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Spatial patterns in the understorey shrub genus *Psychotria* in central Amazonia: effects of distance and topography

V. F. Kinupp*[1] and William E. Magnusson†[2]

* Instituto Nacional de Pesquisas da Amazônia (INPA), Coordenação de Pesquisas em Botânica, CP 478, 69011-970 Manaus AM, Brazil
† INPA, Coordenação de Pesquisas em Ecologia, CP 478, 69011-970 Manaus AM, Brazil

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Abstract: We evaluated the effects of topography on the distribution of understorey herbs, shrubs and small trees of the pantropical genus *Psychotria* (Rubiaceae) in a 10 000-ha rain-forest reserve in central Amazonia. As plots were long and thin, and followed altitudinal isoclines, we were able to avoid the trade off between plot size and precision of measurement of topographical variables. The minimum distance between plots (1 km) was sufficient to avoid spatial autocorrelation in topographical variables. However, indices of plot similarity based on species composition were spatially autocorrelated to distances of at least 4 km. Although Multivariate Analysis of Covariance (MANCOVA) indicated significant effects of altitude, slope, and watershed on species composition within plots, topographical variables were generally poor surrogates for species distributions. Differences between eastern and western watersheds within the reserve were not due to distance effects, and most species occurred in both watersheds, indicating that differences in species assemblages between watersheds are determined by ecological factors. Habitat specialization and local density were not clearly associated with rarity. At scales of 1–10 km, both distance and habitat affect the distribution of understorey shrubs of the genus *Psychotria*, but much of the variation in species abundances remains unexplained.

Key Words: Amazonia, biological survey, landscape, reserve design, Rubiaceae, spatial autocorrelation, species diversity, topography, tropical forest, understorey

INTRODUCTION

There has been considerable debate as to the role of local habitat characteristics in determining the structure of plant communities in tropical forests. Hubbell & Foster (1986), based on their studies of a 50-ha plot in Panama chosen for its uniformity, concluded that much of the structure results from random processes, with little effect of local topography or edaphic conditions. Pitman *et al.* (2001) studied widely distributed plots in Ecuador and Peru, and concluded that the patterns seen could not be the result of largely random assemblages because the dominant species and families were consistent over very large geographic areas. They concluded that the dominant species in the rain forest are habitat generalists, and the apparently rare species tend to be habitat specialists, generating an inverse relationship between population density and the number of sites occupied. However, such a pattern does not exclude neutral models without strong effects of habitat or species-specific adaptations (Hubbell 2001). Tuomisto *et al.* (2003a) showed strong effects of both distance between plots, which presumably reflects stochastic or historic influences, and habitat categories, in a study of understorey plants in plots separated by distances of over 1000 km in western Amazonia. Although both distance and habitat characteristics affect beta diversity of neotropical forest trees (Condit *et al.* 2002), most of the variation in tree floristic similarities remains unexplained (Duivenvoorden *et al.* 2002).

The Pitman *et al.* (2001) model, which indicates that much of the floristic similarity between sites is a result of deterministic processes, and the results of Brosofske *et al.* (2001), Charles-Dominique *et al.* (1998), Clark *et al.* (1999), Condit *et al.* (2002), Harms *et al.* (2001), Itoh *et al.* (2003), Poulsen & Tuomisto (1996), Ruokolainen *et al.* (1997), Tuomisto & Ruokolainen (1994) and Vormisto *et al.* (2000) indicate that topographic and

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[1] Present address: Rua Ângelo Crivellaro, 680, Ed. Vitória Régia, apto. 304, Jardim do Salso, 91410-080 Porto Alegre RS, Brazil. Email: vkinupp@hotmail.com
[2] Corresponding author. Email: bill@inpa.gov.br

edaphic variation over tens or hundreds of kilometres could be an important determinant of biodiversity. Harms *et al.* (2001), Itoh *et al.* (2003) and Palmiotto *et al.* (2004) showed that the distribution of plant species was significantly associated with topographic and soil categories in 50-ha tropical forest plots. Both the habitat-specificity and neutral models of community composition indicate that beta diversity may be much more important than alpha diversity in determining species richness in a site.

Due to their economic importance, and because many species can be identified by forestry workers, much tropical forest ecology has been done with trees. However, studying patterns of trees in tropical forests is difficult because of the high diversity, and most tree species have such low densities that it is usually not feasible to obtain enough data to establish space-use patterns for each species (Tuomisto & Ruokolainen 1994). For these reasons, understorey herbs and shrubs may be more useful for studying distribution patterns (Higgins & Ruokolainen 2004, Ruokolainen *et al.* 1997). The understorey in the tropical rain forest is species rich (Gentry & Emmons 1987, Nebel *et al.* 2001), and often an important source of food for frugivores (Levey 1988).

In this paper, we investigate the distribution of species of *Psychotria* L. (Rubiaceae), a species-rich genus of understorey plants, in the Reserva Florestal Adolpho Ducke (RFAD), near Manaus, central Amazonia, Brazil. *Psychotria* contributes importantly to tropical floristic diversity and comprises a significant proportion of the understorey vegetation in many wet tropical lowland forests around the world. For this reason, this genus has been considered a model for inferring patterns and general mechanisms of speciation in the tropics (Hamilton 1989). Although the genus includes vines, epiphytes and rheophytes (Mabberley 2000), all species in the RFAD are herbs, shrubs or small trees. *Psychotria* species provide nectar and fruits to animals (Almeida & Alves 2000) and many species have medicinal properties (Elisabetsky *et al.* 1995). *Psychotria* is the largest genus in the family Rubiaceae, one of the most species-rich genera of flowering plants, and this huge genus appears to be closely related to two other species-rich genera: *Palicourea* Aubl., and *Rudgea* Salisb. Two subgenera occur in South America: *Psychotria* subg. *Psychotria* (pantropical), and *Psychotria* subg. *Heteropsychotria* (neotropical), a sister group of *Palicourea* (Taylor 1996). Therefore, *Psychotria* is broadly paraphyletic (Nepokroeff *et al.* 1999). RFAD has species of both subgenera.

