

How wide is the riparian zone of small streams in tropical forests? A test with terrestrial herbs

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Abstract: Although it is well known that riparian zones can contribute strongly to between-habitat beta diversity, for most taxa it is not clear how far this ‘zone’ extends, and whether it corresponds to easily recognizable topographic features. Forty 200-m² plots were installed in a terra firme tropical forest to detect compositional variation in terrestrial herbs from the margins of small streams to the uplands. Plots were ordinated by their dissimilarity in species composition with non-metric multidimensional scaling. The riparian zone around streams was distinct in understory herb composition from upland areas for about 100 m from the streams, or about 70 m asl in elevation, the exact distance depending on the size of the stream valley. However, the only assemblage that was almost completely distinct occurred as a narrow band a few metres wide along the streams. The rest of the riparian zone appears to represent an ecotone with continuous change, most of which occurs out to a distance of about half the width of the riparian zone as we defined it. Although riparian zones are legally protected in Brazil, they are frequently degraded. The complex factors leading to zonation around streams need to be understood to effectively manage these areas.

Key Words: Amazonia, community ecology, ecotone, herbs, riparian zone

INTRODUCTION

Most of the studies of floristic variation along edaphic and topographic gradients have shown differences in composition between broad environmental classes, such as uplands and valleys, or between clayey and sandy soils. In a review of the mechanisms that could maintain the high diversity of tropical forests, Wright (2002) concluded that topographic and/or soil specializations could not maintain the high species diversity because there are few ‘environments’, which could act as niche compartments. A similar conclusion was reached for specialization in light use (Hubbell *et al.* 1999), and the hypothesis of light regeneration niches (Denslow 1980) has lost favour in recent years (Brown & Jennings 1998). However, few studies searched for community patterns within the broad environmental categories (Lieberman *et al.* 1985, Svenning 1999, Vormisto *et al.* 2000).

Distinct habitats could result from specialization for specific zones along continuous environmental gradients, which was Whittaker’s original definition of beta diversity (Whittaker 1972). Such specialization

may be hard to detect because mass effects (Clark 2002, Shmida & Wilson 1985, Zobel 1997) tend to blur the species limits. However, when analyses are based on continuous variables, some surprising results may arise, such as evidence of light partitioning in the absence of gaps (Montgomery & Chazdon 2002). Species-rich communities structured by segregation across hydrological gradients were observed in English meadows, even when the spatial variation in soil hydrological conditions thought to cause this occurred in the absence of any obvious topographic variation (Silvertown *et al.* 1999). Therefore, it is possible that variation within broad topographic or soil classes provides opportunities for specialization which have yet to be documented.

Riparian zones around streams (Bren 1993) are one of the broad habitat categories recognized in tropical rain forests (Clark *et al.* 1999, Webb & Peart 2000), including terra firme forests of central Amazonia (Valencia *et al.* 2004). Variation in the riparian vegetation associated with streams is expected as a response to soil saturation, which changes from the stream margins to the slopes (Gregory *et al.* 1992), and to the light regime. Light penetration is expected to be higher at the stream margins,

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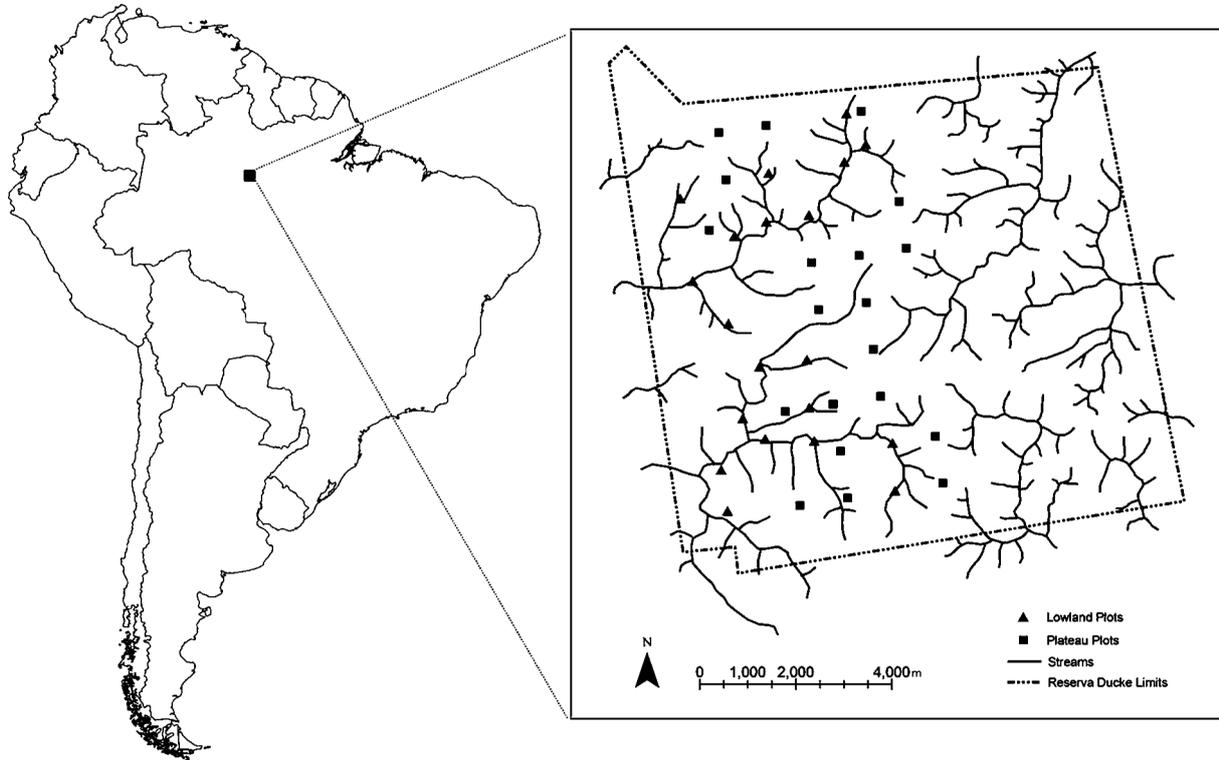


