradients, such as vertical distances from the water table, than deep-rooted plants.

The test of spatially explicit proxies derived from remote sensing to predict plant composition changes is of great importance for extrapolations and production of regional diversity maps (Schulman et al. 2007; Albernaz et al. 2012). Maps of diversity are necessary for conservation planning and for estimates of diversity losses due to forest degradation and environmental changes. Detailed topographic data have become available since 2000 from the Shuttle Radar Topography Mission (SRTM). Even though it represents vegetation-canopy topography, rather than terrain topography, the SRTM digital elevation model (DEM) has high vertical resolution (1 m) and free near-global coverage. As terrain topography usually varies much more than canopy topography, the SRTM DEM highlights geomorphological features and is useful as a surrogate for terrain topography and for hydrological modelling (Valeriano et al. 2006). Therefore, SRTM-HASL has been used as a predictive variable for plant species distribution (Prates-Clark et al. 2008; Raes et al. 2009) and for above-ground live biomass (Saatchi et al. 2007) in tropical forests. An algorithm to calculate the height above the nearest drainage (HAND), a proxy for vertical distance from the water table, based on SRTM-DEM was developed by Rennó et al. (2008). The height above drainage was shown to be correlated with the water table level and hydrological conditions of the terrain (Rennó et al. 2008; Nobre et al. 2011), and therefore might be a better predictor of plant-species distribution than traditional measures, such as HASL and horizontal distances from drainage (HDND).

Predictors of species distributions are important to understand present distributions and likely distributions under climate change. Therefore, we tested the hypothesis that HAND is a better predictor of species composition than terrain topography or horizontal distance from streams for species in six plant life forms: trees, lianas, palms, shrubs, non-fern herbs and ferns. To test if life forms responded differently to vertical distance from water gradient, we compared the strength of the life-form relationships with HAND in a lowland evergreen terra firme forest in the Central Amazonia. We hypothesised that species composition in shallow-rooted life forms should be better related to HAND than for deep-rooted life forms.

Materials and methods

Study area

The study was conducted in the Reserva Ducke, or Ducke Forest Reserve of the Instituto Nacional de Pesquisas da Amazônia (INPA) in central Amazonia, located 26 km north of Manaus (2°55′ 47.80″ S; 59°58′ 30.34″ W). The Reserve covers 10,000 ha (10 × 10 km) of lowland evergreen terra firme tropical rain forest, with a 30–37 m high closed canopy and emergent trees reaching 40–45 m (Ribeiro et al. 1999). Soils are derived from tertiary marine sediments from the Alter do Chão formation. The local relief is dissected by the hydrographic system, resulting in a landscape formed by plateaux and valleys, where the clay fraction decreases as elevation decreases (Chauvel et al. 1987). The dominant soil type is clayey yellow latosol typic Haplorthox or Acrorthoxon on the plateaux where the water table is deep, transitioning to less clayey red-yellow (Orthoxic Tropohumult or Palehumult) soils on slopes. Soils are sandy on the valley bottoms with hydromorphic podsols (Tropohumods–Troporthods) (Chauvel et al. 1987) where the water table is close to the surface and the soils are almost permanently waterlogged during the rainy season. Reserva Ducke is generally considered to contain relatively uniform dense forest and is not subject to flooding by large rivers.

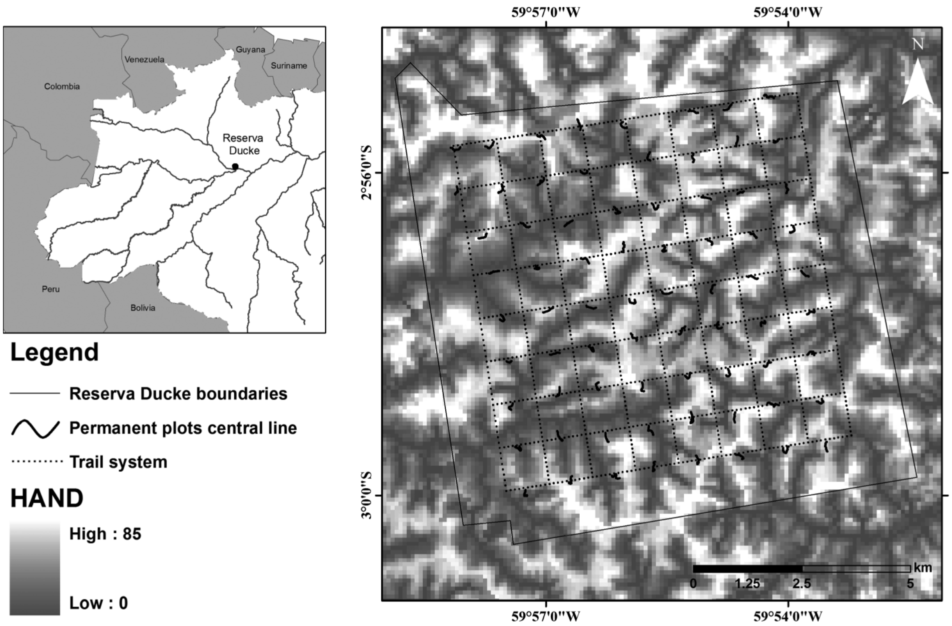

Figure 1. The Reserva Ducke, Manaus, Brazil grid system with 72 uniformly-distributed permanent plots and height above the nearest drainage (HAND) data in the background. Centre lines of plots follow terrain contours.

The mean annual temperature at Reserva Ducke between 1965 and 1980 was 26°C and the annual rainfall ca. 2400 mm with the monthly maximum in March (∼330 mm) and minimum in August with <100 mm (Marques-Filho et al. 1981). The dry season occurs between July and September, but on average only two months have rainfall lower than 100 mm (Marques-Filho et al. 1981). The drainage system in Reserva Ducke is formed by streams of first- to third-order (Figure 1), ranging from less than a metre to ca. 10-m wide. The valley bottoms (flat areas along the streams, known locally as baixios) vary in size up to about 150 m from stream margins (D. Drucker, unpublished data), and often contain swampy pools due to the proximity of the water table to the surface in these areas.

Reserva Ducke has a grid of regularly spaced east-west and north-south trails covering 64 km^2. Trails allow access to 72 permanent plots regularly distributed across the landscape that were installed in 2000 (Costa and Magnusson 2010). The plots are separated from each other by a minimum distance of 1 km (Figure 1). In each plot, a 250-m long centre line follows the contour to minimise variation in depth to water table and soil variables within the plots. The width of the plot varies according to the taxa of interest (Magnusson et al. 2005; Costa and Magnusson 2010).

Floristic datasets

Reserva Ducke has been the site of numerous studies of plant assemblages in association with soil/topographical gradients (Costa et al. 2005; Kinupp and Magnusson 2005; Costa 2006; Drucker et al. 2008; Costa et al. 2009; Nogueira et al. 2011) and an extensive floristic dataset exists for the area. We compiled six datasets of plants with different life forms frequently used in ecological studies: (1) trees, (2) lianas, (3) palms, (4) shrubs, (5) non-fern herbs and (6) ferns, and a combined dataset of (7) all species in the six groups sampled in Reserva Ducke. These datasets include 741 plant species sampled over 72 plots (all life forms were sampled together in a sub-sample of 22 plots). All plants were recorded along the entire length of the 250-m long plot centre line in each plot. The width of the plot varied according to the relative abundance of groups, ranging from 1 m for ferns to 40 m for trees over 30 cm diameter at breast height (DBH) (see Table 1). Details on the sampling protocols are available in the metadata associated with the data for each life form at http://ppbio.inpa.gov.br/repositorio/dados.