RFAD is square and covers approximately 100 km^2 on the outskirts of the city of Manaus, Amazonas State, central Amazonia. The surrounding areas are rapidly being converted for urban and rural uses (Ribeiro *et al.* 1999), and the reserve will soon be isolated from other areas of continuous forest. The vegetation of RFAD is diverse (Ribeiro *et al.* 1999) and relatively well studied. It is typical of Central Amazonia and lacks distinct 'anomalous' formations, such as bamboo, that might result from intensive recent human occupation. Topographic variation is low (∼ 30 m–∼ 120 m asl) compared to many regions of the world, but is representative of the range found in Central-Amazonian *terra firme* forests. Therefore, the Reserve is a reasonable model for patterns occurring in other relatively undisturbed Amazonian lowland *terra firme* forests.

The vegetation of the reserve has generally been considered to be relatively uniform, and the flora of the reserve was based on studies conducted almost entirely in the north-west corner of the reserve (Ribeiro *et al.* 1999). However, the RFAD lies on the divide between two major watersheds. Streams in the eastern half of the Reserve flow to tributaries of the Amazon River. Streams in the western half flow to tributaries of the Negro River. Each watershed has several drainage basins that are isolated from each other within the reserve. It is not known whether individual basins or watersheds have distinct plant communities.

Using *Psychotria* as a model, we asked the following questions: Is the understorey community structure in RFAD related to topographic features? Is the understorey community randomly distributed across the reserve, or are there distinct assemblages in different parts of the reserve? Do topographic generalists occupy more sites within the reserve than topographic specialists?

METHODS

Study area

The study was conducted in Reserva Florestal Adolpho Ducke (RFAD) of the Instituto Nacional de Pesquisas da Amazônia (INPA), 26 km north-west of Manaus in the Brazilian State of Amazonas (02°55′S, 59°59′W). The reserve covers 10 000 ha (10 km × 10 km) of terra firme non-flooded rain forest with closed canopy, and the understorey is characterized by abundant sessile palms, such as species of *Astrocaryum* and *Attalea* (Ribeiro *et al.* 1999). Canopy height of trees is generally 30–37 m with individuals that reach 40–45 m. The mean annual temperature is 26 °C and mean monthly rainfall is 362 mm (SD = 400 mm), with a short dry season between July and September (Marques Filho *et al.* 1981). The mean monthly rainfall is less than 100 mm for 3 months.

Data collection

Field work was conducted between February and September 2001. Each plot was 250 × 5 m. This is similar to the size (0.1 ha) of plots used by Gentry & Dodson (1987) for non-tree species, except that, in this study, the plots followed the topographic isoclines to reduce variation in soils, which are closely related to altitude in this region (Chauvel *et al.* 1987, Luizão *et al.* 2004). In two cases, plots were on small knolls and doubled around onto themselves, and in these cases we extended the plot to account for the area of overlap.

There is a high correlation (r = 0.94) between soil clay content and altitude in Reserva Ducke (F. Luizão, unpubl. data). Therefore, it was not possible to include topographic and edaphic variables in the same analyses. Topographic variables were used in analyses, but the relationships found may represent edaphic effects. No lower size limit was imposed on stem size, and all individual stems that could be identified as belonging to *Psychotria* species were counted. All stems could be confidently identified to species. Many plots were surveyed in periods that species were not flowering, so it is not possible to determine whether individuals were adults. However, adult-sized individuals were found in most plots in which each species was found, so the results are unlikely to be distorted by sink populations of juvenile individuals. The 61 plots were distributed across the reserve on an 8 × 8-km grid (Figure 1). All plots were at least 1 km from the edge of the reserve.

Measures of altitude and plot position were made by a professional surveyor. Slope across the plot orthogonal to the isocline was measured with a clinometer each 50 m along each plot, for a total of five points per plot. Slope data for each plot were averaged for analysis. The mean altitudes of plots reflected the variation in altitude across the reserve (mean = 74.9 m, range = 39.4–109.8, SD = 19.8). No direct measures of altitudinal variation between the lower and upper edges of the plots were made. However, the within-plot variation in altitude can be calculated from the mean slope and the known width of the plot (5 m). The maximum within-plot altitudinal range was 1.2 m (mean = 0.46 m, SD = 0.33 m, min. = 0.03 m). The mean variation in slope within plots (mean SD = 3.9°, median SD = 3.2°) was only about half the variation among plots (mean = 10.7°, max. = 27.8°, min. = 0.7°, SD = 7.7°).

As some of our questions, such as biomass per ha, required extrapolation of local densities to map densities, we used horizontal measurements to define plot boundaries. In our plots, mean slope across the plot ranged from 0–27.8°. This means that plots effectively sampled up to 13% more ground area than the map area indicates.

All individual stems were counted in each plot, each stem being considered as an individual for species with vegetative reproduction because it was not possible to verify underground connections without damaging the permanent plot. Fertile vouchers were collected, photographed and incorporated in the INPA Herbarium. Sterile vouchers were collected when it was not possible to collect fertile specimens for confirmation of identifications.

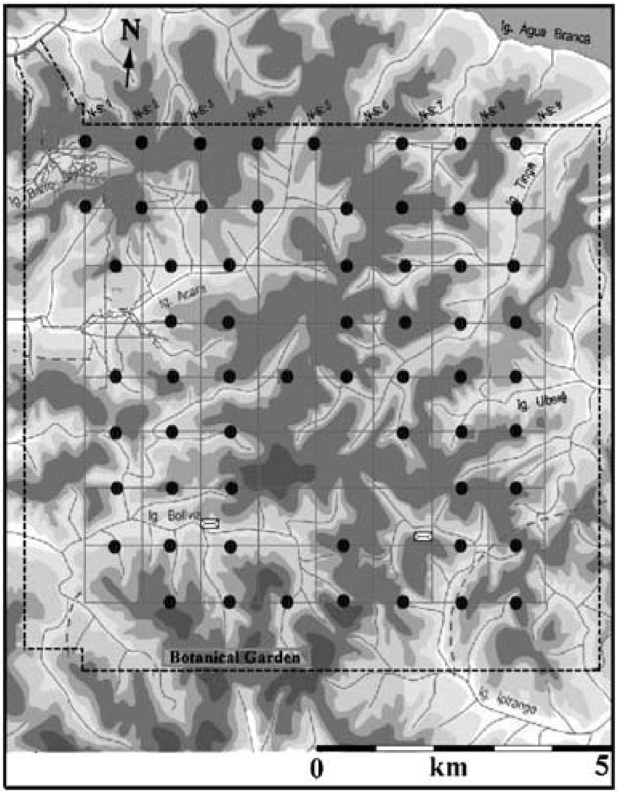

Figure 1. Map of Reserva Florestal Adolpho Ducke showing the trail system (fine straight lines) and the positions of plots (filled circles). Shading indicates gradients in altitude from the lowest areas (lightest shading, < 40 m asl) to the highest areas (darkest shading, > 100 m asl). Streams are shown as curved lines in valley bottoms. The limit of the reserve is shown by the dotted line.

