CHARACTER CONVERGENCE, DIVERSITY, AND DISTURBANCE IN TROPICAL RAIN FOREST IN GUYANA

Hans ter Steege[1,2] and David S. Hammond[2,3]

[1]*The Department of Plant Ecology and Evolutionary Biology, Utrecht University, P.O. Box 80084, 3508TB Utrecht, The Netherlands*
[2]*Tropenbos Guyana Programme, 12 E Garnett Street, Campbellville, Georgetown, Guyana*
[3]*Iwokrama International Centre for Rain Forest Conservation and Development, P.O. Box 10630, 67 Bel Air, Georgetown, Guyana*

Abstract. The level of tree diversity varies greatly between sites in Guyana and decreases along a gradient from south to north. We conducted a study to understand what controls this gradient of diversity using data from country-wide forest inventories. Analysis of tree diversity on the basis of soil and rainfall effects in an area of 15×10^6 ha showed that soil exerts a strong local effect on tree diversity, whereas rainfall, potential evapotranspiration, and length of the dry season do not.

Community averages of disturbance-sensitive attributes of trees, such as seed mass or wood density, were not correlated with variation in either rainfall or soil, but were strongly correlated with tree diversity. As such, the forests in central Guyana were characterized by generally a high average wood density, large seeds, and rodent or unassisted dispersal. These forests also displayed the highest single dominance, thus lowest diversity and low percentages of pioneers in the community. The more highly diverse forests in south Guyana showed much lower average community wood density and seed mass, and bird and primate dispersal were more common than in central Guyana.

Large-scale spatial variation in diversity and community averages of life history characteristics are here considered the product of local convergence of species with similar characteristics. Characteristics bestowing competitive superiority in environments with little disturbance ultimately lead to a decline in diversity through competitive exclusion, much as that predicted by the intermediate disturbance hypothesis and dynamic equilibrium theory. The more diverse communities are associated with characteristics of superior colonizers: low wood density, small seeds, and good dispersal. Variation in diversity at smaller spatial scales is strongly affected by soils.

Key words: alpha diversity; competitive exclusion; dispersal; disturbance; Guyana; rain forest, tropical; seed mass; soil heterogeneity; wood density.

INTRODUCTION

Generally speaking, tropical rain forests are characterized by high tree diversity, with some inventories recording up to ~300 species of trees with diameter at breast height (dbh) > 10 cm per hectare (Gentry 1988, Valencia et al. 1994). Various explanations have been offered for the maintenance of high diversity in tropical forests. One well-substantiated explanation suggests that diversity peaks at intermediate levels of productivity or disturbance (see Huston 1979, 1994 and Rosenzweig 1995 for reviews). Huston (1979, 1994) later expanded this explanation into the "dynamic equilibrium hypothesis," which predicts that the highest diversity will be found where disturbance and population growth are in "optimal" balance. When disturbance is greater (or more frequent), populations of certain (slow-growing) species will no longer recover after disturbance and fast-growing (pioneer or r-type) species

will prevail. Under low disturbance regimes the most competitive (climax or k-type) species will exclude other species. The species that will finally dominate the two low-diversity ends of the continuum predictably differ in a large number of key characteristics associated with ecological responses to varying environmental conditions (Huston and Smith 1987, Swaine and Whitmore 1988, Huston 1994). The most significant difference in ecological response between species groups is thought to be caused by a trade-off between the capacity to achieve high growth under high light conditions and high survival under low light conditions (e.g., Bazzaz 1979, Hubbell 1995).

Disturbance and productivity are not uniform throughout the tropics and spatial variation in tree diversity as a response to changes in these key environmental factors is predicted by the dynamic equilibrium hypothesis (Huston 1979). Not all tropical forest communities show particularly high tree alpha diversity (Richards 1952, Connell and Lowman 1989, Hart et al. 1989) and low diversity typifies forests in central Guyana (e.g., Fanshawe 1952, Richards 1952, ter Steege

et al. 1993, Johnston and Gillman 1995, ter Steege 1998*a,* ter Steege et al. 2000*b*).

Low diversity, as in some monodominant forest types of central Guyana, has been attributed to adverse moisture or nutrient properties of the soil on which such forests exist (Richards 1952, Connell and Lowman 1989, Hart et al. 1989, but see ter Steege et al. 2000*b*). The dynamic equilibrium hypothesis suggests that these forests could be either early successional (Huston 1994) or, as speculated for Guyana (Hammond and Brown 1995), late successional forests (Hart et al. 1989, Huston 1994). In late successional forests, with infrequent and/or low-intensity disturbances, shade tolerance of seedlings is a prerequisite to survival. One way to achieve such shade tolerance is by utilizing an internal energy source, in the form of seed endosperm or bulky cotyledons, that can support juvenile plant growth and maintenance when the quantity and quality of light available at the forest floor alone is not enough. When recovery after herbivory or other forms of biomass loss do not disproportionately absorb remaining seed reserves (e.g., Clark and Clark 1991, Hammond and Brown 1998), larger seeds generally produce larger seedlings (e.g., Hart et al. 1989). The woody plants of central Guyana are renowned for their large seeds (Hammond and Brown 1995) (see Plate 1, left and middle photographs). It has been hypothesized that this abundance of large-seeded trees is symptomatic of positive selection for individuals with traits that enhance shade tolerance and competitive ability in a region subject to relatively infrequent larger-scale disturbances (Hammond and Brown 1995) that are more common at other neotropical forest sites (Saldarriaga and West 1986, Salo et al. 1986, Boucher 1990, Horn and Sanford 1992, Bush and Colinvaux 1994, Nelson et al. 1994, Zimmerman et al. 1996, Lugo and Scatena 1997).

In Guyana, a gradient in diversity was observed by ter Steege (1998*a*) but this gradient remained largely unexplained. In this paper we examine the landscape-scale spatial pattern in tropical canopy tree diversity in Guyana and its relationship with tree and plot attributes over an area of 15×10^6 ha, spanning from $1°30'$ to $8°12'$ N. There is considerable spatial variation in community-level representation of life history character states of canopy trees in these forests, and this is strongly associated with variation in alpha diversity. After evaluating several environmental variables, such as rainfall and soil, posited as explanatory factors for varying tree diversity in other neotropical regions, we preliminarily suggest that the pattern of varying tree alpha diversity in Guyana may be better explained in terms of regional differences in the disturbance history of these forests.

Disturbance regimes

It has been recognized for some time that plant communities are not just random assemblages of species. Certain assembly rules may underlie the communities as we see them (e.g., Keddy 1992, Grime 1993, Weiher and Keddy 1995). Keddy (1992) defined assembly rules as filters acting on a regional set of species. Such environmental filters remove species from the regional set, which are unsuited to a specified set of conditions. Possible filters could include flooding, drought, biotic interactions, and here disturbance regimes. Episodic disturbances that alter canopy cover, such as shifting cultivation, hurricanes, fires, landslides, phytopathogen epidemics, and dynamic fluvial processes, directly or indirectly affect all tree species in a forest stand and may drive tree communities towards character convergence (e.g., see Lugo and Scatena 1997). In forests subject to repeated large-scale disturbances at a wide range of scales, selection should place a premium on trees that are able to reproduce at an early age. Frequent canopy disturbance and an increased likelihood of suffering a terminal injury would diminish the reproductive success of individuals maturing late. As a consequence, species unsuited to survival and growth in these highly dynamic environments are slowly filtered out of the regional assembly. Similarly, if a forest community is only subject to relatively small-scale minor disturbances, such as tree or branch-fall gaps, then certain species characteristics in this community should show greater convergence towards those states that convey the greatest fitness under low disturbance conditions (Hammond and Brown 1995).