Figure 1. Reserva Florestal Adolpho Ducke and plot distribution within the study site. Triangles represent riparian plots and squares represent upland plots.

and to decrease towards the slopes. However, riparian environments are complex, because flooding patterns, water and litter accumulation, and light availability to the understorey can change rapidly in space and time.

Patterns of vegetation zonation along margins are well-documented for large rivers. In Amazonian floodplains, plant composition varies with flood duration, which depends on terrain elevation (Ferreira 1997, 2000; Ferreira & Prance 1998, Junk & Piedade 1997, Keel & Prance 1979, Salo *et al.* 1986, Worbes 1997). This strong gradient selects plants according to their life cycle duration, growth rate and wood density. It is not known, however, if the weaker gradients on the margins of small streams can play the same role as selective forces shaping community composition.

Many of the early studies of plant ecology in the tropics were concentrated on tree species (Gentry 1988, Hubbell 1979). However, environmental variations relevant for understorey plants may not be important for canopy trees (Wiens 1989). More recently, there has been a growing interest in understanding the ecology of palms, shrubs and herbs (Duque *et al.* 2002, Poulsen & Balslev 1991, Svenning 1999, Tuomisto & Ruokolainen 1994), and surveys of these groups can be conducted more rapidly than for trees. Shrub species composition was shown to be more correlated with light incidence and edaphic conditions than was canopy composition (Duque *et al.* 2002, Duque Montoya 2001). Therefore, the understorey

may respond to finer gradients than do trees. Riparian zones have been shown to contribute to between-habitat beta diversity (Sabo *et al.* 2005), but there is no guarantee that the width of the 'riparian zone' is similar for groups with different life forms.

In this paper, we investigate how terrestrial herb species composition varies from stream margins to the uplands, and how it varies within the riparian zone, from stream margins to the edge of slopes, in Reserva Florestal Adolpho Ducke, Amazonas, Brazil. We tested the hypotheses that composition differs between the riparian zone and uplands, and that species composition varies within the riparian zone along a gradient in water saturation, flooding and light availability associated with distance from the stream.

STUDY SITE

The study was conducted at Reserva Florestal Adolpho Ducke of the Instituto Nacional de Pesquisas da Amazônia (INPA), located 26 km north-west of Manaus, central Amazonia ($2^{\circ} 55' - 3^{\circ} 01'S$, $59^{\circ} 53' - 59^{\circ} 59'W$, Figure 1). The reserve covers 10 000 ha (10 km \times 10 km) of *terra firme* tropical rain forest, with a closed canopy 30–37 m high and emergents growing to 40–45 m. The understorey is characterized by abundant sessile palms, such as *Astrocaryum* spp. and *Attalea* spp. (Ribeiro *et al.* 1999).

Mean annual temperature at RFAD is around 26 °C and mean annual rainfall is 2362 mm, with a dry season between July and October (Marques-Filho *et al.* 1981).

Soils are derived from Cretaceous sediments from the Alter do Chão formation. Topography is an important determinant of soil formation in central Amazonia. Soils are clayey on the ridges, predominately formed by oxisols, constituted by kaolinite, iron oxide and gibbsite (Chauvel 1982). The clay fraction decreases as elevation decreases, and lowlands have predominately hydromorphic podzolic sandy soils (Chauvel *et al.* 1987, Ranzani 1980). The maximum altitudinal variation is about 87 m between the tops of ridges (max. observed elevation 115 m asl) and the lowlands (min. observed elevation 28 m asl). However, maximum variation between ridge tops and adjacent streams is generally only about 30 m.