Identifications were made from the Reserve field guide (Ribeiro *et al.* 1999); by comparison with material in the INPA and Museu Paraense Emílio Goeldi Herbaria; and using taxonomic keys available in Steyermark (1974), descriptions in the Flora Brasiliensis (Müller-Argoviensis 1881) and Steyermark (1972), and unpublished material produced by the Projeto Flora team. For taxonomic confirmation of doubtful material, digital images were sent to Charlotte M. Taylor (Missouri Botanical Garden) for confirmation.

Multivariate analyses

The dimensionality of compound variables, such as species composition, was reduced by multivariate ordination. These techniques were used to test for the existence of floristic gradients, and to assess the relative importance of topographical characteristics (altitude and slope) on species distributions. Plant community studies have used similar multivariate analyses to describe plant communities, to classify vegetation, and to relate environmental variables to dissimilarities in plant communities in Amazonia (Oliveira & Nelson 2001, Terborgh & Andresen 1998, Tuomisto *et al.* 2003a).

Most analyses used data from the two watersheds combined. However, separate analyses were also made for eastern and western watersheds to check the consistency of patterns. The western watershed has two stream basins, associated with the streams Igarapé Acará and Igarapé Bolívia. The eastern watershed includes the drainage basins of three streams: Igarapé Tinga, Igarapé Uberê and Igarapé Ipiranga. The stream basins were nested within watersheds, and preliminary analyses indicated significant differences between stream basins for presence–absence data. However, as subsequent analyses indicated spatial autocorrelation of community composition over distances of about 4 km, and stream basins were generally less than 4 km in their greatest dimension, we do not present statistical analyses for stream basin.

The effects of stream basin and watershed could represent proximity effects rather than indicating ecologically significant units. There were insufficient replicates to differentiate the effects of proximity from those of location for individual stream basins. However, a test of the significance of the watershed can be made by using an arbitrary division of the reserve into northern and southern sections with the same relative numbers of sites as the eastern and western watersheds. If the difference between watersheds was due solely to the effects of distance, the northern and southern sections would be expected to show the same degree of difference in species composition.

The distributions of species densities generally do not conform to the assumptions of multivariate inferential analyses such as Multivariate Analysis of Variance (MANOVA), Canonical Correlation Analysis (CCA) and Multivariate Analysis of Covariance (MANCOVA) (Legendre & Anderson 1999). Therefore, Principal Coordinates (PCoA) analyses were performed on the dependent variables to obtain linear, orthogonal variables (axes) describing the community composition that met the assumptions of the multivariate inferential analyses (Anderson & Willis 2003). The first four axes derived from the PCoA analyses were used in the MANCOVA analyses because these axes explained 82% of the variance in the original variables for quantitative data and 99% of the variance for presence-absence data.

Ordinations were performed in the PATN statistical package (Belbin 1992). The Bray–Curtis distance measure was used to describe dissimilarity between sites after the data had been range standardized (number of individuals of each species converted to relative frequency within plots). This combination of transformation and distance measure has been shown to be one of the best for describing ecological gradients based on species occurrence data (Faith *et al.* 1987, Kenkel & Orlóci 1986, Minchin 1987). When used on presence-absence data, the Bray–Curtis index is known as the Sørensen distance measure (Legendre & Legendre 1998).

Ordination by Multidimensional Scaling (MDS) may be a better method to describe ecological gradients (Faith *et al.* 1987, Minchin 1987). Lima *et al.* (2000), Magnusson *et al.* (1999), and Costa & Magnusson (2002) have used multivariate regression on axes derived from hybrid multidimensional scaling analyses. However, Anderson & Willis (2003) claimed that such analyses are valid only for axes derived from eigen analyses, such as Principal Components Analysis (PCA) or Principal Coordinates Analysis (PCoA), because axes derived from multidimensional scaling analyses are not perfectly orthogonal in terms of the original variables. As we are not aware of any studies using simulations to examine the implications of non-orthogonality of the dependent variables evaluated in multivariate regression analyses, we used PCoA axes in the inferential analyses we present. However, the PCoA analyses apparently captured the same patterns captured by MDS analyses because MANCOVA with MDS axes (not presented) gave similar results.

Ordinations were undertaken for quantitative (range standardized within sites) and for qualitative (presence–absence) data. The quantitative data reveal patterns based on the most common species, which tend to have the greatest quantitative differences among sites. The presence–absence data tend to give more weight to uncommon species as common species tend to occur in most sites, and therefore contribute little to qualitative differences among sites (Clark & Warwick 2001).

Locally weighted (LOWESS) regression (Cleveland 1979) was used to generate empirical curves for the relationship between floristic similarity and distance between plots. The intersection of curves was estimated by piecewise regression (Toms & Lesperance 2003). LOWESS, piecewise, simple and multiple regressions, MANOVA and MANCOVA were performed in the SYSTAT 8.0 statistical program. The Pillai Trace statistic was used to evaluate the significance of multivariate tests. This statistic has been shown to be less sensitive to deviations from assumptions than other multivariate statistics (Johnson & Field 1993, Olson 1976).

Mantel tests of the significance of relationships between floristic similarity and distance (spatial autocorrelation) between plots were undertaken in the PATN program. Other resampling tests were conducted in the RT program (Manly 1997).