Seed mass, establishment, and dispersal

To deal with different growth and reproductive strategies, tropical trees have traditionally been divided into pioneer and climax groups (see, e.g., Swaine and Whitmore 1988). During early stages of succession, fast growth and high sapling establishment are considered important characteristics for success, whereas shade tolerance is more important during later stages (Huston and Smith 1987). Similarly, low disturbance conditions would favor shade tolerance, mostly achieved through large seed reserves (Hart et al. 1989, Hammond and Brown 1995), and physiological adaptations that also reduce the growth rate (Smith and Huston 1989). Whereas size and residence time determine success of seedlings in the understorey and small gaps in central Guyanan forests, the ability to increase relative growth rate (RGR) under high light conditions may determine to a large extent success in large gaps (Boot 1996, ter Steege and Hammond 1996). Because larger seeds produce larger seedlings with greater structural mass, RGR in seedlings of a similar (young) age is negatively correlated with seed mass (Kitajima 1994, Osunkoya et al. 1994, ter Steege 1994). In the functional classification of trees, seed mass also plays a prominent role in the distinguishing of groups (e.g., Brzeziecki and Kienast 1994, Grime et al. 1997). Thus seed mass may be one reasonable estimator of the place of a species in the continuum of regeneration strategies.

Seeds are dispersed by a variety of mechanisms and

PLATE. 1. (Left) A freshly germinated seed/young seedling of *Eperua rubiginosa* in ''mora forest'' along the main creek in the Forest Reserve Mabura Hill, Central Guyana. The fresh seed mass of this species is ~65 g. (Middle) A germinating seed/young seedling of *M. excelsa*. The average fresh seed mass of this species is near 120 g. Due to the presence of an air chamber between the cotyledons (visible as impressions in them) the seeds float and are often dispersed by water. (Right) A large *Mora excelsa* tree, also in ''mora forest'' along the main creek. Most of the seedlings in the photograph are *M. excelsa*, a species capable of tolerating heavy shade.

dispersal may help seeds to escape heavy mortality near the parent tree (Howe and Smallwood 1982). The adaptation to a particular mechanism, however, can constrain other seed attributes, such as size. Dispersal type explained >30% of the variation in seed mass near Mabura Hill, Guyana (Hammond and Brown 1995). Most of the variation is not found at the species level: only 22% of the variation in seed mass is accounted for by species included in the woody flora of the Guianas; the remainder is explained at the genus (53%) and family levels (25%) (Casper et al. 1992). Most species within a genus are dispersed by the same dispersal mechanism (only 4% variation explained at species level) and are either all dry or fleshy, dehiscent or indehiscent (Casper et al. 1992). This obviously also reflects our way of classifying species. In the Guianas, the highest species richness is found in genera associated with vertebrate dispersers: e.g., *Psychotria, Miconia,* and *Ocotea* with birds; *Piper, Solanum,* and *Ficus* with bats; *Licania* and *Swartzia* with bats and rodents; and *Protium* and *Pouteria* with primates (Charles-Dominique 1993). We have no a priori hypothesis of how dispersal should be related to larger spatial and temporal scales of disturbance in a rain forest. However, wind-dispersed seeds may tend to arrive first in large gaps (Schupp et al. 1989), followed by bird-, bat-, and rodent-dispersed seeds. Autochorous and barochorous species, due to their larger average seed mass, are expected to arrive last or less often in large openings (see also Foster et al. 1986). Thus

wind-, bird-, bat-, and primate-dispersed species may be expected to be more common than gravity- or rodent-dispersed species in forests that repeatedly experience extensive canopy fragmentation over the course of centuries or millennia (Hammond and Brown 1995). The latter species may regenerate more through the presence of a shade-tolerant seedling bank present at the time of gap formation (see Plate 1, right photograph). Their large seed mass and, hence, large seedling size, are beneficial in this respect (Boot 1996, ter Steege and Hammond 1996).

Wood density and growth rates

Like large seed mass, large stem size and long life span typify climax species (Huston and Smith 1987), and maximum height and diameter have been found to be important characters when grouping both temperate (Brzeziecki and Kienast 1994) and tropical (Favrichon 1994) trees. We showed earlier (ter Steege and Hammond 1996) that increasing disturbance rates should disproportionately limit recruitment in slower growing species. Individuals that reside in smaller size classes for longer periods, due to slow growth, are more likely to be incidentally involved in treefall events (see Clark and Clark 1991). Data on the maximum intrinsic growth rates of most tropical trees is lacking. This ''information gap'' complicates any effort to understand the relationship between long-term growth and long-term fluctuations in external conditions. There is evidence to suggest, however, that high growth rates

in tropical trees are associated with low wood density (Favrichon 1994, Suzuki 1999; H. ter Steege, *unpublished data*). The advantages given to fast-growing trees in a highly disturbed environment suggests that wood density, as a measure of long-term growth performance, may also be a proximate measure of disturbance sensitivity.

METHODS

Field data collection details

From 1966 to 1973 a low-level strategic reconnaissance survey, the ''Forest Industries Development Survey'' (FIDS) was carried out with Food and Agricultural Organisation/United Nations Developmental Programme (FAO/UNDP) funding to ''assist the Government of Guyana in determining the extent and composition of accessible forest'' (de Milde and de Groot 1970). The survey consisted of 1029 plots of 0.2–0.4 ha in size, spread across the entire country, amounting to 243 ha of enumerated forest. Sample plots were established, after extensive air-photo interpretation, in the main forest types of a region. In each plot, soil type, presence of rocks, topography, forest type, and height of the highest tree (for each subplot) were recorded. All trees with dbh >30.5 cm (breast height = 1.3 m) were recorded and identified by trained treespotters (de Milde and de Groot 1970, ter Steege 1998*a*). No voucher specimens were collected. Vernacular names in Guyana are relatively constant (but see ter Steege 1998*a* for some problems) and were converted to scientific names using Mennega et al. (1988) and Boggan et al. (1997). Because the exact location of each plot could not be reliably reconstructed from the survey archives for all plots, the plots were grouped into 77 clusters, each consisting of a constellation of plots that were within a few kilometers of each other. Cluster analysis carried out on these 77 clusters resulted in five floristic groups that were well separated geographically and were considered ''forest regions'' (ter Steege 1998*a*). Five clusters from the original set of 77 were identified as gross statistical outliers in a multivariate vegetation analysis (ter Steege 1998*a*) and have been omitted from the analyses undertaken here.

Plot cluster and taxa attribute data sources and compilation

We constructed a relational database containing information on: (1) plot composition (plot number, species, dbh), (2) plot attributes (including location, soil, rainfall, and potential evapotranspiration [PET]), (3) taxa-specific attributes, and (4) tree community attributes.

Plot attribute data.—1. *Location* (see *Field data collection details*).—Plots were identified with location information that was written on the field sheets and summary sheets. Usually this information was in the form of a river, creek, small village, or mountain.

Sometimes no geographical information was present but, as plots were enumerated sequentially in each area, it was then possible to deduce the approximate location by using the date of the plot and the name of the recording person. Only in one zone (northwest of Guyana) was there no geographic information, and plots were assigned to three geographical locations based on their numbering.

2. *Soil* (see *Field data collection details*).—Soils were classified during the FIDS as ''pegasse'' (terric and fibric Histosol), clay (Fluvisol/xantic Ferralsol), loam (mostly haplic and xanthic Ferralsol), brown sand (ferralic Arenosol and possibly some haplic Ferralsol), laterite (Leptosol with possibly some xanthic Ferralsol included), white sand (albic Arenosol), and rocky (Lithosol). In a number of cases soil type was not recorded and labeled unclassified.

3. *Rainfall*.—Monthly and yearly data were obtained from interpolated maps, based on the very many rainfall stations present in Guyana (Persaud 1994, Persaud and Persaud 1995).