Height above the nearest drainage (HAND)

HAND values were shown to be correlated with water table level categories within the same geological formation with dissected clayey-plateau and sandy-valley landscapes (Chauvel et al. 1987), about 60 km from Reserva Ducke (Rennó et al. 2008). Conceptually, HAND represents the relative water gravitational potential (or vertical relative draining potential), although no direct correlation of HAND values and soil-water potential or soil moisture has yet been made. The water gravitational potential is a component of the soil water potential, which reflects difficulty for plants to extract soil water or to avoid excess water. High HAND values mean large gravitational potential (high vertical draining potential) and low HAND values mean low gravitational potential (low vertical draining potential) and proximity to the water table, where lack of drainage leads to waterlogging (Nobre et al. 2011).

The HAND algorithm developed by Rennó et al. (2008) calculates the vertical distance between points on the terrain and their nearest drainage, based on a DEM (SRTM in this study). The nearest drainage for each terrain point is

Table 1. Numbers of species and sampling design for the six life forms sampled in the permanent plots of the Reserva Ducke, Manaus, Brazil.

Life form	Taxon included	Number of species	Number of plots	Plot area	Inclusion limit
Trees			72	0.5–1 ha	>10–30 cm DBH
	Burseraceae	40			
	Chrysobalanaceae	46			
	Euphorbiaceae	31			
	Fabaceae	139			
	Lauraceae	100			
	Lecythidaceae	42			
	Moraceae	32			
	Myristicaceae	21			
	Sapotaceae	69			
Lianas			32	0.25–1 ha	>1–5 cm *D*
	Bignoniaceae	42			
Palms			72	0.1 ha	>100 cm *H*
	Arecaceae	44			
Shrubs			57	0.1 ha	No limit
	Rubiaceae (*Psychotria*)	23			
	Piperaceae (*Piper*)	26	57	0.1 ha	>50 cm *H*
Herbs			56	0.05 ha	>5 cm *H*
	Poales	22			
	Zingiberales	27			
	Other	12			
Ferns			54	0.025 ha	>5 cm *H*
	Pteridophyta	21			
	Lycophyta	4			
All species	All above	741	22	All above	All above

D, diameter measured at 130 cm from the rooting point; *H*, height from the ground.

the stream to which the water from that point is drained. Therefore, the nearest drainage is not defined based on Euclidean distances but using flow-direction paths, which follow the topography (from one point to its steepest downslope neighbour) and has topological continuity. The most important step in the calculation of HAND values is the definition of the drainage network density because this is the base for the calculations of terrain vertical distances from drainage. This step needs field calibration for the establishment of the stream origins (the headwaters), which are defined by the minimum-contributing-area threshold. The lower this minimum-contributing-area threshold the higher the drainage network density (more streams are taken into account). If this threshold is too low, the algorithm can create false small streams and low HAND values will be attributed to terrains close to these false streams. Conversely, if the minimum-contributing-area threshold is too high, small streams will not be included in the drainage network and HAND values will be higher than the real vertical distance from the terrain and its nearest drainage. Different minimum-contributing-area thresholds can be used to represent differences in the drainage density from dry season to wet season for seasonal streams.

We calculated HAND values for Reserva Ducke based on SRTM-DEM (90 m spatial resolution) using a 30-pixel minimum contribution area (= 0.41 km^2) and validated several small streams and headwaters along the trail system in the field.

Using a geographical information system (GIS), we extracted (with bilinear interpolation) HAND values for 25 locations along the permanent-plot centre lines (Figure 1). Values of HAND obtained for each location were averaged per plot. The mean HAND values for the 72 plots ranged from 1–53 m (mean = 22 m).

Horizontal distance from nearest drainage (HDND)

HDND are usually related to soil drainage classes (Campling et al. 2002; Kravchenko et al. 2002). Areas horizontally close to streams are also more likely to waterlog and to receive sediment deposits from streams. We calculated HDND from plots to nearest drainage using two types of distances: Euclidian distance (HDND-Euclidean) and water-flow direction distance (HDND-flowdir). The HDND-Euclidean is the usual horizontal distance calculated with GIS tools in which the smallest distances are calculated between plots and nearest drainages, without regard to hydrological connection between plots and drainage. The HDND-flowdir is calculated using flow paths between plots and drainages, so the plots are always hydrologically connected to drainage. HDND-Euclidean and HDND-flowdir are highly correlated in Reserva Ducke (r = 0.95) and HAND is correlated with HDND-Euclidean (r = 0.80) and with HDND-flowdir (r = 0.86), based on data for the 72 plots of this study.

Using GIS we extracted (with bilinear interpolation) HDND values for 25 locations along the permanent-plot centre lines. Values of HDND obtained for each location were averaged per plot. The HDND-Euclidean values for the 72 plots ranged from 27–601 m (average = 234 m) and HDND-flowdir values ranged from 27–756 m (average = 250 m).

Height above sea level (HASL)

HASL was obtained from radar data (SRTM-HASL) and from direct ground measurements (ground-HASL). Ground-HASL and SRTM-HASL were highly correlated ($r = 0.94$), and HAND was correlated with SRTM-HASL ($r = 0.89$) based on data for the 72 plots. SRTM-HASL was compared with HAND and HDND as a predictor of floristic composition changes. Ground-HASL was used only to estimate the accuracy of the SRTM-HASL measurements.

SRTM-HASL data for Reserva Ducke was obtained from http://www2.jpl.nasa.gov/srtm/, with a horizontal resolution of 3 arc-seconds (90 m near the equator) and a vertical resolution of 1 m. The C band of the radar has a strong interaction with the vegetation canopy, so the SRTM data represents mostly the canopy surface in densely forested areas (Valeriano et al. 2006). We used the same procedure described for HAND and HDND to extract SRTM-HASL data for 25 locations along the central line of each plot. Values were averaged per plot and the SRTM-HASL ranged from 53–114 m. The average for all plots in Reserva Ducke was 82 m.

Ground-HASL for the centre lines in the 72 plots was accurately measured by a professional topographer (A.T. Cardoso e Silva) using a theodolite and the Brazilian High Precision Altimetric Network (http://www.ibge.gov.br). As the 250-m centre line of the plots follows the terrain contour, the elevation above the sea level is the same at all points along the centre line of the plots. Ground-HASL values are available from http://ppbio.inpa.gov.br/knb/style/skins/ppbio/. The values of ground-HASL ranged from 39–110 m in the 72 plots. The average ground-HASL was 76 m.

Data analyses

Plant species composition matrices of each life form were reduced to one dimension using non-metric multidimensional scaling (NMDS). Ordinations were based on relative abundance (quantitative composition) and on presence-absence of species (qualitative composition). Ordinations of presence-absence data used the Sørensen dissimilarity index; and quantitative ordinations were based on data standardised by total abundance per plot and used the Bray-Curtis dissimilarity index. The adjusted r^2 of the dissimilarity matrices of original data regressed against the dissimilarity along the one-dimensional ordination was used to evaluate the adequacy of the ordinations for each life form (McCune and Grace 2002). Most variation in ordinations based on plant-species relative abundance and presence/absence was captured by one dimension in the NMDS. The percentage variance captured by one-dimension-NMDS ranged from 57% for shrubs to 92% for palms (Table 2).

Table 2. Percentage variance captured by quantitative and qualitative non-metric multidimensional scaling (NMDS) ordination in one axis for six life forms individually and all six combined (all life forms), based on data from 72 permanent forest plots, Reserva Ducke, Manaus, Brazil.