Habitat specialization

The range of habitat variation (altitudes and slopes) occupied by a species is expected to be related to the number of sites occupied, independent of habitat specificity, because more occurrences would result in a greater number of habitats occupied if the occurrences were random with respect to habitat (Clark *et al.* 1999). Therefore we developed an index of habitat specificity that is independent of the number of sites occupied. To determine the variation in habitat variables expected to be found in occupied sites when the null hypothesis (no habitat specificity) was true, we used a resampling procedure. For the number of sites occupied by a species (N), we randomly sampled the survey sites and determined the standard deviations of altitude and slope in the sample. This process was repeated 99 times for each species that occurred in more than two plots.

The proportion of standard deviations in the 99 random samples that were equal to, or less than, the observed standard deviation can be used to test the null hypothesis of no specialization for each species. However, such analyses would require a correction for the number of tests undertaken, and individual tests would be weak. Rather than analyse the results for each species separately, we tested whether the tendency to reject the null hypothesis of the species being no more specialized than expected by chance, based on the probabilities from the randomization tests, was related to the distribution or abundance of the species. The probabilities were arcsine square-root transformed before use in the regression analyses.

RESULTS

Species richness of *Psychotria* in the reserve

A total of 9722 stems of 22 species were recorded in the sample plots. Four species were new records for RFAD: *Psychotria variegata*, *P. turbinella*, *P. stipulosa* and a possibly undescribed species, *Psychotria* sp. 1. Two species not previously recorded from the reserve (*P. microbotrys* and *P. egensis*) were found beside trails between plots (Table 1).

Similar total densities ($t_{59} = 0.799$, $P = 0.427$) and total numbers of species were recorded in the plots in the eastern and western basins (19 and 20 respectively), even though the mean number of species per plot was significantly higher ($t_{59} = 3.7$, $P = 0.001$) in the east (mean = 7.6, SD = 1.6) than in the west (mean = 5.9, SD = 2.1).

Table 1. Numbers of stems, and number of plots occupied by species of *Psychotria* in 61 plots of 250 × 5 m. * New records for the reserve; ** new record and undescribed species; *** species found only during travel between plots. PH, prostrate herb or sub-shrub; EH, erect herb or sub-shrub; S, Shrub; ST, small tree.

Species	Life form	Stems	Plots
P. astrellantha Wernham	S - ST	639	50
P. bahiensis DC. var. *cornigera* (Benth.) Steyerm.	EH - S	2669	18
P. brachybotrya Müll.Arg.	S	280	43
P. cincta Standl.	S	398	34
P. deinocalyx Sandwith	S	45	43
P. egensis Müll.Arg.***	S	0	0
P. iodotricha Müll.Arg.	PH	2014	40
P. manausensis Steyerm.	S	323	27
P. mapourioides DC.	ST	6	4
P. medusula Müll.Arg.	EH	207	16
P. microbotrys Ruiz ex Standl.***	S	0	0
P. pacimonica Müll.Arg.	S - ST	31	11
P. platypoda DC.	S	5	3
P. podocephala (Müll.Arg.) Standl.	ST	309	29
P. poeppigiana Müll.Arg. subsp. *barcellana* (Müll.Arg.) Steyerm.	S	2	1
P. polycephala Benth.	EH - S	277	5
P. prancei Steyerm.	S - ST	107	36
P. rhombibractea C. M.Taylor & M. T.Campos	S - ST	460	50
P. sciaphila S.Moore	PH	1795	23
P. sphaerocephala Müll.Arg.	EH	35	6
P. stipulosa Müll.Arg.*	S – ST	1	1
P. turbinella Müll.Arg.*	S	1	1
P. variegata Steyerm.*	PH	67	1
P. sp. 1**	S - ST	51	2

Effect of habitat on community structure

Due to the spacing on the grid, no plot was closer than 1000 m from any other, and there was no relationship between dissimilarities in altitude or slope, and distance between plots (Mantel test: $P = 0.49$ and $P = 0.145$, respectively), indicating no spatial autocorrelation at this scale for these variables. However, there was a significant relationship between differences in community composition and distance for both quantitative data ($P < 0.001$) and presence–absence data ($P < 0.001$). Association-matrix correlations in mantel tests are always much lower than correlations between the original variables (Tuomisto *et al.* 2003b), making visual interpretation of the graphs difficult. However, in both cases, LOWESS regression, which represents the general trend in the data, indicated a linear increase in dissimilarity in *Psychotria* species composition out to a distance of 4–5 km, and little or no effect of distance beyond those points (Figure 2). Piecewise regression, which represents the approximately linear segments of the LOWESS regression as straight lines, estimated the distance at which the lines intersected as 4.3 km for the quantitative data and 4.2 km for the presence–absence data.

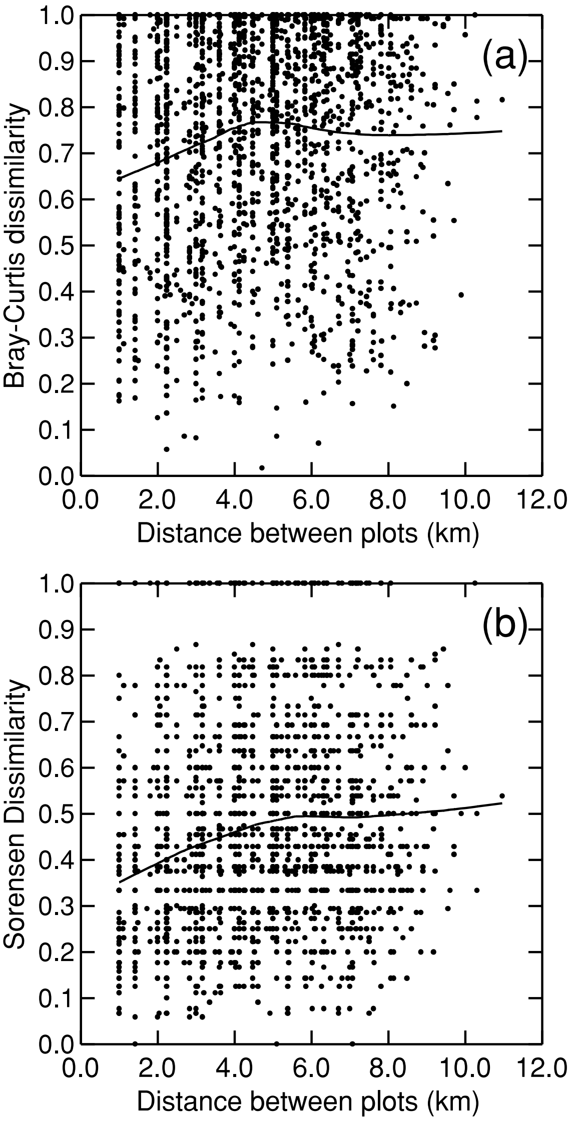

Figure 2. Relationship between dissimilarities in species composition and geographical distance between plots for (a) quantitative data (Bray–Curtis index) and (b) qualitative data (Sørensen index). The lines represent locally weighted (LOWESS) least–squares regressions (tension = 0.5).