4. *Potential evapotranspiration*.—Yearly potential evapotranspiration data were obtained from interpolated maps (Persaud and Persaud 1993).

5. *Length of dry season*.—Length of dry season was determined based on the monthly data gathered from the interpolated maps (see 3. *Rainfall*; Persaud 1994, Persaud and Persaud 1995).

6. *Sunshine hours*.—Sunshine hours were determined based on yearly data obtained from interpolated maps (Persaud 1982).

Taxa-specific attribute data.—1. *Seed mass*.—Average seed mass was classified in $\log_{10}$-classes to account for the range in seed mass found in Guyanan forests (10^{-5}–10^2 g dry mass; see van Roosmalen 1985, Hammond and Brown 1995, Hammond et al. 1996; D. S. Hammond, *unpublished data*). The log classes also account to some extent for the high variability in seed mass within a species, which in some large-seeded species can range from 10 to 240 g (ter Steege 1990, 1994). In cases in which more than one scientific species could be associated with a vernacular name, the average seed mass of all species in the group (if known) was used. Generally, the seed class was identical for all species (see also Casper et al. 1992 and *Introduction: Seed mass, establishment, and dispersal*) associated with the same vernacular name, and the error due to unknowns was small.

2. *Dispersal type*.—Seed dispersal type was classified as primate, bird, bat, rodent, wind, water, and unassisted (gravity and explosive). We allowed more than one dispersal type per species, as this is frequently the case (van Roosmalen 1985, Hammond and Brown 1995, Hammond et al. 1996).

3. *Wood density, at 12% moisture content (or air-dry timber)*.—If more than a single scientific species was referred to by vernacular name, the average wood density for all scientific species associated with the

vernacular name was used, where known. In cases in which a vernacular name referred to a single group of congenerics, the average of the genus was assumed (e.g., in many *Inga* spp.; Fanshawe 1961, Détienne and Jaquet 1982, Vink 1983, Favrichon 1994, Gérard et al. 1996). As wood density is relatively constant within genera (in Guyana), except for *Ocotea,* the error due to estimation was again believed to be relatively small.

4. *Endemic status.*—An endemic is defined here as a species or higher taxon associated with a vernacular name with 90% of its known distribution confined to Guyana (Polak 1992): *Aldina* spp., *Chlorocardium rodiei, Dicymbe* spp., *Eschweilera potaroensis, Licania buxifolia* (Marishiballi), *Licania cuprea* (Konoko), *Maburea trinervis, Swartzia leiocalycina, Swartzia* spp. (Itikiboroballi), and *Vouacapoua macropetala.*

5. *Pioneer status.*—Trees were determined to be either short- or long-lived pioneer tree taxa as identified by Favrichon (1994) and Finegan (1996). We did not attempt to identify new pioneer taxa.

Tree-community attribute data.—1. *Alpha diversity.*—Fisher's alpha was calculated for each of the 72 plot clusters (Fisher et al. 1943). This index was used because of its independence of sample size (Taylor et al. 1976, Leigh 1995, Rosenzweig 1995).

2. *Dominance.*—Dominance is a measure of the relative abundance of the most common species within the tree community. This was defined as

$$\text{dominance} = 100 \times N_{sp1}/N_{tot}$$

where N_{sp1} is the number of individuals of the most common (or dominant) tree species and N_{tot} is the total number of individuals in the community.

3. *Percentage of pioneers.*—Percentage of pioneers is a measure of the relative proportion of stems within a plot cluster that have been typified as pioneer taxa (see *Taxa-specific attribute data*). Because dominance was thought to be inversely related to disturbance frequency or intensity and therefore inversely related to pioneer abundance, we defined the percentage of long-lived pioneers as

$$\text{percentage of pioneers} = 100 \times N_{pioneers}/(N - N_{sp1}).$$

Where $N_{pioneers}$ is the number of short- and long-lived pioneers in the tree community and N_{sp1} is the number of individuals of the most common (or dominant) tree species. This definition was chosen to avoid the situation in which a high dominance score would be pseudocorrelated with the percentage of pioneers due to the inclusion of the most common tree species in calculating plot cluster scores for both dominance and pioneer variables.

Statistical analyses

The relationship of diversity (Fisher's alpha) with rainfall, PET, length of dry season, and sunshine hours was investigated with regression analysis (Statistica; Statsoft 1993 [Statsoft, Tulsa, Oklahoma]). Regional

effects on diversity and the effects of soil type on diversity were assessed with ANOVA. Because there was no replication and an unbalanced design, the ANOVA was carried out with the generalized linear model (GLM) module of Systat 8.0 as a Model I, two-way ANOVA without replication (Wilkinson 1998). Geostatistical analyses, previously performed on the same data set (ter Steege 1998a), had already shown that in terms of diversity and forest composition (based on correspondence analysis) there was strong spatial autocorrelation, and the plots could be viewed as a gradient from south to north both in terms of diversity and composition. Thus, for regional groups we used the clusters that were obtained through a Twinspan cluster analysis (ter Steege 1998a; see also *Methods: Field data collection details*), these being broadly grouped along a south to north gradient.

We examined the relationship between the plot and species attributes by carrying out a principal components analysis (PCA, Statistica; Statsoft 1993) for 72 sites. Seed mass and wood density were log transformed, and percentages of soil type per site and percentage of individuals per dispersal type per site were arcsine transformed. The PCA was conducted on a correlation matrix (Pearson's r) of the transformed data. For each soil type, the percentage of plots on that soil type was calculated per geographical site and arcsine transformed.

RESULTS

A total of 15 397 trees >30.5 cm dbh were found on the plots. They comprised 251 identified taxa in 53 families (ter Steege 1998a) and 17 unknowns. The most abundant family in the sample was Caesalpiniaceae, which accounted for 8% of all species and nearly 30% of all individuals.

The wood density, seed mass, and dispersal mode were available for 243 tree species (Appendix). Average wood density ranged from 0.26 to 1.29 g/cm³. Seed mass ranged from just over 10 µg to 120 g or eight orders of magnitude. Seed mass and wood density showed a weak positive correlation ($r^2 = 0.11$, $P < 0.001$; Fig. 1). Wood density and seed mass were not equally distributed over dispersal types and/or taxa (Tables 1 and 2). Dispersal type had a significant effect on seed mass (ANOVA: $F_{6, 394} = 6.16$, $P < 0.001$) and on wood density (Kruskal-Wallis: $H_{6, 401} = 98.45$, $P < 0.0001$; Table 1). Wind-, bird-, and bat-dispersed species had the smallest seeds. Primates and rodents can handle larger food items and seed masses of species dispersed by them were larger. Seeds that are not dispersed by animals, wind, or water were largest on average (Table 1).

Several of the most common tree taxa in Guyana are characterized by large seeds (see also Hammond and Brown 1995) and dense wood (Table 2). The Lauraceae encompasses a large variation in wood density (Table 2). Within the Legumes, Mimosaceae have the lowest
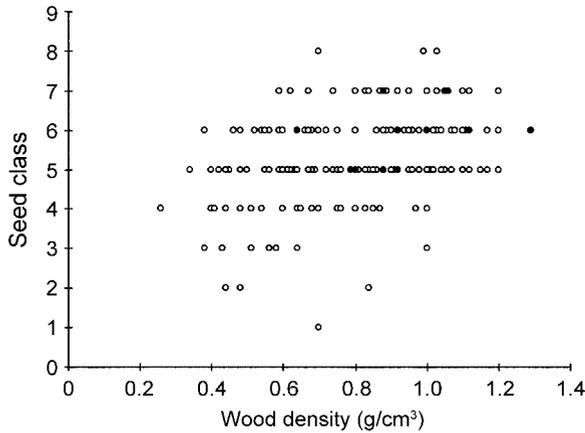
FIG. 1. Seed mass (log classes: $1 = 10^{-5}-10^{-4}$, $2 = 10^{-4}-10^{-3}$, ... $8 = >100$) and wood density for 243 species found in the National Forest Inventory in Guyana. There is a significant correlation between seed class and wood density ($r^2 = 0.11$, $P < 0.001$). Solid circles are species endemic to Guyana.