METHODS

Sampling design

We installed forty 2 × 100-m plots that followed altitudinal contours, to minimize internal variation in elevation (Magnusson *et al.* 2005). Twenty plots were installed on well-drained soils, in the higher portions of the topographic gradient, at a minimum distance of 1000 m from each other. The other 20 plots were installed in the riparian zone along the lower portions of the topographic gradient, with the main axis parallel to the streams, at a minimum distance of 600 m from each other.

Riparian plots were at distances up to 100 m from the Acará and Bolívia streams, which constitute the western drainage of the reserve. The headwaters of both streams are in the reserve, and they are up to 7 km long and third order within the reserve limits. Minimum distance among the forty upland and riparian-zone plots was 300 m. Distances of riparian plots to the stream margin were randomly assigned to 0, 25, 50 or 75% of the width (from the stream margins to the edge of slopes) of the valley around the stream. Percentages of width were used to describe the environmental gradient instead of actual distances because drainage patterns vary according to the size of the drainage area (Hodnett *et al.* 1997). This means that a plot 20 m from the stream margin is relatively closer to the margin when it is in a wide drainage area than when it is in a narrow one. Four plots per distance class were established. Plots in the 0% class were split in two subplots of 1 × 100 m, one on each side of the stream.

Herb community sampling

The herb community sampled in this study was restricted to the obligate terrestrial species (*sensu* Poulsen 1996),

i.e. those that germinate and spend their entire life cycle on the ground. Hemi-epiphytes and epiphytes fallen to the ground were not considered.

Herbs were sampled between July 2001 and July 2002 in the uplands and between February and September 2004 in the lowlands. All individuals greater than 5 cm in height were counted and identified. The varieties of *Lindsaea lancea* (var. *lancea* and var. *falcata*) and *Calathea mansonis* (var. 1 and var. 2) were treated as species, as they were morphologically distinct. For species with clonal growth (Poaceae and the Marantaceae genera *Calathea* and *Ischnosiphon*) in which individuals are difficult to separate, each clump at least 20 cm from another was counted as an individual.

Identifications were based on the field guide *Flora da Reserva Ducke* (Ribeiro *et al.* 1999), identification keys (Alston *et al.* 1981, Kramer 1957, Mori *et al.* 1997, Steyermark *et al.* 1995, Tryon & Stolze 1989a,b; Tuomisto & Groot 1995, Windisch 1996) and comparison with material deposited in the Herbarium of the Instituto Nacional de Pesquisas da Amazonia (INPA). Voucher material was deposited in the INPA Herbarium.

Environmental variables

Elevation was measured by a professional topographic surveyor using a theodolite in all plots. Distance from stream margin was obtained with direct measurements with a measuring tape and compass for riparian plots and with a cartographic map for upland plots.

In each riparian plot, environmental variables were measured at five points (0, 25, 50, 75 and 100 m) along the main axis, and summarized as averages. Width of the riparian zone was measured with a clinometer, measuring tape and compass from the water margin to the edge of slope, the latter being defined as the point where elevation was 2 m above stream margin. Canopy openness was measured with a convex spherical crown densiometer (Model-A, Forestry Suppliers Inc.) at 1.0 m height. Water-table levels were measured once in each riparian plot at the end of the dry season in 50-mm-diameter dipwells augered to about 1 m below the ground surface, which was sufficient to reach the water table between 15 and 20 October 2004.

Data analysis

Plots were ordinated by their dissimilarity in species composition with non-metric multidimensional scaling (NMDS), to reduce dimensionality and allow the visualization of major patterns structuring the community. Ordinations were carried out with the whole set of 40 plots to detect differences in the herb community between the riparian zone and uplands, and separately

using only the 20 plots installed in the riparian zone to detect community variation within the riparian zone. Two ordinations were carried out with the plant data for each group of plots (40 or 20), one based on quantitative data and another using presence-absence data. Quantitative ordinations used the Bray–Curtis distance measure on site-standardised (percentage of each species in each site) data. Ordination of quantitative data was used to capture the patterns displayed by the most abundant species, as these will have the greatest quantitative contribution to the differences between sites. Presence-absence ordination was performed using the Sørensen index. This ordination tends to capture the patterns of the rarer species, because the more abundant species generally occur in most sites and therefore contribute little to the differences between sites.