The four PCoA axes captured much of the variance in the original variables for quantitative data (Cumulative proportion of total variance (C_{PV}) = 0.82) and presence–absence data ($C_{PV} = 0.99$). For quantitative data on species composition, MANCOVA indicated that these axes were significantly related to $\log_e$ altitude (*Pillai trace* = 0.67, $F_{4,52} = 26.4$, $P < 0.001$), slope (*Pillai trace* = 0.48, $F_{4,52} = 12.0$, $P < 0.001$), and watershed (*Pillai trace* = 0.24, $F_{4,52} = 4.2$, $P = 0.005$), that there was a significant interaction between watershed and $\log_e$ altitude (*Pillai trace* = 0.22, $F_{4,52} = 3.8$, $P = 0.009$), and that there was a low probability for the null hypothesis of no interaction between watershed and slope (*Pillai trace* = 0.16, $F_{4,52} = 2.5$, $P = 0.055$).

For species presence–absence data, MANCOVA indicated that the PCoA axes were significantly related to $\log_e$ altitude (*Pillai trace* = 0.57, $F_{4,52} = 17.2$, $P < 0.001$), slope (*Pillai trace* = 0.21, $F_{4,52} = 3.6$, $P = 0.012$), and watershed (*Pillai trace* = 0.39, $F_{4,52} = 8.4$, $P < 0.001$), that there was a significant interaction between watershed and $\log_e$ altitude (*Pillai trace* = 0.36, $F_{4,52} = 7.4$, $P < 0.001$), and that there was a low probability that the null hypothesis of no interaction between watershed and slope was correct (*Pillai trace* = 0.15, $F_{4,52} = 2.2$, $P = 0.081$).

The simple effects of altitude and slope together explained only about 20% of the variance in the PCoA axes for quantitative data (about 18% of the variance in the proportions of species per plot in the original data matrix standardized by site totals) and about 20% of the variance in the PCoA axes for presence–absence data (about 19.6% of the variance in the original presence–absence matrix).

Community differences between watersheds

When the north–south division was substituted for watershed in the analysis of the presence–absence data, the effects of $\log_e$ altitude and slope remained significant ($P = 0.001$ and $P = 0.026$, respectively). There was no significant simple effect of the north–south division ($P = 0.770$), its interaction with altitude ($P = 0.767$), or its interaction with slope ($P = 0.832$). When the north–south division was substituted for watershed in the analysis of the quantitative data, the effects of altitude and slope remained significant ($P < 0.001$ and $P < 0.001$, respectively), and there was no significant simple effect of the north–south division ($P = 0.672$) or its interaction with altitude ($P = 0.660$). However, there was a significant interaction between the north–south division and slope ($P = 0.023$). Despite the single possible interaction for the quantitative data, which could be a type II error due to the lack of correction for the number of comparisons, the general lack of effect of the north–south division indicates that the very strong effects of watershed were due to ecological differences, and did not result only from distance effects.

Visualization of watershed by topography interactions

The complex effects of the geographic variables (watershed, stream basins and distance between plots) increase the dimensionality of the questions and require several dimensions in the dependent variable in order to avoid type II errors in the inferential tests. However, these local variables may not be of general interest and impede the recognition of general patterns related to the topographical variables. Therefore, in an attempt to permit visualization of the topographic patterns, we analysed the first PCoA axis separately for the quantitative and presence–absence data on species distributions. Although the analyses in one dimension will be weaker, they should reveal the major patterns.

The ordinations in one dimension captured less of the variance in the original data for presence–absence ($C_{PV} = 0.41$) and quantitative data ($C_{PV} = 0.33$), but all of the variables and their interactions remained significant for the presence–absence data ($P < 0.006$ in all cases), and $\log_e$ altitude, slope and the watershed by slope interaction remained significant ($P < 0.03$ in all cases) for the quantitative data. Probabilities of no effect of watershed ($P = 0.071$) and the watershed by altitude interaction ($P = 0.142$) for the quantitative data were much higher.

Regression of the species composition ordination in one dimension on altitude and slope was used to produce partial plots (plots of the relationship of the dependent variable with one predictor variable after relationships with other predictor variables have been removed statistically) for the presence–absence data. These plots illustrate the interaction between watershed and altitude (Figure 3a), and watershed and slope (Figure 3b). Plots at high altitudes and slopes were similar in the two basins and the general direction of the effects was similar in both watersheds. However, the effects of altitude and slope were less in the eastern watershed, resulting in greater differences between high- and low-altitude plots, and between plots with small and large slopes in that area.

Distributions of individual species

Plots of abundance of individual species against altitude revealed two groups of species (Figure 4). One, in the upper part of Figure 4, consists of generalist species, such as *Psychotria astrellantha* and *P. rhombibractea*, that occur across most of the gradient in altitude. A smaller number of species, such as *P. bahiensis* var. *cornigera* and *P. polycephala*, in the lower part of Figure 4, occurred only in a limited range within the altitudinal gradient. Those habitat specialists were mostly confined to the lower altitudes.

Plots of abundance of individual species against slope revealed little pattern (Figure 5). That the simple direct gradient analysis was unable to reveal habitat specificity contrasts with the multivariate, multifactorial analyses (Figure 3b) which indicated that slope is a significant niche dimension for species of *Psychotria* in the reserve.