TABLE 1. Mean wood density and median seed mass per seed dispersal type for trees surveyed in Guyana. The range is given in parentheses.

Dispersal type	Mean wood density (g/cm³)	Median seed mass (g)
Wind	0.69 (0.26–1.04)	0.1 (10^{-3}–10)
Birds	0.74 (0.34–1.20)	0.1 (10^{-5}–10)
Bats	0.89 (0.44–1.29)	1 (10^{-4}–10)
Water	0.77 (0.36–0.99)	0.1 (10^{-3}–100)
Primates	0.80 (0.34–1.29)	0.1 (10^{-4}–100)
Rodents	0.89 (0.4–1.29)	1 (10^{-2}–10)
Unassisted	0.87 (0.62–1.10)	10 (10^{-1}–100)

Notes: Wood density differs significantly between classes (ANOVA: $F_{6, 394} = 16.07$, $P < 0.001$). Median seed mass also differs significantly between classes (Kruskal-Wallis: $H_{6, 401} = 98.45$, $P < 0.0001$).

wood density and smallest seeds, whereas Caesalpiniaceae have the densest wood and largest seeds (Table 2).

Guianan endemics are among the species with the heaviest wood (all >0.75 g/cm³) and largest seeds (Fig. 1). The most common 15 species, occurring with >250 individuals in the survey, were characterized by large seeds (range 6–8, median = 7).

Species diversity, as expressed by Fisher's alpha, was highest in the southern part of the country and declined along a gradient towards the north ($r^2 = 0.469$; $P < 0.01$; Figs. 2A and 3A). Total annual rainfall was a poor estimator of diversity over the 72 sites ($r^2 = 0.01$, $P = 0.48$), and PET did not explain any significant variation in diversity ($r^2 = 0.02$, $P = 0.28$) either. All other climatic parameters tested, viz. length of dry season, difference between rain and PET and total annual sunshine, showed a strong correlation with rainfall and did not explain significant variation in diversity.

Plots on mesic soil types, such as brown sand and loam (Ferralsols, ferralic Arenosol), clay (Fluvisols/xanthic Ferralsol), and laterite (Leptosols/xanthic Ferralsol), showed higher tree diversity than plots on more xeric soils, such as rock and white sand (Albic Arenosols), or plots on hydric soil types, such as peat soils (terric/fibric Histosols; Table 3). This relationship was consistent throughout the country. The southern sites, however, were generally more species rich than the northern sites (Table 3), consistent with the gradient in alpha diversity described above.

Community averages of species attributes, weighted by the abundance of each species (i.e., averaged by the number of individuals of each species, rather than number of species alone), showed distinct spatial variation when all plots were mapped onto a countrywide grid (Fig. 2). A high median (and mean) seed mass (Fig. 2C) was most typical of plots in central Guyana while

most plots in the south had a median seed mass that was one to two orders of magnitude smaller than those in the central region. Average wood density (Fig. 2B) of the plots in the south was also less than in central or northwestern sites. Bird-dispersed trees were especially common in the forest communities in the southern parts of Guyana, where 36% of the individuals on average were bird dispersed, compared to 14–19% in the rest of the country (Fig. 2E). This was also the case, to a lesser extent, for primate-dispersed trees, with an average of 68% of the individuals in the south being dispersed by primates, compared to 40–50% in the other parts of the country (Fig. 2F). Rodent-dispersed trees were more abundant in central Guyana, accounting for 60% of all individuals, compared to 50% in the northwest and 40% in the south of the country (Fig. 2G). Trees with seeds dispersed by gravity or water typified both central and northwestern areas (41 and 43% respectively; Fig. 2H), but were relatively uncommon in the southern plots (13% of all individuals).

The results of the principal components analysis are shown in Fig. 4. Initially, climatic data, soil data, and tree species attributes were included in the PCA. Both annual rainfall and the difference between rainfall and

TABLE 2. Mean wood density and median seed mass for some of the most important taxa in Guyana. Ranges are given in parentheses.

Species	Mean wood density (g/cm³)	Median seed mass (g)
Licania	1.08 (1.03–1.20)	10 (1–10)
Lecythis/Eschweilera	1.02 (0.90–1.12)	1
Swartzia	0.97 (0.72–1.29)	1 (1–10)
Pouteria s.l.	0.99 (0.67–1.20)	1 (0.1–100)
Lauraceae	0.67 (0.38–1.12)	1 (0.1–10)
Mimosaceae	0.69 (0.40–1.12)	0.1 (0.01–1)
Fabaceae	0.87 (0.52–1.29)	1 (0.1–10)
Caesalpiniaceae	0.89 (0.68–1.15)	1 (0.1–100)

Notes: Wood density differs significantly between these taxa (ANOVA: $F_{7, 97} = 8.88$, $P < 0.001$). Median seed mass also differs significantly between these taxa (Kruskal-Wallis: $H_{7, 105}$ 30.49 $P < 0.0001$).

PET had no significant direct correlation with diversity (see above), and their inclusion or exclusion did not alter the PCA results (communality of rainfall with factor 1, 0.42). Thus, rainfall data were excluded from the final PCA. There was considerable variation in tree diversity among soil types (Table 3). However, soil type also had no effect on the PCA (communalities of soil variables with PCA factor 1 varied from −0.37 to 0.45) and did not correlate well (most r's were between −0.2 and 0.2) with any of the community characteristics when analyzed per site. Soil information was therefore also removed from the analysis.

The first factor of the PCA (Fig. 4) shows that large seed mass, high wood density, and dispersal by rodents were associated, while on the other hand low seed mass, low wood density, and primate and bird dispersal were associated. To understand how tree diversity and disturbance were related to the PCA axes, we included (1) alpha diversity (Fisher's alpha), (2) the percentage of (short- and long-lived) pioneers, (3) the dominance of the most abundant species, and (4) the abundance of endemics at each site into the existing PCA variable set and reran the PCA. The inclusion of these four site characteristics did not change the PCA with regard to the previous analysis. The subsequent and final analysis revealed (Fig. 4) that alpha diversity and a high occurrence of pioneer species were related to small seed mass, low wood density, and primate and bird dispersal. That is to say, they grouped with the characteristics on the left side of PCA factor 1. Dominance grouped well with characteristics on the right side of PCA factor 1. A biplot of factor scores for PCA factor 1 and 2 is given in Fig. 4 (inset). There were no real clusters within the sites but rather the sites form a continuous gradient with the main variance distributed over factor 1.

Table 4 lists the correlation coefficients for the parameters used. As suggested by the PCA, a strong positive correlation exists between dominance and seed mass ($r = 0.69$, $P < 0.01$), whereas dominance is negatively correlated with the percentage of pioneers and primate and bird dispersal.

Geographically, the plots with the highest PCA factor 1 scores (0 to 1.7), being those sites with high wood density, large seeds, and a high degree of dominance, were situated in central and northwest Guyana (Figs. 2D and 3B). Most sites below 4° N have a negative score on the first PCA factor, whereas most sites above 4° N have a positive score.