Life form Variance explained NMDS (quantitative/qualitative) (%/%)	Predictor	Quantitative composition changes					Qualitative composition changes					
		y_0	a	b	r^2	Δ AIC	y_0	a	b	r^2	Δ AIC	P
Tree	HAND	**−0.31**	**1.54**	**0.13**	**0.72**	0.00	**−0.21**	**1.31**	**0.17**	**0.74**	0.00	<**0.001**
(80/80)	HDND	−0.32	1.41	0.01	0.48		−0.21	1.29	0.01	0.48		<0.001
	SRTM-HASL	−0.47	15.35	0.05	0.57		−0.41	8.72	0.04	0.56		<0.001
Liana	HAND	**−0.68**	**2.75**	**0.16**	**0.82**	16.06	**−0.48**	**2.49**	**0.23**	**0.72**	22.81	<**0.001**
(60/79)	HDND	−0.75	3.30	0.01	0.77		−0.48	3.12	0.02	0.64		<0.001
	SRTM-HASL	−0.85	78.88	0.06	0.77		−0.49	347.67	0.10	0.61		<0.001
Palm	HAND	**−0.38**	**2.40**	**0.18**	**0.67**	13.98	**−0.16**	**1.16**	**0.21**	**0.41**	9.88	<**0.001**
(92/87)	HDND	−0.31	2.96	0.02	0.42		−0.13	1.36	0.02	0.22		<0.001
	SRTM-HASL	−0.52	36.00	0.06	0.44		−0.21	18.20	0.06	0.23		<0.001
Shrubs	HAND	**−0.23**	**2.30**	**0.28**	**0.49**	24.83	**−0.19**	**2.10**	**0.31**	**0.63**	9.81	<**0.001**
(57/72)	HDND	−0.23	3.13	0.03	0.35		−0.18	3.30	0.03	0.43		<0.001
	SRTM-HASL	−0.35	33.10	0.06	0.26		−0.39	17.50	0.05	0.42		<0.001
Herbs	HAND	**−0.23**	**1.13**	**0.13**	**0.26**	8.97	**−0.23**	**1.13**	**0.13**	**0.26**	16.61	<**0.001**
(64/65)	HDND	−0.20	1.45	0.17	0.20		−0.20	1.43	0.68	0.21		<0.001
	SRTM-HASL	−0.25	46.71	0.07	0.16		−0.25	49.64	0.07	0.17		<0.004
Ferns	HAND	**−0.49**	**3.63**	**0.20**	**0.58**	44.73	**−0.27**	**1.75**	**0.17**	**0.56**	33.51	<**0.001**
(75/86)	HDND	0.45	4.67	0.02	0.43		−0.24	1.91	0.02	0.37		<0.002
	SRTM-HASL	−0.67	80.54	0.06	0.32		0.32	−0.40	24.86	0.32		<0.001
All life forms	HAND	**−0.38**	**1.73**	**0.17**	**0.84**	–	**−0.20**	**1.19**	**0.25**	**0.68**	–	<**0.001**
(83/84)	HDND	−0.39	2.00	0.01	0.76		−0.19	1.63	0.02	0.62		<0.001
	SRTM-HASL	−0.48	123.92	0.08	0.72		−0.24	78.44	0.08	0.42		<0.002

Probabilities (P), r^2_{adj} (r^2) and parameters y_0, a and b of the exponential decay model (Equation (1)) between life form/all life forms species composition, given by the NMDS axis, and the three predictors: height above the nearest drainage (HAND), horizontal distance from nearest drainage (HDND) and Shuttle Radar Topography Mission – height above sea level (SRTM-HASL). The results of the best model for predicting changes in composition for each life form are given in bold. Delta Akaike information criterion (Δ AIC) values for a subset of 18 plots are presented for comparisons among models of plant composition for the six life forms. Δ AIC was calculated in relation to tree species composition versus the HAND model, which had the most support.

To investigate if plant quantitative- and qualitative-composition changes were related to HAND, we tested this predictor for the six life forms and for all species using an exponential-decay function with three parameters:

$$\text{Species composition} = y_0 + a\,\exp^{-b*\,\text{predictor}} \qquad (1)$$

We tested other non-linear functions (inverse polynomial of first- and second-order, quadratic and exponential decay with two parameters) but the exponential decay function with three parameters captured relationships as well or better than the other functions in all cases. Therefore, we only report the results of the exponential decay with three parameters (Table 2). The delta Akaike information criterion (Δ AIC) was calculated to compare differences in model strength among life forms. Δ AIC > 2 indicates stronger support for a given model than other models in the comparison (Burnham and Anderson 2004). As the AIC values are sensitive to the number of sampling units (Burnham and Anderson 2004), we used only the plots where all life forms were sampled for model-fit comparisons among life forms.

In order to locate positions along the HAND gradient where the rates of change in plant-species composition slowed along the exponential-decay gradient, we calculated HAND values corresponding to the part of the curve at which a change of 90% in species composition occurred. The same threshold (90%) was used for all plant groups to standardise the comparisons among groups. We identified this HAND threshold for the six life forms and for all species combined.

To compare the predictive power, related to plant composition changes, of HAND with that of HDND and SRTM-HASL, we tested these three predictors together in multiple linear regressions where we selected the minimum adequate model (Calcagno and De Mazancourt 2010). The automated model selection, implemented by the package glmulti (Calcagno and de Mazancourt 2010) finds the best model among all possible models based on their AIC ranking. The variables were log-transformed prior to analysis to meet the assumptions of linear regression models. All analyses were carried out in the R environment, version 2.15.1 (R Core Team 2011).

Results

Patterns of floristic composition changes

Changes in plant-species composition were closely related to the HAND. HAND alone explained between 26% and 82% of variance in the ordination using quantitative species composition, and all life forms had the same pattern of change in species composition along the HAND gradient. Higher rates of change in species composition occurred close to the drainage, with a decrease to almost no change as the vertical distance from the nearest drainage increased (Figure 2). However, the strength of this relationship differed among life forms (Δ AIC > 2 for all groups, Table 2). Major changes in plant species composition (90% of the changes) occurred within vertical distances from drainage of 8 to 18 m (corresponding horizontal distances of about 60 to 350 m), indicating that a strong change in composition takes place in the transition between the valley bottoms and higher elevations (Figure 3). This threshold of plant-species composition change varied among life forms, from a HAND value of 8 m in shrubs to 18 m above the nearest drainage in trees and herbs (Figure 2).

Qualitative-composition changes were consistent with the results of quantitative changes, with similar relative rates of change along the HAND gradient. However, the explanatory power of HAND for lianas, palms and all life forms combined was lower for qualitative-composition compared to quantitative-composition changes (Table 2). The strengths of relationships with HAND were similar between palms and shrubs (Δ AIC < 2) but differed among other plant groups. The distance above the nearest drainage below which 90% of the changes in plant composition occurred for qualitative data was 8 m for shrubs, 10 m for lianas, 11 m for palms, 13 m for ferns, 14 m for trees and 18 m for herbs.

Predictors of floristic-composition changes: HAND versus HASL and HDND

Changes in species composition of the plant life-form types examined and all species combined were more closely related to HAND than to HASL and HDND. HAND was the best single predictor of floristic composition, and the addition of HASL and HDND to models did not increase model support (Δ AIC < 2, Table S1 (available online)). There was no support (Δ AIC < 2 in all cases) for differences between Euclidean distance and flow-direction paths for predicting floristic-composition changes (Δ AIC < 2), so we report only results for HDND-flowdir (Table 2).