Relationships between habitat specialization, distribution and abundance

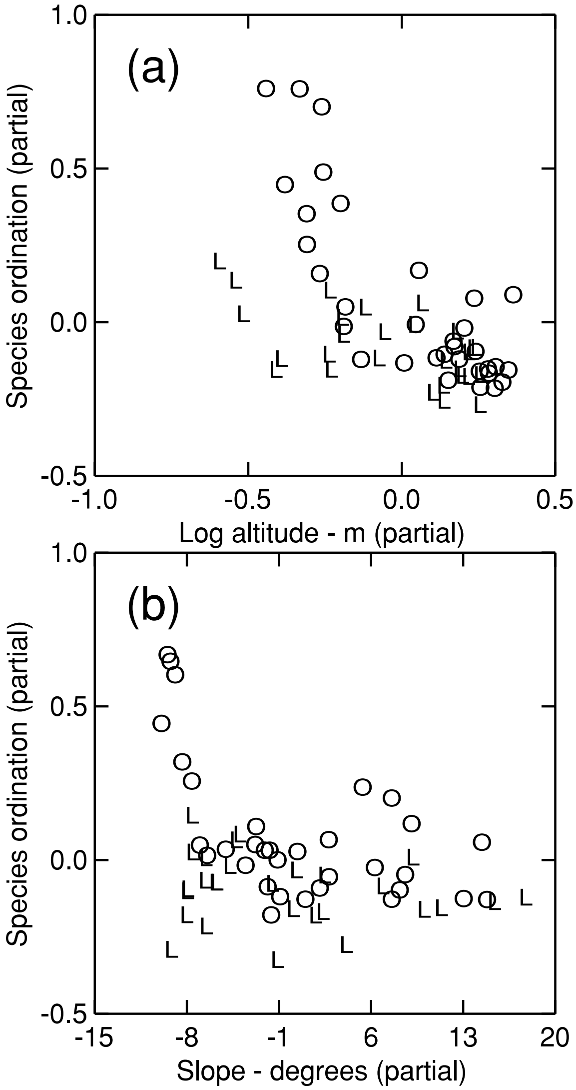

Figure 3. Partial regressions of the first PCoA axis for presence–absence data (Sørensen index) on (a) altitude, and (b) slope. Plots in the eastern watershed are represented by the letter L, and plots in the western watershed are represented by the letter O.

As expected, the ranges of habitat variables (R_H) in sites occupied by a species were significantly related to the number of sites occupied (N_S) for altitude ($R_H = -15.9 + 0.28N_S$, $r^2 = 0.46$, $P = 0.002$, $N = 18$) and slope ($R_H = 36.4 + 0.77N_S$, $r^2 = 0.56$, $P = 0.0004$, $N = 18$). The tendency to be considered a habitat specialist in altitude in the randomization tests was not related to the number of sites occupied ($r^2 = 0.007$, $P = 0.747$), or the mean density of stems per plot ($r^2 = 0.161$, $P = 0.111$). However, there was a tendency for species with higher mean densities in sites in which they occurred (D_E) to have lower probabilities (P_{HoA}) associated with the null hypothesis of no specialization in altitude ($P_{HoA} = 0.72 - 0.005D_E$, $N = 17$, $r^2 = 0.229$, $P = 0.052$). This indicates that species with higher local densities may tend to be more specialized in altitude.