As results of the analyses for presence-absence and quantitative data revealed the same patterns in all cases, we only present results for qualitative data for the overall community, and quantitative data for plots in the riparian zone. Scores of the NMDS ordinations, which represent the major patterns in herb community composition, were used as dependent variables in models of univariate or multivariate regression to test for the effects of environmental variables.

Ordinations were done in PCord version 4.25 and inferential analyses with the statistical package Systat version 8.

RESULTS

Herb community composition from the stream margins to the uplands

The ground-herb community sampled along the complete topographic gradient of Reserva Ducke was composed of 75 species or morphotypes, distributed in 22 families and 8332 individuals (Table 1). Four morphotypes could not be identified to the species level. Nineteen species were pteridophytes (8 families), 18 were Marantaceae, 10 were Cyperaceae, 6 Poaceae, 5 Araceae and 17 species of 10 other angiosperm families. Most individuals (6195) and species (61 of 75) were recorded within the riparian zone, of which 29 species did not occur elsewhere. Thirty-two species occurred along the complete topographic gradient and 14 species were recorded only in the uplands. Thirteen species occurred in only one plot (9 in the riparian zone and 4 in the uplands).

Ordination with NMDS captured 77.7% of the variation in the original distances between plots in one dimension, for qualitative data. There were strong curvilinear relationships between the one-dimensional NMDS ordination and distance from the stream (Figure 2a) and elevation (Figure 2b).

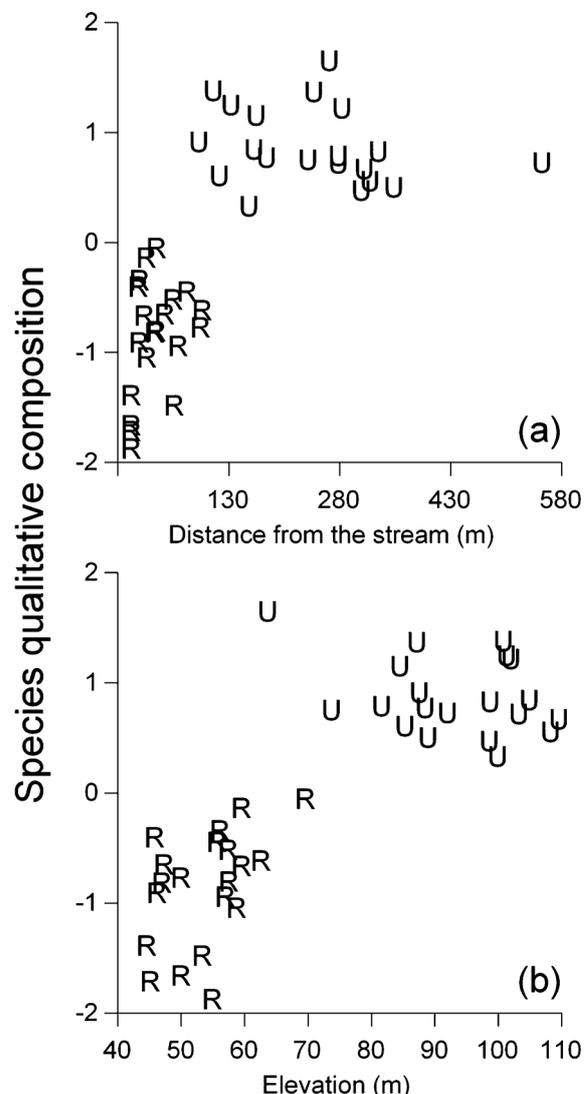


Figure 2. Herb species composition represented by one-dimensional NMDS ordination scores of qualitative data plotted against distance from stream (a) and elevation (b). U represents plots located in uplands and R represents plots located in the riparian zone.

Riparian and upland plots formed distinct groups in both figures. Herb-species qualitative composition, represented by the NMDS ordination scores, changed significantly ($r^2 = 0.75$, $P < 0.001$) along the gradients of distance from stream and elevation. Most variation occurred at distances from stream < 100 m (Figure 2a) and elevations < 70 m (Figure 2b), indicating that species composition in riparian plots was more heterogeneous than in upland plots.

Herb community variation within the riparian zone

The ground-herb community sampled within the riparian zone was composed of 61 species or morphotypes,

Table 1. Number of individuals and frequency of ground herbs in 20 riparian and 20 upland plots at Reserva Ducke, Manaus, Brazil. FR = frequency in riparian plots, TR = total number of individuals in riparian plots, FU = frequency in upland plots, NU = number of individuals in upland plots, TI = total number of individuals, summed over riparian and upland plots.