We used SRTM-HASL as the altitudinal predictor in the model selection procedures because SRTM data are spatially explicit, similar to HAND and HDND, allowing extrapolations, while ground-HASL data are available for few locations in Amazonia, restricting extrapolation to other areas. The comparison between SRTM-HASL and ground-HASL however, showed different supports for models of floristic composition. When only HASL predictors were considered, SRTM-HASL had more support for predictions of tree, palm and shrub species composition changes than ground-HASL (Δ AIC > 2 in all cases). The other plant life forms (lianas, herbs and ferns) were better predicted by ground-HASL than SRTM-HASL (Δ AIC > 2 in all cases).

Discussion

Changes in floristic composition along the HAND gradient

In this study, plant-composition changes at the mesoscale were closely related to vertical distance from the nearest drainage (HAND), with an exponential decay of changes in

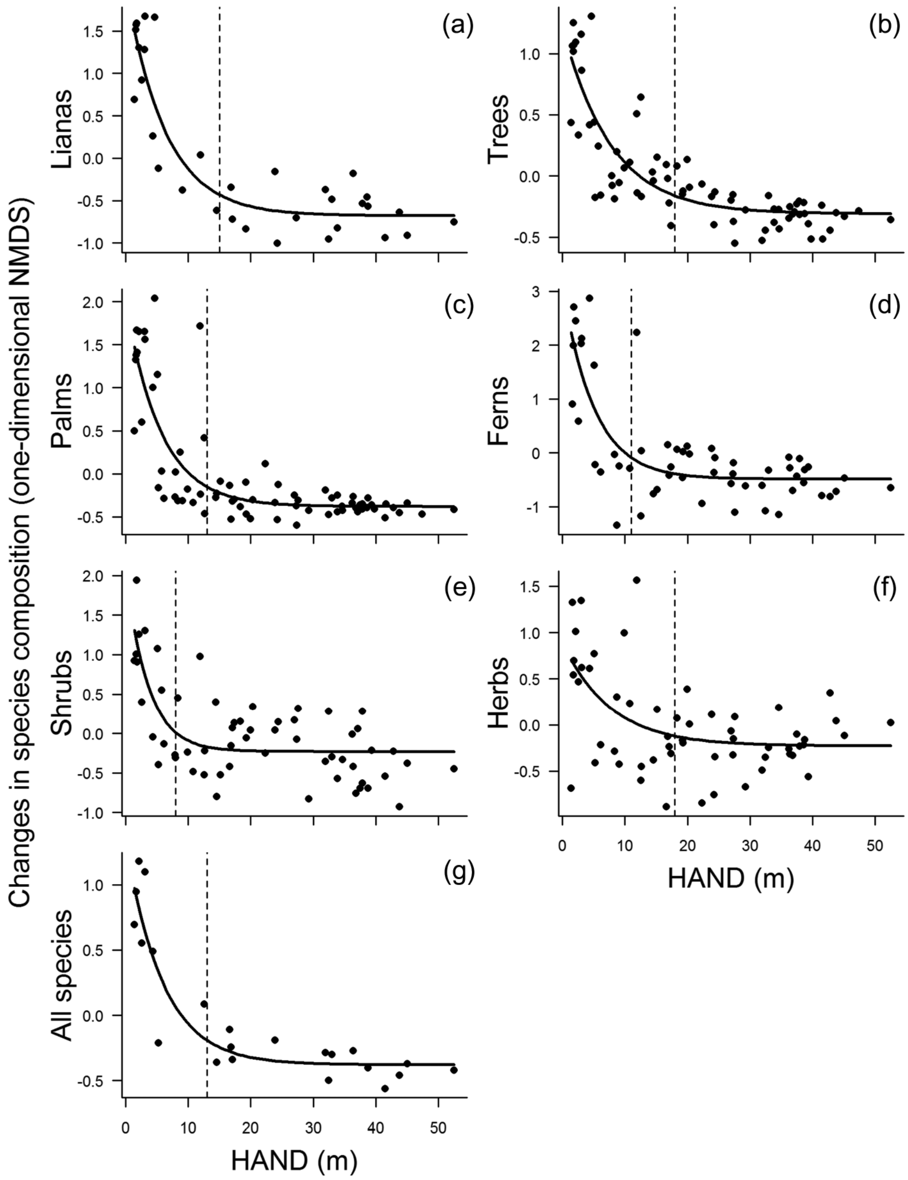

Figure 2. Relationships between quantitative composition changes of six life forms and all species combined and height above the nearest drainage (HAND), Reserva Ducke, Manaus, Brazil. Dashed lines show the thresholds of vertical distance from drainage below which 90% of the changes in species composition take place. (a) Lianas, $r^2_{adj} = 0.82$ and threshold of 15m; (b) trees, $r^2_{adj} = 0.72$ and threshold of 18 m; (c) palms, $r^2_{adj} = 0.67$ and threshold of 13 m; (d) ferns, $r^2_{adj} = 0.58$ and threshold of 11 m; (e) shrubs, $r^2_{adj} = 0.49$ and threshold of 8 m; (f) herbs, $r^2_{adj} = 0.26$ and threshold of 18 m; (g) all life forms, $r^2_{adj} = 0.84$ and threshold of 13 m. Changes in species composition were reduced to one dimension, using non-metric multidimensional scaling (NMDS).

species composition as HAND increased. About 90% of the changes in species composition took place below a HAND threshold of 8 to 18 m, depending of plant life form (13 m for all life forms combined), suggesting that soil hydrology, probably in combination with other edaphic features, plays an important role in determining plant-assemblage composition.

That 90% of changes in species composition occur up to 8 to 18 m above the drainage, depending on life form, indicates that most changes in composition take place in areas affected by seasonal water table fluctuations. The upper limit of the water table in a well-studied micro-catchment close to the Reserva Ducke has been estimated as 16 m above the drainage (Tomasella et al. 2008). This zone of water table fluctuation encompasses the valley bottom and the lower parts of slopes, and the water table level in the valley ranges from water at the ground surface (waterlogged) to less than 1 m below the surface at the end of dry season in average years (Hodnett et al. 1997; Drucker et al. 2008). This suggests that the seasonal water table fluctuations leading to frequent waterlogging in valleys may promote a distinct plant-species composition in these areas, possibly related to higher stem mortality and recruitment (see Phillips et al. 1994). In the Reserva Ducke, the mortality of small trees (4 ≥ DBH < 30 cm) in the valleys and on the slopes was 40% higher (between 2003–2008) than on plateaux; and uprooting was an important mode of death (Toledo et al. 2012). Uprooting may be caused by

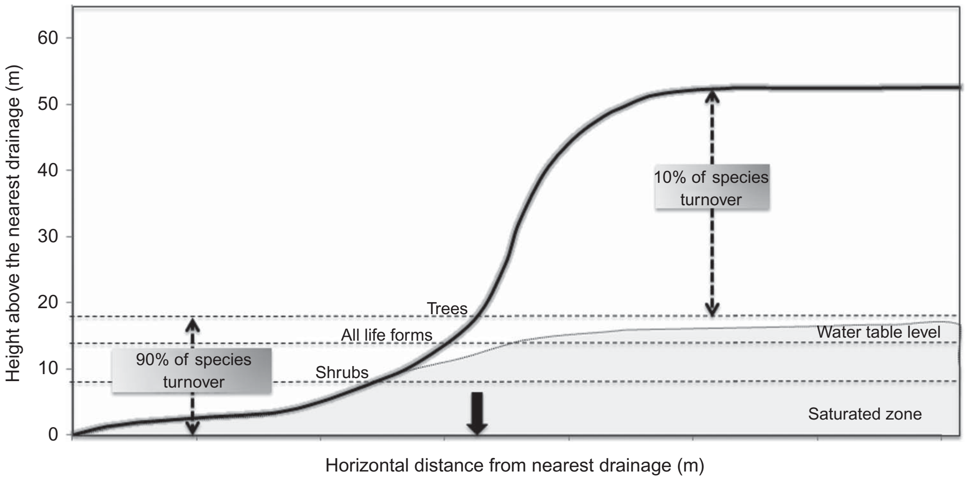

Figure 3. A schematic view of where the major part of floristic composition changes takes place along the vertical distances from the nearest drainage (HAND) gradient. Horizontal dashed lines show HAND thresholds for 90% of composition changes in shrubs (8 m), all life forms combined (13 m) and trees (18 m). Water table fluctuation zone is shown in grey. Horizontal distance from drainage (HDND) that corresponds to a 18 m HAND threshold in the Reserva Ducke, Manaus, Brazil extends 350 m and is highlighted by the black arrow in the schema.