DISCUSSION

Exploring spatial variation in canopy tree diversity

Soil effects.—There exists a clear gradient of alpha diversity of canopy trees across Guyana (Figs. 2A and 3A). The gradient in diversity covaries with gradients in community averages of life history characteristics such as seed mass, wood density, and dispersal type (see *Methods*) but also with a floristic gradient (see ter

Steege 1998*a*). As diversity is also affected by soil type (Table 3), it is reasonable to assume that regional differences in geology and soils may be in part responsible for the differences in diversity found (ter Steege 1998*a*). Soil types at the site level, however, had no significant effect on diversity, as shown by the PCA analysis. This may appear surprising but is caused by the fact that the 77 sites (72 used for PCA analysis) are made up of a kilometer-scale constellation of neighboring plots. Because the main objective of the national reconnaissance tree survey was to give a timber assessment of the most common regional forest types, several forest types on different soils may thus be included in single sites. In the PCA this obscures the effect that local substrate has on diversity and only the regional effect remains. In Table 3 the interaction between regional and local substrate effects can be seen. The overall soil effect, given in the rightmost column, shows that there are clear differences in diversity among soil types. The overall regional effect, given in the bottom line of Table 3, shows a steady increase of diversity from northwest Guyana towards the south, as did the general gradient (Fig. 3A). The pattern within this table is rather consistent. Soils supporting the highest overall tree diversity are also the most diverse in each region. Furthermore, the diversity on each soil type increases towards the south. Forests on white sand were the exception to this pattern, being most diverse in the Pakaraimas area, where some of the main concentrations of white sands are situated.

Among soil types in Guyana there are also very clear differences in forest composition (Fanshawe 1952, ter Steege et al. 1993) as elsewhere (Gentry 1988, Tuomisto et al. 1995). The relationship between varying soil attributes and forest composition are thought to consist of effects at three spatial scales, viz.: (1) macro-scale differences in soil parent material (ter Steege 1998*a*); (2) meso-scale changes in the edaphic quality of the soil (Fanshawe 1952, ter Steege et al. 1993); and (3) micro-scale hydrological variation within soil types (ter Steege et al. 1993). The effects of soil on composition may be explained in general terms by the filtering effect that important soil characteristics, such as water retention capacity, high water tables, and nutrient quantity and quality, can have on the pool of species present. The effect of soil type on diversity is more difficult to explain but differences in soil water and nutrients may affect diversity through productivity (e.g., Huston 1994 for a review but see ter Steege et al. 2000*b*).

Rainfall effects.—Yearly rainfall was a poor estimator of diversity. We conclude that geographical variation in rainfall is not important in explaining spatial patterns in tree diversity at the scale studied, even though annual rainfall at the sample plots varies from 1650 to 3550 mm. This is in sharp contrast to Gentry (1988) and Clinebell et al. (1995), who found rainfall to be highly correlated with tree alpha diversity. However, a more recent and more expansive analysis of tree
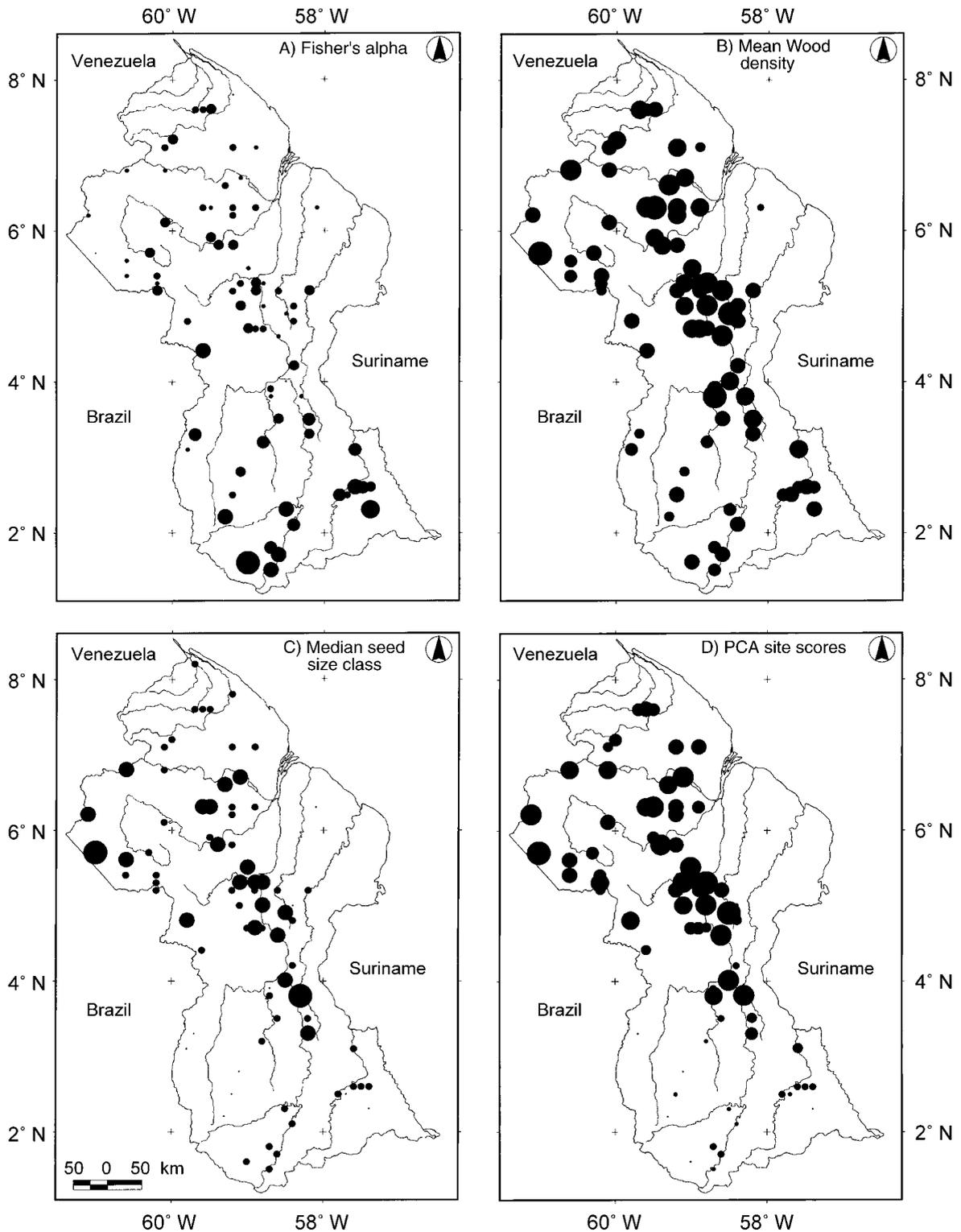
FIG. 2. Maps of community characteristics of Guyana's rain forest. The diameter of each circle is a reflection of the value of the characteristic at a location. The value ranges are: (A) Fisher's alpha, 1–68 (after ter Steege 1998a; see also Fig. 3A); (B) mean wood density of the forest, 0.61–0.98 g/cm^3; (C) median seed mass of the forest, 1–100 UNITS, three logarithmic classes; (D) PCA factor 1 score of forest sites, −1.91–1.93 (see also Fig. 3B); (E) percentage of individuals in the forest community the seeds of which are dispersed by birds, 4–53%, (F) dispersed by primates, 18–83%, (G) dispersed by rodents, 0–87%, and (H) dispersed without assistance, 0–74%.
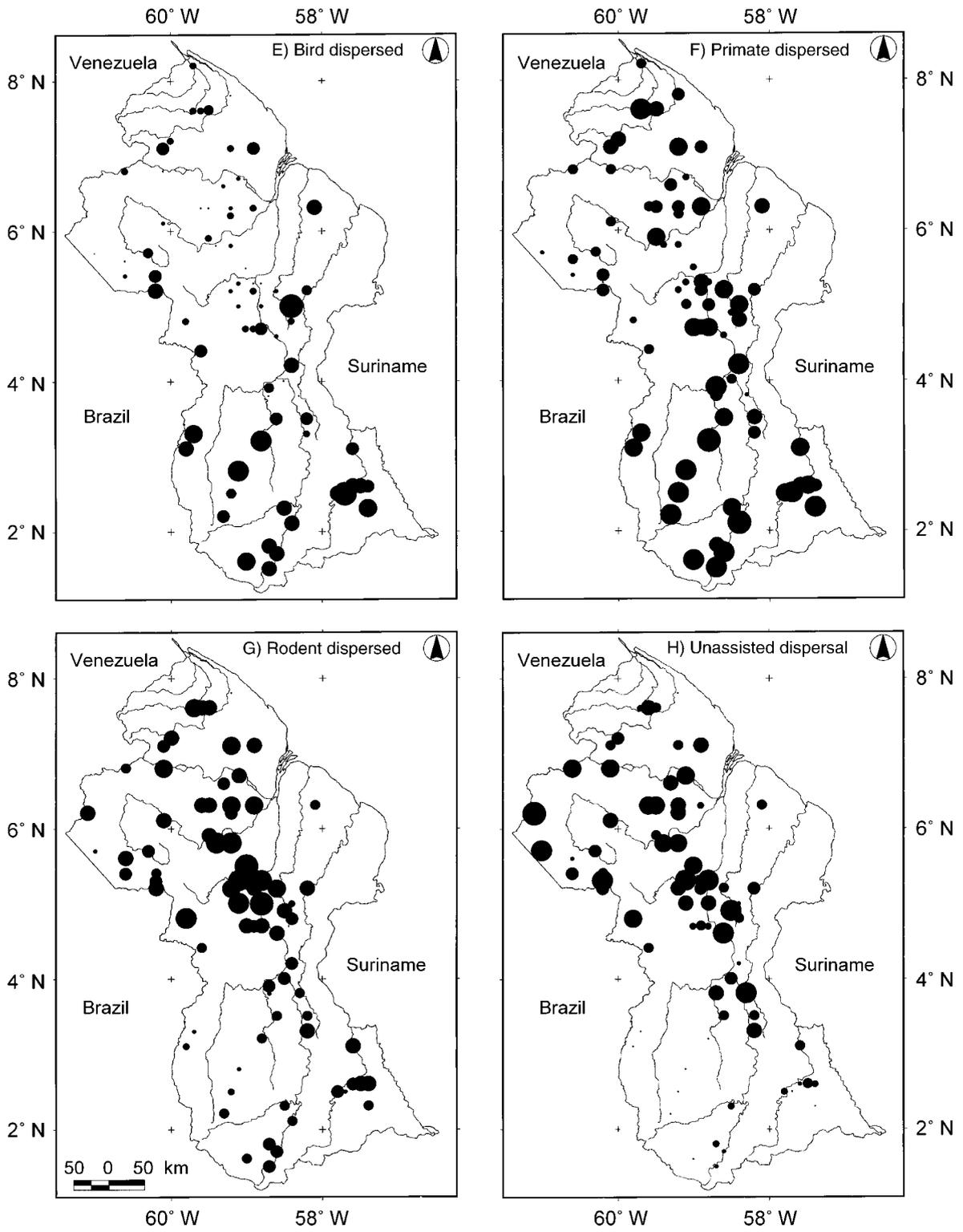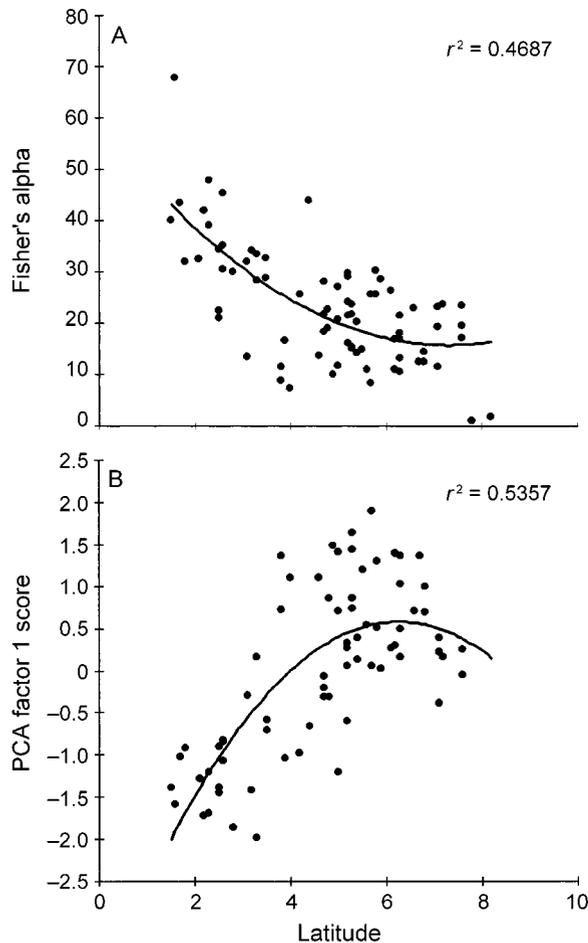
Fig. 2. Continued.