	FR	TR	FU	NU	TI
(Angiospermae)					
Araceae					
<i>Dieffenbachia elegans</i> Jonker	6	23	1	2	25
<i>Dracontium longipes</i> Engl.			2	4	4
<i>Philodendron barrosoanum</i> G.S. Bunting	2	9	1	3	12
<i>Spathiphyllum maguirei</i> G.S. Bunting	3	81			81
<i>Urospatha sagittifolia</i> Schott	6	108			108
Bromeliaceae					
<i>Bromelia tubulosa</i> L.B. Sm.	2	3	5	7	10
<i>Disteganthus</i> aff. <i>lateralis</i> (L.B. Sm.) Gouda			2	3	3
<i>Pepinia sprucei</i> (Baker) G.S. Varad. & Gilmartin	12	1245			1245
Costaceae					
<i>Costus arabicus</i> L.			1	1	1
<i>Costus sprucei</i> Maas	1	8			8
Cyclanthaceae					
<i>Cyclanthus bipartitus</i> Poit.	5	104			104
Cyperaceae					
<i>Calyptrocarya bicolor</i> Nees	1	15			15
<i>Calyptrocarya glomerulata</i> Urb.	10	220	3	7	227
<i>Calyptrocarya poeppigiana</i> Kunth	3	15	2	12	27
<i>Diplasia karataefolia</i> Rich.			1	1	1
<i>Hypolytrum schraderianum</i> Nees	7	31			31
<i>Mapania macrophylla</i> H. Pfeiff.	1	4			4
<i>Mapania pycnostachya</i> (Benth.) T. Koyama	6	739			739
<i>Mapania sylvatica</i> Aubl.			2	5	5
<i>Pleurostachys sparsiflora</i> Kunth	2	11	16	103	114
<i>Scleria secans</i> Urb.			1	20	20
Heliconiaceae					
<i>Heliconia acuminata</i> A. Rich.	20	361	19	367	728
<i>Heliconia psittacorum</i> L. f.			2	2	2
Marantaceae					
<i>Calathea altissima</i> Horan.	4	15	19	52	67
<i>Calathea cannooides</i> (Nicolson, Steyerem. & Sivad.) H. Kenn.	3	23	8	120	143
<i>Calathea exscapa</i> Körn.	1	3			3
<i>Calathea mansonis</i> Körn.	4	16	2	16	32
<i>Calathea mansonis</i> var. 2	1	1			1
<i>Calathea panamensis</i> Rowlee ex Standl.	7	26	2	4	30
<i>Calathea</i> sp. 1	13	119	1	6	125
<i>Ischnosiphon arouma</i> Körn.	13	75	9	19	94
<i>Ischnosiphon gracilis</i> Körn.	2	4	6	12	16
<i>Ischnosiphon hirsutus</i> Petersen.	1	42	1	12	54
<i>Ischnosiphon killipii</i> J.F. Macbr.	3	10	2	8	18
<i>Ischnosiphon martianus</i> Eichler	12	38	18	89	127
<i>Ischnosiphon puberulus</i> Loes.	14	39	5	6	45
<i>Monotagma densiflorum</i> (Koern.) K. Schum.	3	10	2	4	14
<i>Monotagma</i> sp. 5			2	5	5
<i>Monotagma spicatum</i> J.F. Macbr.	17	377	6	41	418
<i>Monotagma tomentosum</i> K. Schum. ex Loes.	6	57			57
<i>Monotagma vaginatum</i> Hagberg	5	27			27
Orchidaceae					
<i>Palmorchis sobralioides</i> Barb. Rodr.			2	2	2
Poaceae					
<i>Ichmanthus panicoides</i> P. Beauv.	1	2	8	10	12
<i>Pariana</i> aff. <i>simulans</i> Tutin	2	3	1	1	4
<i>Pariana campestris</i> Aubl.	1	1	16	184	185
<i>Pariana gracilis</i> Döll			4	6	6
<i>Pariana radicyflora</i> Sagot ex Döll	20	414			414
<i>Pariana</i> sp. 1	2	4			4

Table 1. (Contnd.)