low anchorage due to limited production and establishment of roots in waterlogged anoxic conditions in valleys, by poor anchorage in the sandy soils of valley bottoms, and by the higher phosphorus availability in valleys and lower-slope soils that may reduce the investment in roots (see Toledo et al. 2012). The high stem mortality may create greater recruitment opportunities than on the plateaux, and that, combined with diverse seed rain (Harms 1997), could lead to higher species turnover through space and time in riparian areas. Conversely, the lower soil-water availability on the plateaux, especially in the dry season (Hodnett et al. 1997), associated with lower mortality (Toledo et al. 2012), could be selecting for establishment of a more drought-tolerant assemblage composition on the upper slopes and higher lands (Newbery et al 1996; Gibbons and Newbery 2002). This could explain the lesser differences in plant species composition found in areas with higher vertical distances to the drainage.

Other processes that may affect the pattern of compositional changes along a HAND gradient are differential tolerance to anoxic conditions (Joly and Crawford 1982; Junk 1997; Scarano et al. 1997; Svenning 2001; Parolin 2002), differential root:shoot biomass ratios (Joslin et al. 2000) and dispersal patterns and limitations (Dalling et al. 1998; Ozinga et al. 2005; Parmentier and Hardy 2009). Most of these processes affect seed germination, individual establishment, survivorship and recruitment, and may contribute to the higher rates of change in species composition with distance from stream in areas vertically close to the drainage.

Other factors, such as soil physical and chemical properties, are correlated with HAND in the Reserva Ducke and should also be considered as possible determinants of patterns of changes in composition. Soil texture affects water retention (Hodnett and Tomasella 2002) in soil surface layers and in some circumstances this could counterbalance the effects of higher vertical distances. Clay content is highly correlated with HAND in the Reserva Ducke ($r = 0.88$) and clay content can affect soil water availability for plants (Hodnett and Tomasella 2002). Nutrient availability is linked to soil physical properties and water availability (Baldwin and Mitchell 2000) and should also interact with the HAND gradient. Further studies in sites with distinct correlations between topography and soil characteristics, e.g. Iquitos region (Western Amazonia) where clayey and nutrient-rich soils are at lower elevations and sandy, nutrient-poor soils are at higher elevations (Vormisto et al. 2000), are necessary for disentangling the effects of soil nutrients, soil physical properties and HAND on plant-composition changes.

Plant life forms

The strength of the relationship between plant composition and HAND varied among life forms. The six life forms differed in mean maximum plant size, resource use and reproductive patterns, but soil-water gradients should play an important role in establishment and maintenance for all plants. Tropical rainforest herbs, ferns, shrubs and palms have shallow root systems (Becker and Castillo 1990; Ramos et al. 2009) and our expectation was that compositional changes in these plant groups would be more closely related to the HAND gradient due to their limited access to groundwater. However, contrary to this expectation, deep-rooted plants, such as lianas and trees, had more variation explained by HAND than ferns, shrubs and herbs. A possible reason is that the life forms, with shallow roots and smaller sizes, may depend more than the other life-history types on the small-scale and seasonal variation in soil water in the surface layers (see Marthews et al. 2008), rather than on access to deep water. Drucker et al. (2008) documented fine-scale changes in herb species' composition along a gradient of horizontal distance from streams in the Reserva Ducke, and ferns' life cycle are highly dependent on free water (Page 2002). The weaker relationships with HAND for herbs, shrubs and ferns may be due to the fact that HAND is a proxy with stationary measurements of vertical distances to the water table, and with relatively coarse spatial resolution in this study (90 × 90 m pixels).

Given the differences in rooting depth of the life forms, changes in turnover rates would be expected to occur at higher HAND thresholds for deep rooting plants and at lower HAND thresholds for shallow rooted-plants. Deep-rooted plants, however, may have access to water even at higher vertical distances from the water table, and therefore not show changes in composition until well away from streams. To provide further understanding of the role of root depth for the turnover rates, we regressed the HAND thresholds for the major changes of the six life forms against their respective maximum rooting depth. We compiled data on rooting depth in tropical forests for the six plant groups from published papers and unpublished information. Root depth can reach up to 18 m for trees (Nepstad et al. 1994), 0.6 m for palms (Ramos et al. 2009), 0.7 m for shrubs (Becker and Castillo 1990), 0.7 m for herbs and 0.3 m for ferns (F.R.C. Costa, unpublished data). No published data was found for root depth of adult lianas, but Restom and Nepstad (2004) reported 10 m for vine seedlings. Therefore, we used the same depth for lianas as for trees. Based on these data, there was no relation between HAND thresholds for major changes in composition and maximum rooting depth ($r^2 = 0.27$; $P = 0.29$; $n = 6$), indicating that this trait might not be linked to the differences among life forms. There is a large variation in rooting depths within life forms and their ontogeny (Canadell et al. 1996; Jackson et al. 1996), but the lack of available information on species' rooting depth presently restricts detailed analysis.

Despite the large variation in rooting deep among plant life forms, Jackson et al. (1996) and Galbraith (forthcoming) have shown that the majority of the roots in tropical forests are within the first 2 m of the soil surface, and that root biomass decreases exponentially with depth. Therefore, the deep roots of trees and lianas may not contribute greatly to water balance. There is surprisingly little literature on this subject and further detailed studies are needed to investigate the relationship between rooting depth, species turnover along edaphic gradients and access to the water table.

HAND versus HASL and HDND

Earlier studies have shown that tree (Valencia et al. 2004), palm (Costa et al. 2009), shrub (Kinupp and Magnusson 2005) and herb, including fern (Costa et al. 2005) assemblage compositions are correlated with HASL in Amazonian forests. In this study, we showed that ordinations of all species, considering the life forms listed above and lianas together, also can be predicted by HASL and HDND. However, we found that, on its own, HAND was a better predictor of plant-composition changes at the mesoscale than HASL or HDND, even in the Reserva Ducke, where HASL is correlated with soil physical properties, nutrients and water availability (Chauvel et al. 1987; Hodnett et al. 1997). The main difference between HAND and HASL is that HAND values are relative to the local drainage (not to sea level), so it is a quantitative descriptor of the vertical distance from the saturated zone or the water table (Rennó et al. 2008; Nobre et al. 2011). For plants, access to groundwater will be lower in areas with high HAND values, independent of HASL. Hydrologically similar terrains, such as valleys (or riparian areas), can be located at different HASL, but their HAND values will be near zero because they are vertically close to the saturated zone. As HAND measures distance to the local drainage, it should be a robust proxy for comparisons between areas located at different HASL.