FIG. 3. Scatterplots of community characteristics vs. latitude. Regressions are second-degree polynomials. (A) Fisher's alpha decreased from the south to the north in Guyana ($r^2 = 0.469$; $P < 0.0001$). Most values >30 were found below 4° N latitude. (B) Principal components analysis (PCA) factor 1 scores were highest in central Guyana, from 5° to 6.5° N latitude ($r^2 = 0.536$; $P < 0.0001$).

alpha diversity in rain forests plots of Amazonia and the Guiana Shield showed that rainfall is in fact a poor estimator of tree alpha diversity (ter Steege et al. 2000*b*).

Latitudinal effects.—The gradient in diversity we detect over a large area from 1° to 8° N in Guyana should not be confused with the latitudinal gradient in diversity that is apparent when moving from the tropics to the temperate and boreal areas. This latitudinal gradient is largely the product of changes occurring from 60° to 20°. Within the tropics, the gradient disappears, mainly because all areas within the tropics are subject to similar annual amounts of incoming radiation (Rosenzweig 1995). Furthermore, diversity also increases from central Guyana towards Amapa, Brazil (ter Steege et al. 2000*b*) and this gradient too is accompanied by a decline in wood density (ter Steege 1998*b*). Community average wood densities are also low in the re-

mainder of the Amazon (Fearnside 1997) when compared to the high values reported from Guyana here.

Tree attributes.—Diversity is strongly correlated with other community characteristics, such as dominance, pioneer abundance, seed mass, and wood density as shown in the PCA analysis (Table 4). Plots with a high score on this factor had low canopy tree diversity, often verging on monodominance, as well as a high average seed mass and wood density. Rodent-, gravity-, or water-dispersed species and relatively high endemism also characterized these plots. The plots also had a high occurrence of typical Guyanan taxa such as Lecythidaceae and Chrysobalanaceae (ter Steege 1998*a*). In contrast, plots with low scores on PCA 1 were mainly situated in the south of Guyana. These plots were characterized by a highly diverse set of trees with small seeds, typically dispersed by birds and primates, and stems with relatively low wood density.

Competitive exclusion and spatial character convergence

Relatively low disturbance, as we think is normal for central Guyana, results in a stable forest in which mainly small gaps occur. We therefore think that the current forest composition in this part of Guyana is largely a reflection of competitive exclusion, as predicted by the Dynamic Equilibrium Hypothesis (Huston 1994, and many references therein). Shade tolerance of seedlings is expected under such conditions (Huston and Smith 1987, Hart et al. 1989, Huston 1994, Hammond and Brown 1995) and is considered to be achieved through having large seeds (Hart et al. 1989, Hammond and Brown 1995). In small gaps, a large seedling, being the result of a large seed, may be more important than a high relative growth rate in determining establishment success (Boot 1996, ter Steege and Hammond 1996). If disturbance increases, mostly leading to larger and more frequent gap-forming events, more opportunities are created for canopy tree species whose relatively small seeds can be transported to greater distances and can achieve much greater relative growth rates than those of large-seeded species (Boot 1996, ter Steege and Hammond 1996). Also, we showed with a very simple model (ter Steege and Hammond 1996) that species with dense wood, and hence lower growth and recruitment rates, are more likely affected by an increase in disturbance than faster growing species. Thus, we interpret the first PCA factor as a factor of disturbance.