	FR	TR	FU	NU	TI
Rapateaceae					
<i>Rapatea paludosa</i> Aubl.	17	547			547
<i>Rapatea ulei</i> Pilg.	2	2			2
<i>Saxofridericia subcordata</i> Körn.	14	79	2	4	83
<i>Spathanthus unilateralis</i> Desv.	187	470			470
Rubiaceae					
<i>Geophila cordifolia</i> Miq.			1	3	3
Strelitziaceae					
<i>Phenakospermum guianensis</i> Aubl.	10	48	3	8	56
Thurniaceae					
<i>Thurnia sphaerocephala</i> Hook. f.	4	133			133
Zingiberaceae					
<i>Renealmia floribunda</i> K. Schum.	1	2	3	5	7
(Pteridophyta)					
Cyatheaceae					
<i>Sphaopteris hirsuta</i> (Desv.) R.M. Tryon	8	41			41
Dennstaedtiaceae					
<i>Lindsaea divaricata</i> Klotzsch	3	13			13
<i>Lindsaea guianensis</i> (Aubl.) Dryand	5	17	1	1	18
<i>Lindsaea lancea</i> (L.) Bedd. var. <i>falcata</i> (Dryand.) Rosenst.	10	127			127
<i>Lindsaea lancea</i> (L.) Bedd. var. <i>lancea</i> Christ	3	5	18	80	85
<i>Saccoloma inaequale</i> (Kunze) Mett.	1	1			1
Hymenophyllaceae					
<i>Trichomanes cellulosum</i> Klotzsch	2	4			4
<i>Trichomanes elegans</i> Poir.	4	26			26
<i>Trichomanes pinnatum</i> Hedw.	12	303	15	258	561
<i>Trichomanes</i> sp. 1			17	247	247
Marattiaceae					
<i>Danaea elliptica</i> Sm.	1	7			7
<i>Danaea trifoliata</i> Kunze	2	5	2	2	7
Metaxyaceae					
<i>Metaxyia rostrata</i> (Kunth) C. Presl	8	47	1	1	48
Pteridaceae					
<i>Adiantum amazonicum</i> A.R. Sm.	1	1			1
<i>Adiantum cajennense</i> Willd. ex Klotzsch			10	22	22
<i>Adiantum terminatum</i> Kunze ex Miq.	1	1			1
<i>Adiantum tomentosum</i> Klotzsch	6	8			8
Schizaeaceae					
<i>Schizaea elegans</i> (Vahl) Sm.			3	4	4
Tectariaceae					
<i>Triplophyllum dicksonioides</i> (Fée) Holttum	1	26	18	367	393
Total		6196		2136	8332

distributed in 20 families and 6195 individuals. Most individuals (3659) occurred in the four plots installed immediately adjacent to the stream (Table 2).

Ordination of quantitative data with NMDS captured 70.7% of the variation in the original distances between plots in one dimension. Community quantitative composition, represented by the ordination in one dimension, changed significantly with distance from the stream ($r^2 = 0.77$, $P < 0.001$). The best fit, however, was a negative logarithmic function of distance, which explained 82.3% of the variation in composition ($P < 0.001$; Composition = $-1.71 - 0.506 \times \log(\text{distance from the margin})$).

Species quantitative composition turned over continuously with the distance from the margin, but one group of species was clearly restricted to the margins of streams (Table 2). The gradual change in species composition was evident when species composition ordinated by quantitative dissimilarity was plotted against the relative distances from the margin (Figure 3a), but not for absolute distances (Figure 3b).

We hypothesized that canopy openness and water-table depth should be the main environmental factors varying with distance from the stream that affect community variation. Also, distance alone is possibly an indicator of the probability of flooding. Therefore, we tested a model

Table 2. Number of individuals of ground herbs in 20 riparian plots in Reserva Ducke, Manaus, Brazil. Plots are grouped in five classes, defined as increasing proportions of distance between the stream and the upper limit of the riparian zone.