HDND, together with HAND, is an important variable for determining soil draining because long horizontal distances from streams have higher draining potential, and areas close to streams are usually poorly drained (Bell et al. 1994; Campling et al. 2002; Kravchenko et al. 2002). The finding that HAND was a better predictor of floristic composition than HDND indicates that changes in HDND should be less important for plants than vertical distances from the water table. It also indicates that HDND might be inappropriate to represent flat areas near streams (i.e. large-bottomed valleys), because these are waterlogged and poorly drained areas that sometimes can have relative high values of HDND. In the Reserva Ducke, there was a positive correlation between horizontal and vertical distances from drainage, even in large valley bottoms, but the shape and direction of this relation may vary across sites with distinct parent material and hydro-geological histories (e.g. in the case of terrain depressions far from streams). The consistency of HAND being a better predictor than HDND of floristic composition should be tested on different geomorphologies, given the geological complexity of the Amazon Basin.

Implications for conservation strategies and climate change

The finding that the areas of higher species turnover and distinct floristic composition are also the areas directly affected by the water table fluctuation has implications for conservation planning and prediction of climate-change effects. In Brazil, environmental legislation protects the riparian zones that vary in width (horizontal distance from the stream margins) according to the stream size. Streams up to 10 m wide, such as those found in the Reserva Ducke, have protected zones that are 30 m wide on each margin. Our results indicate that zones of 30 m width along streams margins are insufficient for conservation of riparian areas because they do not include the areas of highest assemblage turnover (see Figure 3). In the Reserva Ducke, vertical distances from drainage of 8 to 18 m, where the composition changes slow down, correspond to horizontal distances of about 60 to 250 m (but one plot 15 m above the drainage was horizontally 350 m distant from a stream). Vertical distance from drainage, rather than only the horizontal distance, should be considered in the defining riparian habitats for conservation of riparian ecosystems. The critical vertical distance from drainage for conservation purposes could be defined by the upper limits of the water table fluctuation zone and this should vary across Amazonian landscapes due to variations in precipitation, topography and soil properties.

Although the long-term climate variability in Amazonia is complex, with opposite trends in precipitation or no clear patterns over different regions of the basin (Marengo 2004), large-scale numerical models project significant Amazonian drying and shift in vegetation types in the twenty-first century (Cox et al. 2000, 2008; Oyama 2003; but see Malhi et al. 2009). Evidence for a transition to a disturbance-dominated regime in some parts of the Amazon Basin was found recently (Davidson et al. 2012), and tree-ring chronology indicates increasing severity of El Niño events in the last two centuries (Schöngart et al. 2004). If the climate becomes dryer, with more severe droughts, the soil-water storage and water table will decrease. A decrease in the water table level would narrow the areas of highest floristic turnover into smaller horizontal distances from streams. Further, this would cause shifts in species composition in riparian areas, because of differences in drought tolerance (Engelbrecht et al. 2007). Plants confined to plateaux areas could migrate downhill to track water table level changes. However, plants already confined to environments near drainages may not have many options to migrate to similar environments, because there are locally no similar environments and most species in tropical forests are not adapted for long-distance dispersal (Clark et al. 2005; Colwell et al. 2008; Terborgh et al. 2011). These species could become endangered by lack of suitable habitat.

Conclusions

This study has shown that changes in floristic composition are closely related to HAND in central Amazonia, suggesting an important role of soil hydrology for species composition and turnover in terra firme forests. The highest floristic turnover was found to occur in areas influenced by seasonal water table fluctuations, and this finding has important implications for forest conservation. Brazilian environmental legislation protects riparian forests in strips of 30 m wide from small stream margins. Our results indicate that these 30-m strips are far too narrow to protect the areas of high species turnover close to the water table. In the Reserva Ducke, we found that these areas can reach 250 m from the streams. We recommend that vertical distances from the drainage (and seasonal water table fluctuation) rather than only horizontal distances should be used in the delimitation of riparian habitats for conservation of plant diversity and ecosystem functioning.

The strong relationships found between plant composition and HAND opens a promising opportunity to investigate plant species distribution and assemblage composition changes over larger scales, since HAND is based on SRTM data, available for the entire Amazon Basin.

Acknowledgements

Data used in this paper were obtained from data repositories maintained by the Brazilian Programme for Biodiversity Research (PPBio) and the National Institute for Amazonian Biodiversity (INCT-CENBAM). The field infrastructure was installed by the Programa Norte de Pós-Graduação (PNOPG-CAPES) and maintained by the Brazilian PELD (LTER) Program financed by National Council for Scientific and Technological Development CNPq. J.S. and T.E. were supported during this study by a CNPq fellowship. Part of this manuscript was developed during the workshops of PPBio/PPGECO-INPA at Reserva Ducke and RAINFOR (Gordon and Betty Moore Foundation)-UFAC workshop in Rio Branco, Brazil, 2011. We thank Laszlo Nagy, Toby Marthews and one anonymous reviewer for the positive insights and suggestions on the manuscript structure.

Notes on contributors

Juliana Schietti is a Ph.D. student interested in understanding how variation in forest structure and functioning are related to hydrological processes.

Thaise Emilio is a Ph.D. student. She has been working with plant species and vegetation distribution across Amazonia. She is especially interested in palms and how environmental conditions drive their distribution and abundance.

Camilo D. Rennó is a researcher working mostly on hydrology, image processing and geotechnologies.

Debora P. Drucker is an analyst in technology transfer and is interested in information management advancements to enable synthesis studies in ecology and biodiversity and foster dissemination of scientific knowledge.

Flávia R.C. Costa is a researcher, working mostly on the ecological determinants of plant species and assemblage distributions and the impacts of human use upon them.

Anselmo Nogueira is a post-doctoral researcher interested in understanding factors related to plant distribution, specially of lianas, and also the evolution and ecology of animal-plant interactions.

Fernando O.G. Figueiredo is an M.Sc. researcher interested in understanding the distribution of tropical herbs along edaphic and climate gradients.

Fabricio B. Baccaro is a Ph.D. student, interested in the ecology and evolution of parasite-host interactions.

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.

Valdely Kinupp is a professor interested in wild food plants, ethnobotany, economic botany, agroecology and plant taxonomy.

Jean-Louis Guillaumet works on tropical phytogeography.

Ana Raquel M. Garcia is a biologist who has studied the distribution and abundance of shrubs in the Reserva Ducke.

Albertina P. Lima works on different aspect of Amazonian biodiversity.

William E. Magnusson coordinates the Programme for Biodiversity Research (PPBio) in western Amazonia.

References

Albernaz AL, Pressey RL, Costa LRF, Moreira MP, Ramos JF, Assunção PA, Franciscon CH. 2012. Tree species compositional change and conservation implications in the white-water flooded forests of the Brazilian Amazon. Journal of Biogeography 39:869–883.

Baldwin DS, Mitchell AM. 2000. The effects of drying and re-flooding on the sediment and soil nutrient dynamics of soil lowland river-floodplain systems: a synthesis. Regulated Rivers: Research and Managment 467:457–467.

Balvanera P, Quijas S, Pérez-Jiménez. 2011. Distribution patterns of tropical dry forest trees along a mesoscale water availability gradient. Biotropica 43:414–422.

Becker P, Castillo A. 1990. Root architecture of shrubs and saplings in the understory of a tropical moist forest in lowland Panama. Biotropica 22:242–249.

Bell JC, Cunningham RL, Havens MW. 1994. Soil drainage class probability mapping using a soil-landscape model. Soil Science Society of America Journal 58:464–470.

Brown DJ, Clayton MK, McSweeney K. 2004. Potential terrain controls on soil color, texture contrast and grain-size deposition for the original catena landscape in Uganda. Geoderma 122:51–72.