Many canopy trees typically referred to as pioneers are expected to have low- to medium-density wood and small seeds, and those classified as climax species are expected to have dense wood and large seeds (Swaine and Whitmore 1988). Yet, the correlation between wood density and seed mass in our data set is weak (but significant, Fig. 1). Grime et al. (1997) suggested that patterns of functional attributes of the mature plant do not covary well with those of the regenerative phase.

TABLE 3. Canopy tree diversity, expressed as Fisher's alpha, for five TWINSPAN forest regions in Guyana and per major soil class within that region.

Soil group	Drainage quality	nwwf	cgwf	plwf	sdf	swf	Overall soil effect
Brown sand	good	28.8	33.4	38.9	42	46.9	47.8
Clay	good–poor	26.4	29.6	38.6	37.8	40.9	43.7
Laterite	good–poor	16.6	29.9	23.2	⋯	51.8	48.2
Loam	good	25.4	9.8	39.3	36.7	46.4	45.0
Pegasse	waterlogged	5.6	6.5	16.9	⋯	18.8	21.4
Rock	excessive	⋯	⋯	20.1	8.5	⋯	26.3
White sand	excessive	5.3	4.0	16.6	9.5	7.8	23.3
Unclassified		⋯	10.9	34.7	46.5	13.1	43.8
Overall regional effect		30.0	35.0	41.4	43.6	52.2	47.6

Notes: Alpha was calculated with the total number of species and total number of individuals in each cell. The abbreviations are: nwwf = northwest wet forest; cgwf = central Guyana wet forest; plwf = Pakaraima central lowland wet forest; swf = southern wet forest; sdf = southern dry forest. Soil groups are (according to the Forest Industries Development Survey; see *Methods: Field Data collection details*): brown sand = ferralic Arenosol/haplic Ferralsol; clay = mainly dystric fluvisol and some xanthic Ferralsol; laterite = Leptosol/Cambisol/xantic Ferralsol; loam = Ferralsol; pegasse = Histosol; white sand = albic Arenosol (adapted from ter Steege 1998*a*). The ANOVA was carried out with the generalized linear model module of Systat 5.1 as a Model I, two-way ANOVA without replication (F_{soil} = 7.87, $P < 0.001$; F_{region} = 4.93, $P < 0.005$).

This may not be surprising, on second thought, when we realize that growth and mortality in seedlings is much more strongly dependent on gap size (cf. Boot 1996). For saplings and subadults, random mortality, caused by debris, is also an important factor (Clark and Clark 1991, ter Steege and Hammond 1996). Wood density may also be a more plastic character in evo-

lutionary terms. Seed mass must be more constrained by mode of dispersal. Within a study of the woody plants in the three Guianas, the species level accounted only for a very small percentage of the variation in fruit types (Casper et al. 1992), i.e., species within a genus usually have the same fruit type (Casper et al. 1992) and seed mass (Kelly 1995). Kelly (1995), in-
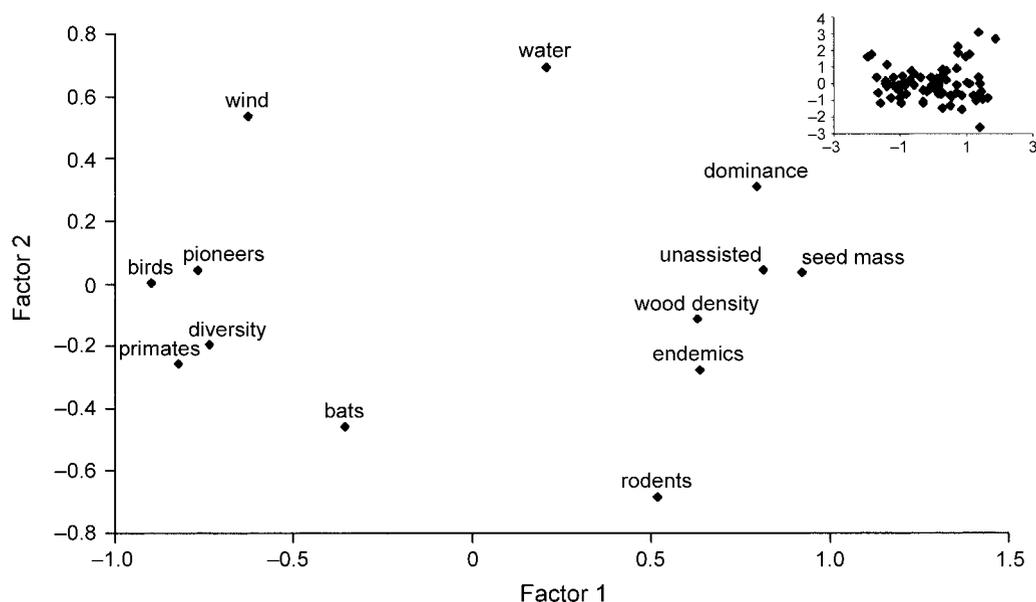

FIG. 4. Factor loadings of community characteristics of Guyana's rain forest based on principal components analysis on 72 sites. Factor 1 has an eigenvalue of 6.40 and explains 49.2% of all variance; factor 2, with an eigenvalue of 1.74, explains 13.4% of all variance. Total explained variance is thus 62.6%. Factor 1 can be interpreted as a factor of disturbance vs. nondisturbance in Guyana's forest, with characteristics of low disturbance (high wood density, high seed mass, and dominance) aggregated at the right of the diagram (i.e., low diversity). Inset: factor scores of the 72 sites on the first two factors (as in main figure) of the principal components analysis.

TABLE 4. Correlation matrix of parameters used in the principal components analysis.

Parameter	Domi-nance	Fisher's Alpha	Pioneers	Seed mass	Wood density	Seed dispersion by:			
						Primates	Birds	Bats	Rodents
Percentage of dominance	1.00	−0.72	−0.54	0.69	0.56	−0.65	−0.66	−0.31	−0.15
Fisher's alpha	−0.72	1.00	0.48	−0.45	−0.43	0.56	0.66	0.23	0.19
Percentage of pioneers	−0.54	0.48	1.00	−0.59	−0.55	0.55	0.75	−0.24	−0.36
Mean seed mass	0.69	−0.45	−0.59	1.00	0.54	−0.67	−0.70	−0.21	0.35
Wood density	0.56	−0.43	−0.55	0.54	1.00	−0.28	−0.56	0.01	0.20
Primate-dispersed seeds	−0.65	0.56	0.55	−0.67	−0.28	1.00	0.75	0.55	−0.29
Bird-dispersed seeds	−0.66	0.66	0.75	−0.70	−0.56	0.75	1.00	0.19	−0.51
Bat-dispersed seeds	−0.31	0.23	−0.24	−0.21	0.04	0.55	0.19	1.00	0.07
Rodent-dispersed seeds	−0.15	0.19	−0.36	0.35	0.20	−0.29	−0.51	0.07	1.00
Wind-dispersed seeds	−0.36	0.37	0.45	−0.49	−0.37	0.40	0.49	0.10	−0.61
Water-dispersed seeds	0.29	−0.24	−0.12	0.19	0.04	−0.22	−0.26	−0.12	−0.20
Unassisted	0.68	−0.60	−0.60	0.75	0.51	−0.87	−0.78	−0.43	0.50
Percentage of endemics	0.34	−0.49	−0.44	0.36	0.36	−0.40	−0.50	−0.14	0.58

Notes: All correlations: $n = 72$. Correlation coefficients >0.23 or <-0.23 are significant at $P < 0.05$.

deed, argued that seed mass was much more under control of dispersal type (birds vs. mammals) than of successional ecology. In the end, the impact of both dispersal and post-dispersal processes on the fitness of an individual seed also depends greatly on the prevailing conditions at the final landing site (e.g., Schupp et al. 1989).