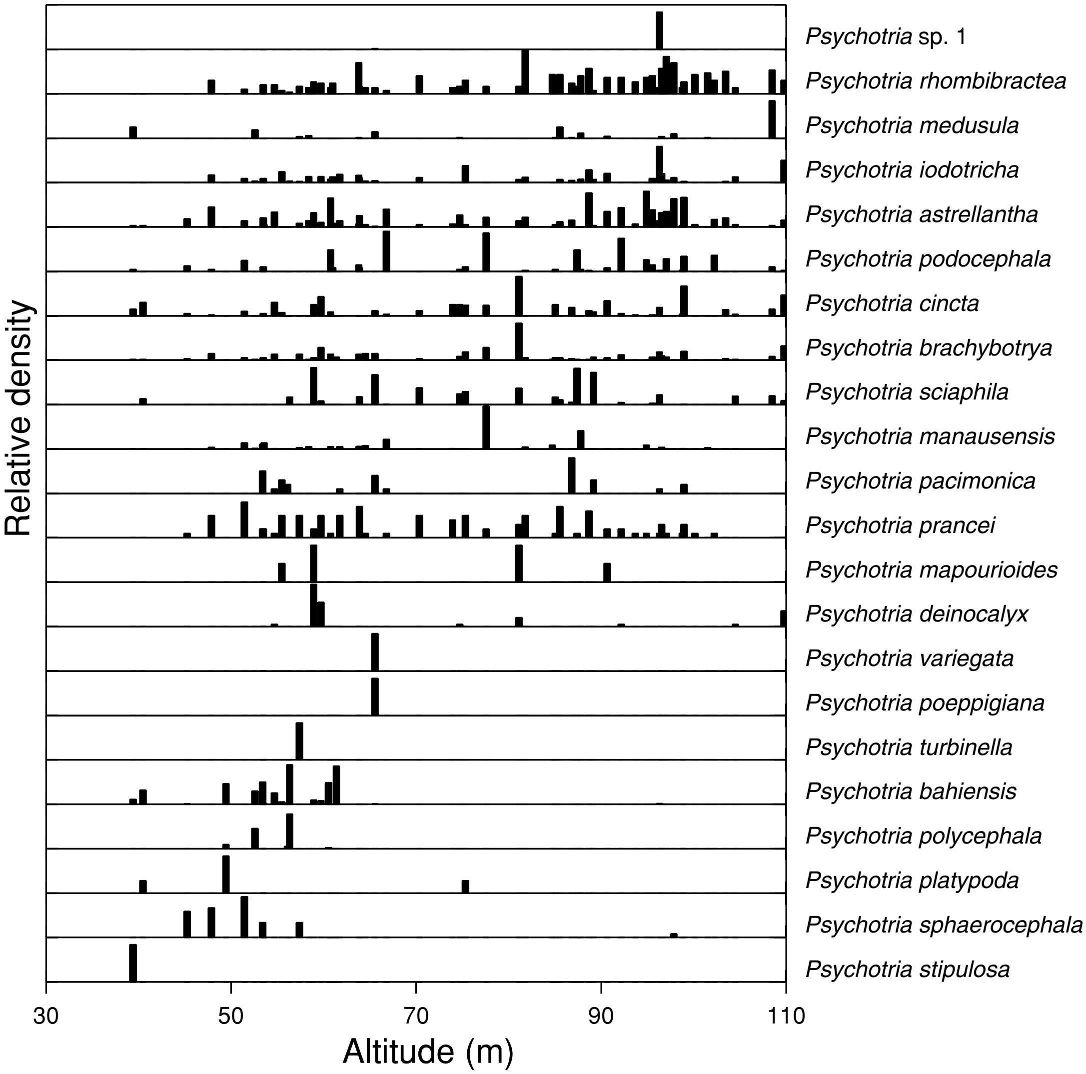

Figure 4. Species distributions in relation to altitude of plots. Maximum values for the Y axis were adjusted to give the same height for each graph. Bars give relative densities within species but are not comparable between species because the number of individuals varied among species (Table 1).

The tendency to be considered a habitat specialist in inclination in the randomization tests (P_{HoI}) was related to the number of sites (N_S) occupied ($P_{HoI} = 0.51 + 0.013N_S, r^2 = 0.352, N = 17, P = 0.012$), indicating that species specialized in relation to inclination tend to occupy fewer sites. However, there was no relationship between P_{HoI} and the mean density of stems per plot ($r^2 = 0.028$, $P = 0.521$) or between P_{HoI} and D_E ($r^2 = 0.162, P = 0.109$).

Species that occurred in only one plot did not have significantly lower densities in the plots in which they occurred than species that occurred in more than one plot (permutation test: $P = 0.399$).

DISCUSSION

Analyses of habitat associations of individual species may suffer from lack of power. There is greater chance of detecting habitat associations for common species (Clark *et al.* 1999), and many species occur at low densities. Therefore, multivariate analyses that take into account overall species associations may be more sensitive indicators of community habitat associations. Results of ordination analysis are sensitive to the choice of dissimilarity measure (Cushman & McGarical 2004). Although there was only moderate correspondence between the multivariate distances based on quantitative and presence–absence data for *Psychotria* ($r = 0.61$), most qualitative conclusions were similar for analyses based on ordinations of either type of data.

Terborgh & Andresen (1998) studied trees in seven neotropical countries, with an emphasis on the Amazonian region, and showed that the dissimilarity in tree composition between sites increases with distance for both flooded and unflooded forests, but very large areas are dominated by predictable associations (Terborgh *et al.* 2002). Tuomisto *et al.* (2003a) found spatial

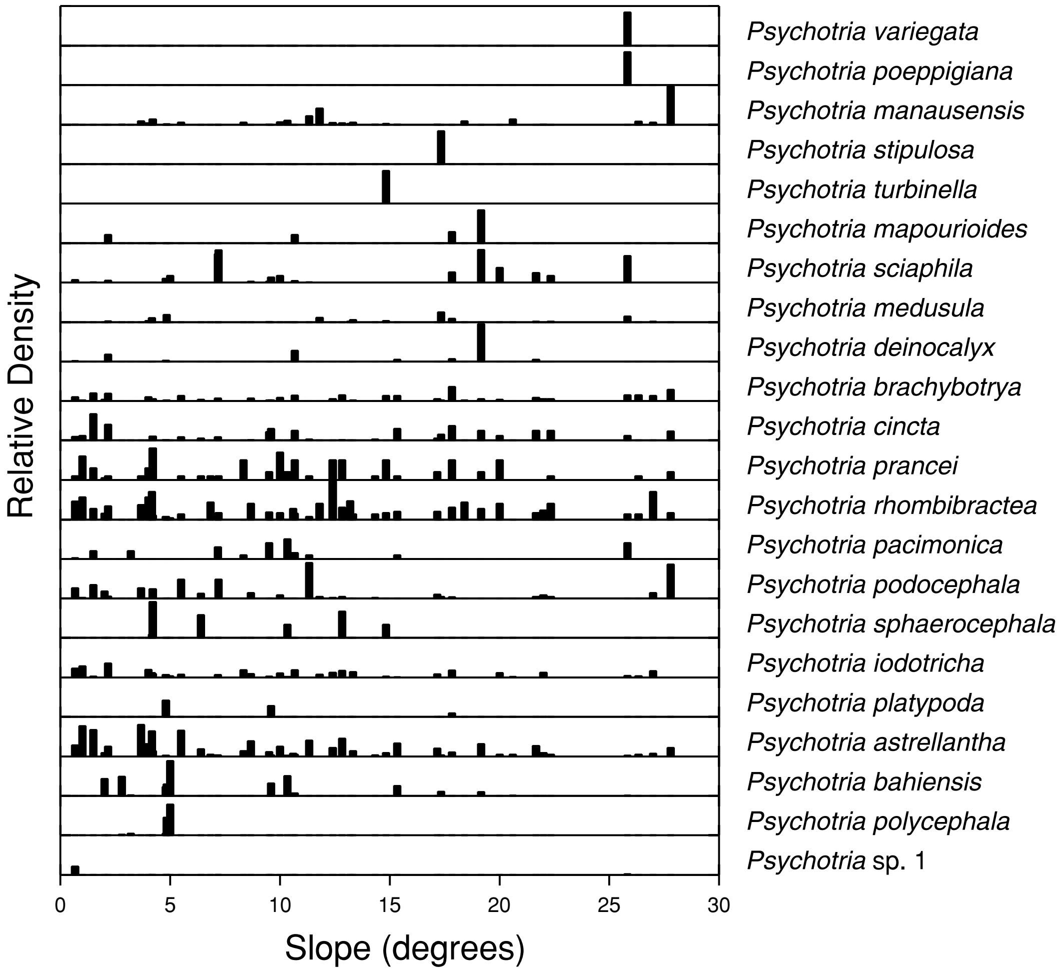

Figure 5. Species distributions in relation to mean slope within plots. Maximum values for the Y axis were adjusted to give the same height for each graph. Bars give relative densities within species but are not comparable between species because the number of individuals varied among species (Table 1).