Species	Relative distance from stream (%)				
	0	25	50	75	100
<i>Pleurostachys sparsiflora</i>					11
<i>Danaea elliptica</i>					7
<i>Adiantum amazonicum</i>					1
<i>Triplophyllum dicksonioides</i>					26
<i>Calathea excapa</i>					3
<i>Adiantum terminatum</i>					1
<i>Calathea mansonis</i> var. 2					1
<i>Pariana</i> sp. 1					4
<i>Calyptrocarya poeppigiana</i>			1	1	13
<i>Rapatea ulei</i>				1	1
<i>Calathea cannooides</i>			3	7	13
<i>Adiantum tomentosum</i>	4				4
<i>Danaea trifoliata</i>		2			3
<i>Renalmia floribunda</i>				2	
<i>Spathanthus unilateralis</i>	1	9	146	127	187
<i>Calathea panamensis</i>	0	0	7	16	3
<i>Ischnosiphon martianus</i>	3	5	8	10	12
<i>Saxofridericia subcordata</i>	1	5	14	44	15
<i>Monotagma spicatum</i>	102	9	82	95	89
<i>Sphaeropteris hirsuta</i>	7	13	1	5	15
<i>Ischnosiphon arouma</i>	3	12	11	20	29
<i>Heliconia acuminata</i>	59	64	63	78	97
<i>Ischnosiphon puberulus</i>	2	10	6	8	13
<i>Calathea altissima</i>		5	4		6
<i>Calathea</i> sp. 1	10	27	16	40	26
<i>Bromelia tubulosa</i>			2		1
<i>Monotagma densiflorum</i>		4			6
<i>Calathea mansonis</i> var. 1	10		2		4
<i>Hypolytrum schraderianum</i>	9	4	6	3	9
<i>Pariana radicyflora</i>	194	63	49	60	48
<i>Metaxya rostrata</i>	29	5	2	4	7
<i>Philodendron barrooanum</i>			9		
<i>Mapania macrophylla</i>			4		
<i>Monotagma tomentosum</i>	4	27	12	4	10
<i>Lindsaea guianensis</i>	12		2	3	
<i>Rapatea paludosa</i>	249	66	90	107	35
<i>Lindsaea lancea</i> var. <i>lancea</i>	3	1			1
<i>Dieffenbachia elegans</i>	11	7	2		3
<i>Pariana</i> aff. <i>simulans</i>		1	2		
<i>Trichomanes cellulolum</i>	3		1		
<i>Phenakospermum guianensis</i>	7	26	7	3	5
<i>Trichomanes pinnatum</i>	244	24	5	10	20
<i>Lindsaea lancea</i> var. <i>falcata</i>	118	3	2		4
<i>Monotagma vaginatum</i>	6	15	6		
<i>Ischnosiphon killipii</i>	6	3			1
<i>Costus sprucei</i>		8			
<i>Pariana campestris</i>		1			
<i>Calyptrocarya bicolor</i>		15			
<i>Ichnanthus panicoides</i>		2			
<i>Trichomanes elegans</i>	24	1			1
<i>Pepinia sprucei</i>	1113	77	8	47	
<i>Calyptrocarya glomerulata</i>	210	0	4	0	6
<i>Lindsaea divaricata</i>	11	2			
<i>Urospatha sagittifolia</i>	105	1		2	
<i>Cyclanthus bipartitus</i>	103			1	
<i>Mapania pycnostachya</i>	735	1		3	
<i>Thurnia sphaerocephala</i>	133				
<i>Spathiphyllum maguirei</i>	81				
<i>Ischnosiphon hirsutus</i>	42				
<i>Ischnosiphon gracilis</i>	4				
<i>Saccoloma inaequale</i>	1				
Total	3659	518	577	701	740

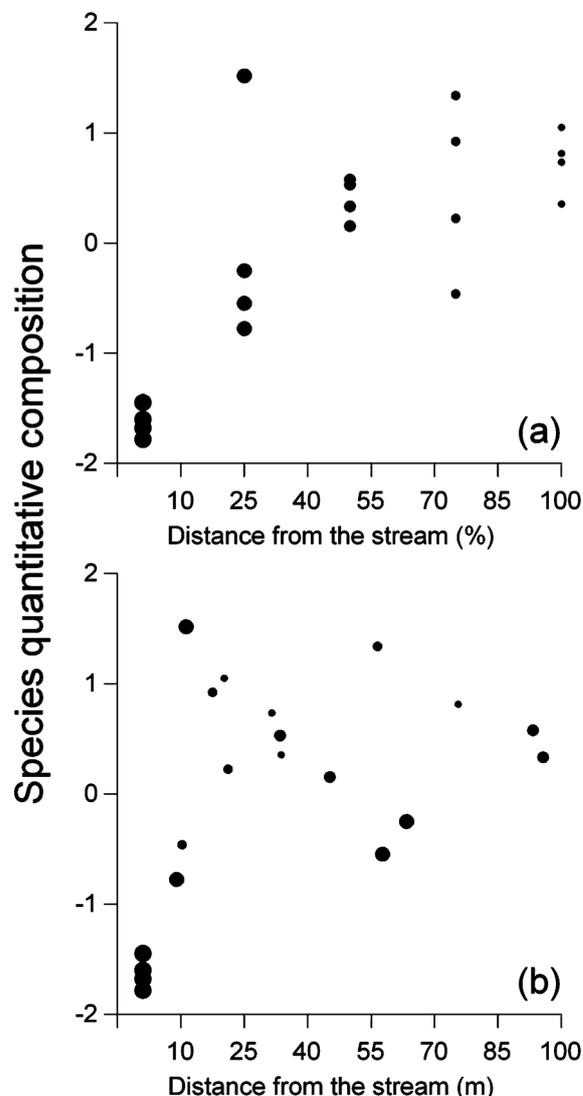


Figure 3. Scores of a one-dimensional NMDS solution of riparian plots based on Bray–Curtis distances plotted against distance from the stream margin, expressed in classes of proportion of riparian-zone width (a) or absolute distance values (b). Relative distance from the margin is represented by the size of dots: the larger the size, the closer to the margin.

to explain community composition that included canopy openness, water-table depth and the log-transformed distances from stream margin. The effect of water-table depth was significant (water-table depth: $t = -3.04$, $P = 0.008$), as was the effect of the log-transformed distances from stream margin (log(distance from margin): $t = -8.98$, $P < 0.001$). Canopy openness did not contribute significantly to the model ($t = 0.58$, $P = 0.57$). This model explained about 90% of the variation in community quantitative composition captured by the ordination ($R^2 = 0.897$, $F_{3,15} = 43.4$, $P < 0.001$).