Burnham KP, Anderson DR. 2004. Multimodel inference: understanding AIC and BIC in model selection. Sociological Methods & Research 33:261–304.

Calcagno V, De Mazancourt C. 2010. glmulti: An R package for easy automated model selection with (generalized) linear models. Journal of Statistical Software 34:1–29.

Campling P, Gobin A, Feyen J. 2002. Logistic modeling to spatially predict the probability of soil drainage classes. Soil Science Society of America Journal 66:1390–1401.

Canadell J, Jackson RB, Ehleringer JR, Mooney HA, Sala OE, Schulze ED. 1996. Maximum rooting depth of vegetation types at the global scale. Oecologia 108:583–595.

Chauvel A, Lucas Y, Boulet R. 1987. On the genesis of the soil mantle of the region of Manaus, Central Amazonia, Brazil. Experimentia 43:234–241.

Clark C, Poulsen J, Bolker B, Connor E, Parker V. 2005. Comparative seed shadows of bird-, monkey-, and wind-dispersed trees. Ecology 86:2684–2694.

Colwell RK, Brehm G, Cardelús CL, Gilman AC, Longino JT. 2008. Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. Science 322:258.

Comita LS, Engelbrecht BMJ. 2009. Seasonal and spatial variation in water availability drive habitat associations in a tropical forest. Ecology 90:2755–2765.

Costa FRC, Guillaumet J-L, Lima A, Pereira O. 2009. Gradients within gradients: the mesoscale distribution patterns of palms in a central Amazonian forest. Journal of Vegetation Science 20:69–78.

Costa FRC, Magnusson WE, Luizao RC. 2005. Mesoscale distribution patterns of Amazonian understorey herbs in relation to topography, soil and watersheds. Journal of Ecology 93:863–878.

Costa FRC, Magnusson WE. 2010. The need for large-scale, integrated studies of biodiversity – the experience of the Program for Biodiversity Research in Brazilian Amazonia. Natureza & Conservação 08:3–12.

Costa FRC. 2006. Mesoscale gradients of herb richness and abundance in central Amazonia. Biotropica 38:711–717.

Cox PM, Betts RA, Jones CD, Spall SA, Totterdell IJ. 2000. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. Nature 408:184–187.

Cox PM, Harris PP, Huntingford C, Betts RA, Collins M, Jones CD, Jupp TE, Marengo JA, Nobre CA. 2008. Increasing risk of Amazonian drought due to decreasing aerosol pollution. Nature 453:212–215.

Dalling J, Hubbell SP, Silvera K. 1998. Seed dispersal, seedling establishment and gap partitioning among tropical pioneer trees. Journal of Ecology 86:674–689.

Davidson EA, De Araújo AC, Artaxo P, Balch JK, Brown IF, C. Bustamante MM, Coe MT, DeFries RS, Keller M, Longo M, et al. 2012. The Amazon basin in transition. Nature 481:321–328.

Daws MI, Mullins CE, Burslem DFRP, Paton SR, Dalling JW. 2002. Topographic position affects the water regime in a semideciduous tropical forest in Panama. Plant and Soil 238:79–90.

Drucker DP, Costa FRC, Magnusson WE. 2008. How wide is the riparian zone of small streams in tropical forests? A test with terrestrial herbs. Journal of Tropical Ecology 24:65–74.

Engelbrecht BMJ, Comita LS, Condit R, Kursar TA, Tyree MT, Turner BL, Hubbell SP. 2007. Drought sensitivity shapes species distribution patterns in tropical forests. Nature 447:80–2.

Gibbons JM, Newbery DM. 2002. Drought avoidance and the effect of local topography on trees in the understorey of Bornean lowland rain forest. Plant Ecology 164:1–18.

Groom PK. 2004. Rooting depth and plant water relations explain species distribution patterns within a sandplain landscape. Functional Plant Biology 31:423–428.

Harms KE. 1997. Habitat-specialization and seed-dispersal limitation in a neotropical forest. Princeton (NJ): Princeton University.

Hodnett MG, Tomasella J. 2002. Marked differences between van Genuchten soil water-retention parameters for temperate and tropical soils: a new water-retention pedo-transfer functions developed for tropical soils. Geoderma 108:155–180.

Hodnett MG, Vendrame I, Marques Filho DO, Oyama M, Tomasella J. 1997. Soil water storage and groundwater behaviour in a catenary sequence beneath forest in central Amazonia: I. Comparisons between plateau, slope and valley floor. Hydrology and Earth System Sciences 1:265–277.

Jackson RB, Canadell J, Ehleringer HA, Mooney HA, Schulze ED, Sala OE. 1996. A global analysis of root distributions for terrestrial biomes. Oecologia 108:389–411.

Jirka S, McDonald AJ, Johnson MS, Feldpausch TR, Couto EG, Riha SJ. 2007. Relationships between soil hydrology and forest structure and composition in the southern Brazilian Amazon. Journal of Vegetation Science 18:183–194.

Joly CA, Crawford RMM. 1982. Variation in tolerance and metabolic responses to flooding in some tropical trees. Journal of Experimental Botany 33:799–809.

Joslin JD, Wolfe MH, Hanson PJ. 2000. Effects of altered water regimes on forest root systems. New Phytologist 147:117–129.

Junk WJ. 1997. The central Amazon floodplain: ecology of a pulsing system. Berlin (Germany): Springer.

Kanagaraj R, Wiegand T, Comita LS, Huth A. 2011. Tropical tree species assemblages in topographical habitats change in time and with life stage. Journal of Ecology 99:1441–1452.

Kinupp VF, Magnusson WE. 2005. Spatial patterns in the understorey shrub genus *Psychotria* in central Amazonia: effects of distance and topography. Journal of Tropical Ecology 21:363–374.

Kravchenko AN, Bollero GA, Omonode RA, Bullock DG. 2002. Quantitative mapping of soil drainage classes using topographical data and soil electrical conductivity. Soil Science Society of America Journal 66:235–243.

Magnusson WE, Lima AP, Luizão R, Luizão F, Costa FRC, Castilho CV, Kinupp V. 2005. RAPELD: a modification of the Gentry method for biodiversity surveys in long-term ecological research sites. Biota Neotropica 5:19–24.

Malhi Y, Aragão L, Galbraith D, Huntingford C, Fisher R, Zelazowski P, Sitch S, McSweeney C, Meir P. 2009. Exploring the likelihood and mechanism of a climate-change-induced dieback of the Amazon rainforest. Proceedings of the National Academy of Science 49:20610–20615.

Marengo JA. 2004. Interdecadal variability and trends of rainfall across the Amazon basin. Theoretical and Applied Climatology 78:79–96.

Marques-Filho A de O, Ribeiro M de NG, Santos HM, Santos JM. 1981. Estudos climatologicos da Reserva Florestal Ducke – Manaus-AM. IV. Precipitacao. Acta Amazonica 11:759–768.

Marshall TJ, Holmes JW, Rose C. 1996. Soil physics. 3rd ed. Cambridge (UK): Cambridge University Press.

Marthews TTR, Burslem DFRPD, Paton SRR, Yangüez F, Mullins CEE. 2008. Soil drying in a tropical forest: three distinct environments controlled by gap size. Ecological Modelling 216:369–384.

McCune B, Grace AJB. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon, USA.

Naiman RJ, Henri D, Décamps H. 1997. The ecology of interfaces: riparian zones. Annual Review of Ecology and Systematics 28:621–658.

Nepstad DC, Carvalho CR, Davidson EA, Jipp PH, Lefebvre PA, Negreiros GH, Silva ED, Stone TA, Trumbore SE, Vieira S. 1994. The role of deep roots in the hydrological and carbon cycles of Amazonia forests and pastures. Nature 372:666–669.