autocorrelation over large distances in understorey Melastomataceae and ferns. This may be expected because of large-scale biogeographical/historical effects. Many studies have suggested that factors associated with soils or topography can partly explain patterns of distribution and abundance of plants in tropical forests (Clark *et al.* 1999, Itoh *et al.* 2003, Kahn 1987, Lieberman *et al.* 1985, Potts *et al.* 2002, Ruokolainen *et al.* 1997, Svenning 1999, Tuomisto & Ruokolainen 1994, Valencia *et al.* 2004, Vormisto *et al.* 2000, Webb & Peart 2000). However, most studies were conducted at small scales, and many did not take into account probable spatial autocorrelation of the variables. Habitat specificity could cause spatial autocorrelation over tens or hundreds of km, but neutral models with dispersal limitation also predict spatial autocorrelation in species distributions in the absence of spatial autocorrelation in values of habitat indices (Hubbell 2001).

Altitude and slope, were significantly associated with the distributions of *Psychotria* species within the RFAD. However there were significant interactions between watershed and the topographical variables. This is probably because 'topography' is a composite variable covarying with many other variables, such as soil type, canopy openness and soil water potential. Screening of a large number of species could help to identify causal factors, but is likely to require very intensive studies (Clark *et al.* 1999). Water availability in the dry season (Mulkey *et al.* 1989) probably restricts some species of *Psychotria* to low altitudes, and this would be a fruitful area for future research. The understorey of the RFAD is relatively poor in herb and shrub species compared with regions in Amazonia that have less-pronounced dry seasons (Gentry 1990, Gentry & Dodson 1987, Ribeiro *et al.* 1999).

Because of the small-scale variation in topography, habitat patches within the reserve are generally not distinct, except for low-lying areas around streams. Most species of *Psychotria* occurred over wide ranges of slopes and altitudes. The most distinct pattern in regard to topography was the presence of a group of species restricted to low altitudes. Lieberman *et al.* (1985), Clark *et al.* (1999) and Valencia *et al.* (2004) also found distinct swamp–upland gradients for forest trees. Many ecological factors are associated with altitude, including light availability in the understorey, soil texture, leaf-litter thickness, depth to water table, and frequency of inundation. However, none of the ecological characteristics peculiar to low-lying areas seemed to exclude the species that occurred at high altitudes from colonizing the areas around streams, because almost all of the species that commonly occurred at high altitudes also occurred at low altitudes, although sometimes at lower densities.

Further studies will be necessary to understand the ecological effects of topographic variables on individual species, but direct-gradient analyses of individual species against single independent variables may not be an appropriate method of evaluating the effect of habitat. There was no obvious pattern to the distribution of species along the slope gradient when this variable was investigated in isolation. However, the multivariate, multifactorial analyses, and the resampling tests, indicated a significant effect of slope on the distribution of *Psychotria* species.

Tuomisto *et al.* (2003b) used long thin plots to study the effect of topography on understorey plants. However, as the plots were oriented to capture the maximum topographic variation, direct analysis of topographic specialization was not possible, and Tuomisto *et al.* (2003b) analysed the relationship between vegetation composition and within-plot variation in topographic variables. In the RFAD, and most Amazonian sites, edaphic variables are closely related to altitude. By orienting the plots to follow the isoclines, we were able to use long thin plots to capture within-habitat variation in vegetation composition, while minimizing within-plot variation in topographic variables. This allowed us to relate vegetation to topographic variables using a relatively low number of plots (61) of 0.125 ha that covered only 0.08% of the reserve. In the RFAD, topographical variables explain about 20% of the local variation in the *Psychotria* community.

In this study, no plot was less than 1 km from any other, and there was no relationship between differences in altitude or slope, and distance between plots. This gives us confidence in the inferential analyses of topographical variables (Legendre *et al.* 2002). However, dissimilarities in species composition increased out to a distance of ∼ 4 km, making interpretation of the ecological effects of the landscape variables, stream basin and watershed, difficult. Before the installation of the 144 km of trails covering 64 km^2 in 2000, the RFAD was considered to represent a fairly homogeneous patch of tropical forest. Satellite images and aerial photographs gave little indication of distinct assemblages, and the eastern and western watersheds are separated only by low (max. ∼ 120 m) ridges, so there are no barriers to plant dispersal. The eastern and western basins have similar species complements of *Psychotria*. Therefore, differences between the watersheds in *Psychotria* assemblages are likely to be ecological rather than biogeographic or historic. However, the eastern watershed drains to tributaries of the Rio Amazonas, the major white-water river draining the Andean highlands. The western watershed drains to the rio Negro, the major black-water river draining the Guianan highlands. Species of frogs (A. P. Lima, pers. comm), shrimps (F. Mendonça, pers. comm), and palms (J.-L. Guillaumet, pers. comm.) that have not been recorded from the western basin have been found in the eastern basin in the 3 y since the trails were installed, so species complements of other taxa may be more distinct than those of *Psychotria*.

Pitman *et al.* (2001) suggested that rare species tend to be habitat specialists and that generalist species tend to be widespread. Duque *et al.* (2002) reported that species that occurred only in one plot had lower local densities than species that occurred in more than one plot, independent of whether the species were considered habitat specialists or not. However, neither of these situations appears to apply to *Psychotria* species in the RFAD. Species that occurred only in one plot did not have lower local densities than species that occurred in many plots. Species more specialized in slope occurred in fewer plots than species less specialized in slope, but species specialized in altitude tended to occur in more plots than species less specialized in altitude.

Alpha (within plot) diversity was not a good predictor of differences in diversity in different parts of the reserve. Similar total numbers of species were recorded in the plots in the eastern and western watersheds (19 and 20 respectively), even though the mean number of species per plot was 29% higher in the eastern drainage than in the western drainage. The differences in species associations between the eastern and western watersheds indicate that they support different ecological processes. Although we have shown that distance and factors related to topography affect beta diversity of *Psychotria*, most of the variation in floristic similarity remains unexplained. Long-term studies of individual survival (Ahumada *et al.* 2004) will be necessary to understand species distributions in the RFAD.

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