DISCUSSION

Species composition of the herb community differed along the topographic gradient in Reserva Ducke. Most species and individuals occurred within the riparian zone, and species did not occupy the riparian zone homogeneously, but changed continuously in response to environmental gradients associated with distance from the stream.

Gradients of change in plant species composition associated with soil or topography have frequently been documented in the tropics, including the herbaceous vegetation at Reserva Ducke (Costa *et al.* 2005). However, in general, the environment is modelled as broad classes (Poulsen & Tuomisto 1996, Tuomisto & Ruokolainen 1994, Tuomisto *et al.* 2003). When the environment is forced into a few gross habitat categories, it may appear that there is less opportunity for specialization than when the environment is modelled as continuous multivariate dimensions. This study has shown that understorey herb composition of the riparian zone around streams is distinct from the upland areas for about 100 m from stream margins and to about 70 m asl in elevation, the exact distance depending on the size of the stream. However, the only assemblage that is almost completely distinct occurs as a narrow band, a few metres wide, along the streams. The rest of the riparian zone appears to represent an ecotone with continuous change, most of which occurs out to a distance of about half the width of the riparian zone as we defined it, based on topography.

Our data do not indicate that understorey herbs recognize a sharp limit of the riparian zone. We used an arbitrary limit of 2 m above the stream level, which in Reserva Ducke is sufficient to attain areas with a very low probability of flooding. Out to this limit, the species composition showed a continuous change in the direction of the composition of the upland areas as summarized by the multivariate ordination. Two metres above stream height is probably higher than many researchers would consider the limit of the riparian zone, but species composition, as represented by the NMDS axes, still had not converged on that of the upland plots.

The logarithmic decay in compositional similarity indicates that differentiation of species composition was stronger at the stream margins, suggesting stronger differences on the environment as well. In the field, we observed unpredictable flooding after heavy rain events that inundated stream margins, and submerged all herbs in plots adjacent to streams. Most plant species are not able to survive in inundated areas due to soil anaerobic conditions (Larcher 2003). The margins of large rivers are usually occupied by habitat specialists (Kalliola & Puhakka 1988, Salis *et al.* 1994). Restriction of species to the margins of small water courses of tropical forests is probably obvious to most observers, but has not previously been documented.

It is possible that adaptations to submergence imply competitive disadvantages in other environmental conditions. *Cyclanthus bipartitus*, *Mapania pycnostachya*, *Pepinia sprucei* and *Urospatha sagittifolia* were highly abundant at stream margins, but rare in other parts of the topographic gradient. *Spathiphyllum maguirei* and *Thurnia sphaerocephala* occurred exclusively on margins, suggesting that they cannot survive in other areas.

The edge of the slopes have greater chance of receiving propagules from herbaceous species established in higher portions of the topographic gradient due to gravity. Species observed at the edge of the slopes in the present study were found associated with steep slopes (*Calyptracarya poeppigiana* and *Danaea elliptica*) and with clayey soils (*Pleurostachys sparsiflora*, *Triplophyllum dicksonioides* and *Calathea cannoidea*) in the study by Costa *et al.* (2005) in Reserva Ducke.

To understand the riparian zonation with distance from the margin it is necessary to understand how different environmental factors vary along the distance gradient. It is likely that important environmental gradients correlated with distance from the stream margin are associated with hydrology. Further understanding of species distribution on riparian zones requires determination of how flooding patterns in response to rain events change subsurface and overland flows along the drainage profile in ways that might affect plants.

One study using data from seven continents and including taxa ranging from Antarctic soil invertebrates to tropical rain-forest lianas and primates (Sabo *et al.* 2005) found that riparian zones had lower alpha diversity than surrounding areas, but contributed to regional species richness because they harboured different species. In contrast, the riparian zones in our study had higher alpha diversity of herb species, as well as harbouring unique species. Also, heterogeneity within the riparian zone was as great as differences between the riparian zone and surrounding areas. We suggest that distributions of other plant and animal groups, specially those with small home ranges, such as ants, may also show strong variation within riparian zones. Riparian zones are critical to water-resource conservation, and are sensitive to changes in land use (Bren 1993). Although riparian zones are legally protected in Brazil, they are frequently degraded, indicating that the complex factors leading to zonation around streams need to be understood to effectively manage these areas.

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