Newbery DM, Campbell EJF, Proctor J, Still MJ. 1996. Primary lowland dipterocarp forest at Danum Valley, Sabah, Malaysia. Species composition and patterns in the understorey. Vegetatio 122:193–220.

Nobre AD, Cuartas LA, Hodnett M, Rennó CD, Rodrigues G, Silveira A, Waterloo M, Saleska S. 2011. Height above the nearest drainage – a hydrologically relevant new terrain model. Journal of Hydrology 404:13–29.

Nogueira A, Costa FRC, Castilho CV. 2011. Liana abundance patterns: the role of ecological filters during development. Biotropica 43:442–449.

Oyama MD. 2003. A new climate-vegetation equilibrium state for tropical South America. Geophysical Research Letters 30:10–13.

Ozinga W, Schaminée J, Bekker R, Bonn S, Poschold P, Tackenberg O, Bakker J, Van Groenendael JM. 2005. Predictability of plant species composition from environmental conditions is constrained by dispersal limitation. Oikos 108:555–561.

Page CN. 2002. Ecological strategies in fern evolution: a neopteridological overview. Review of Palaeobotany and Palynology 119:1–33.

Parmentier I, Hardy OJ. 2009. The impact of ecological differentiation and dispersal limitation on species turnover and phylogenetic structure of inselberg's plant communities. Ecography 32:613–622.

Parolin P. 2002. Submergence tolerance vs. escape from submergence: two strategies of seedling establishment in Amazonian floodplains. Environmental and Experimental Botany 48:177–186.

Phillips OL, Aragão LEOC, Lewis SL, Fisher JB, Lloyd J, López-González G, Malhi Y, Monteagudo A, Peacock J, Quesada CA, et al. 2009. Drought sensitivity of the Amazon rainforest. Science 323:1344–1347.

Phillips OL, Hall P, Gentry AH, Sawyer SA, Vásquez R. 1994. Dynamics and species richness of tropical rain forests. Proceedings of the National Academy of Science 91:2805–2809.

Prates-Clark CDC, Saatchi SS, Agosti D. 2008. Predicting geographical distribution models of high-value timber trees in the Amazon Basin using remotely sensed data. Ecological Modelling 211:309–323.

Pyke CR, Condit R, Aguilar S, Lao S. 2001. Floristic composition across a climatic gradient in a neotropical lowland forest. Journal of Vegetation Science 12:553–566.

R Core Team. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. http://www.R-project.org/.

Raes N, Roos MC, Slik JWF, Van Loon EE, ter Steege H. 2009. Botanical richness and endemicity patterns of Borneo derived from species distribution models. Ecography 32: 180–192.

Ramos A, Folegatti MV, Bovi MLA, Diotto AV. 2009. Distribuição espacial do sistema radicular da pupunheira em função de lâminas de irrigação. Irriga 14:431–440.

Rennó CD, Nobre AD, Cuartas LA, Soares JV, Hodnett MG, Tomasella J, Waterloo MJ. 2008. HAND, a new terrain descriptor using SRTM-DEM: Mapping terra-firme rainforest environments in Amazonia. Remote Sensing of Environment 112:3469–3481.

Restom TG, Nepstad DC. 2004. Seedling growth dynamics of a deeply rooting liana in a secondary forest in eastern Amazonia. Forest Ecology and Management 190:109–118.

Ribeiro JELS, Hopkins MJG, Vicentini A, Sothers CA, Costa MAS, Brito JM, Souza MAD, Martins LH, Lohmann LG, Assunção PA, et al. 1999. Flora da Reserva Ducke. Guia de identificação das plantas vasculares de uma floresta de terra firme na Amazônia Central. Manaus (Brazil): INPA – DFID.

Rodriguez-Iturbe I. 2000. Ecohydrology: a hydrologic perspective of climate-soil-vegetation dynamics. Water Resources Research 36:3–9.

Saatchi SS, Houghton RA, Dos Santos Alvalá RC, Soares J V, Yu Y. 2007. Distribution of aboveground live biomass in the Amazon basin.

Sabo JL, Sponseller MD, Gade K, Harms T, Heffernan J, Jani A, Katz G, Soykan C, Watts J, Welter J. 2005. Riparian zones increase regional species richness by harboring different, not more, species. Ecology 86:56–62.

Salas WA, Ducey MJ, Rignot E, Skole D. 2002. Assessment of JERS-1 SAR for monitoring secondary vegetation in Amazonia: I. Spatial and temporal variability in backscatter across a chrono-sequence of secondary vegetation stands in Rondonia. International Journal of Remote Sensing 23:1357–1379.

Scarano FR, Ribeiro KT, De Moraes LFD, De Lima HC. 1997. Plant establishment on flooded and unflooded patches of a freshwater swamp forest in southeastern Brazil. Journal of Tropical Ecology 14:793–803.

Schnitzer SA. 2005. A mechanistic explanation for global patterns of liana abundance and distribution. The American Naturalist 166:262–76.

Schulman L, Ruokolainen K, Junikka L, Sääksjärvi IE, Salo M, Juvonen S-K, Salo J, Higgins M. 2007. Amazonian biodiversity and protected areas: do they meet? Biodiversity and Conservation 16:3011–3051.

Schöngart J, Junk WJ, Piedade MTF, Ayres JM, Huttermann A, Worbes M, Schongart J. 2004. Teleconnection between tree growth in the Amazonian floodplains and the El Nino-southern oscillation effect. Global Change Biology 10:683–692.

Silvertown J, Dodd M, Gowing D, Mountford J. 1999. Hydrologically defined niches reveal a basis for species richness in plant communities. Nature 400:61–63.

Smith LC. 2002. Emerging applications of interferometric synthetic aperture radar (InSAR) in geomorphology and hydrology. Annals of the Association of American Geographers 92:385–398.

Svenning J-C. 2001. On the role of microenvironmental heterogeneity in ecology and diversification of neotropical rainforest palms (Arecaceae). The Botanical Review 67:1–53.
Terborgh J, Loayza PA, Dexter K, Cornejo F, Carrasco C. 2011. Decomposing dispersal limitation: limits on fecundity or seed distribution? Journal of Ecology 99:935–944.
Toledo JJ, Magnusson WE, Castilho CV, Nascimento HEM. 2012. Tree mode of death in central Amazonia: effects of soil and topography on tree mortality associated with storm disturbances. Forest Ecology and Management 263: 253–261.
Tomasella J, Hodnett MG, Cuartas LA, Nobre AD, Waterloo MJ, Oliveira SM. 2008. The water balance of an Amazonian micro-catchment: the effect of interannual variability of rainfall on hydrological behaviour. Hydrological Processes 22:2133–2147.
Tuomisto H, Poulsen AD. 2000. Pteridophyte diversity and species composition in four Amazonian rain forests. Journal of Vegetation Science 11:383–396.
Valencia R, Foster RB, Villa G, Svenning J, Hernández C, Romoleroux K, Losos E, Magård E, Balslev H. 2004. Tree species distributions and local habitat variation in the Amazon: large forest plot in eastern Ecuador. Journal of Ecology 92:214–229.
Valeriano M, Kuplich T, Storino M, Amaral B, Mendesjr J, Lima D. 2006. Modeling small watersheds in Brazilian Amazonia with shuttle radar topographic mission-90 m data. Computers & Geosciences 32:1169–1181.
Vormisto J, Phillips OL, Ruokolainen K, Tuomisto H, Vásques R. 2000. A comparison of fine-scale distribution patterns of four plant groups in an Amazonian rainforest. Ecography 23:349–359.