Geographically, the plots with the highest PCA factor 1 scores (0 to 1.7) were situated in central Guyana (Figs. 1D and 2B). The fact that these areas are characterized by species-poor forests is interesting as these areas are thought to have been little used by pre-Colombian Amerindians (Evans and Meggers 1960, Dubelaar 1986), now recognized as having had a widespread role in shaping present forest composition and species distributions in the neotropics (Saldarriaga and West 1986, Bush et al. 1989, Bush and Colinvaux 1994, Meggers 1994). This region may have experienced the least environmental disturbance of all regions in Guyana, and possibly Amazonia, whereas the southern and northwestern forests of Guyana are known from the archaeological record to have been important population centers prior to European arrival (see Evans and Meggers 1960, Dubelaar 1986).

Competitive exclusion and disturbance

We believe that these landscape-scale results support the idea that the absence of large-scale disturbance in rain forest can ultimately lead to low tree diversity (Horn 1975, Connell 1978, Huston and Smith 1987, Huston 1994). Species with characteristics adapted to low disturbance converge in space and time as other species with fewer of these adaptations are competitively disadvantaged and therefore are no longer afforded sufficient establishment opportunities to maintain local populations. We further believe that large seed mass, a characteristic limiting dispersability and supporting seedling establishment and persistence in low-light conditions (Hammond and Brown 1995), is directly associated with competitive superiority in low disturbance environments and drives the approach to-

wards monodominance. Interestingly, the percentage of long lived pioneers in the plots was negatively correlated with dominance (Table 4), further suggesting that large disturbance events in low-diversity forests in central Guyana are infrequent enough to suppress widespread colonization of pioneers. It is important to note here that none of the most dominant species are classified as long-lived pioneers and show mostly self-replacing population structures (ter Steege et al. 1993). In contrast, southernmost regions are typified by characteristics, such as small seed mass and high dispersability (via birds and primates), that are normally associated with superior colonizing ability.

One question still remains: "Why is the disturbance in the south of Guyana higher or more large-scale?" We have already suggested that AmerIndian presence may be a key to that. We can think of two possible explanations. (1) The forests in south Guyana are found on better soils (Gross-Braun et al. 1965) and may therefore show higher productivity and hence higher dynamics (see Phillips et al. 1994), and (2) the more fertile soils in the south have attracted more human occupation as agriculture and hunting possibilities were greater and the human disturbances were the cause of the higher dynamics (and the two are not necessarily exclusive). In addition, periodic transitions to savannah conditions may also be of importance in the dry forest area of the south as the savannah–forest border was probably not stationary over long periods. This would be less likely for the wet forest in the south. Guppy (*unpublished manuscript*) suggested that squalls and cyclones were very common in the Acarai Mountains and the FIDS report indicates very common occurrence of liana forest in the southern area between the Essequibo, Kuyuwini, and southern boundary of Guyana (de Milde and de Groot 1970) as well as in forests east of the savannas. Brazil nut was also noted as being common in the south (ter Steege 1998*a*) and may be considered as a possible indicator of past human inhabitation.

TABLE 4. Extended.

Seed dispersion by:			Percentage of endemics
Wind	Water	Unassisted	
−0.36	0.29	0.68	0.34
0.37	−0.24	−0.60	−0.49
0.45	−0.12	−0.60	−0.44
−0.49	0.19	0.75	0.38
−0.37	0.04	0.51	0.36
0.40	−0.22	−0.87	−0.40
0.49	−0.26	−0.78	−0.50
0.10	−0.12	−0.43	−0.14
−0.61	−0.20	0.50	0.58
1.00	0.27	−0.57	−0.40
0.27	1.00	0.20	0.09
−0.57	0.20	1.00	0.58
−0.40	0.09	0.58	1.00

Uncertainties of the data and further research needs

Tree identification.—The collecting of voucher specimens is not general practice during large-scale forest inventories such as the Forest Industries Development Surveys. As a result of that, there is an unknown error associated with the conversion of vernacular names to scientific names. However, as stated above because of the level of consistency among the few, highly trained, tree-spotters and the consistency of life history characteristics among congeners, we believe that the error made is quite small.

Other factors influencing seed size.—Many environmental factors have been associated with a variation in seed size. Soil fertility has been suggested to influence seed size, but the relationship between tree seed size and soil fertility has typically proven to be weak (e.g., Hammond and Brown 1995, Westoby et al. 1997, Grubb 1998). Plant height and growth form have been shown to be more important in explaining variation in seed size (e.g., Hammond and Brown 1995, Leishman et al. 1995). However, the patterns detected in this paper are based entirely on trees >30 cm dbh, eliminating any effect of growth form and limiting the influence of height to the effects of canopy vs. emergent status.

A more compelling uncertainty that could weaken our use of an association between seed size and competitive ability in interpreting the PCA axis 1 as an axis of disturbance is the effect of seed chemical and physical defence structures in dampening attack by vertebrates, invertebrates, and pathogens (Janzen 1969). An investment in defense may not always be correlated with seed mass and could lead to a much poorer association between seed size and competition where this noncollinearity is pronounced.

Factors influencing wood density.—Rainfall may have an effect on community/species average wood density as was shown by Barajas-Morales (1985, 1987), and Borchert (1994) was able to identify several functional groups, with respect to soil water, on the basis of wood density and subsequent water storage of species. On average the species pool of dry deciduous

forest had a higher wood density (0.78 g/cm^3) than that of rain forest in Mexico (0.58 g/cm^3!; Barajas-Morales 1987). In our Guyana data, the community average of wood density showed no relationship with rainfall ($N = 72$, $r^2 = 0.00$). In fact both the dry and wet southern forest show lower average wood densities than the central forests (Fig. 2B). Brazilian data (Fearnside 1997) also do not indicate that deciduous forests have higher community average wood density than evergreen forests. Hence, we do not believe that differences in annual rainfall have distorted our results in any way.

Testing for differences in disturbance.—History of vegetation is difficult to test. Human occupation in southern Guyana is well documented and evidence for similar levels of past inhabitation in central Guyana is very scarce. Testable hypotheses would involve surveys for presence, age, and identification of charcoal (Hart et al. 1996), phytolithic analyses (e.g., Piperno 1994), and further archaeological surveying for signs of human inhabitation and influence. Experimental approaches might involve the parallel monitoring of dynamics and growth rates of forest and regrowth after small-scale clearance within plot clusters in each region. However the cost and time to achieve conclusive outcomes from an experimental approach applied at this scale would be considerable.

Implications for tropical forest conservation and management

Utilization and management.—Timber production in Guyana currently accounts for <1% of total tropical wood production, but Guyana is ranked as the fifth largest sawnwood exporter of timber from the Neotropics (FAOStat 2000 [available online]).[4] While plywood figures significantly in Guyana's timber industry, sawnwood provides a comparative advantage to Guyana on international markets. More than 95% of exported sawnwood consists of those species with high wood density, relatively large seeds, and known geographic ranges restricted to the Guiana Shield region (e.g., see Hammond et al. 1996, *in press*) The strength and durability of these timbers make them suitable for many applications where relatively long-term performance is required or expected (e.g., hardwood flooring, coastal defence works and piers, boat-building). The way in which these species are harvested will ultimately influence their future availability. Overzealous harvesting is expected to lead to recolonization by species with lower wood density, smaller seeds, and broader geographic ranges in central Guyana (e.g., ter Steege and Hammond 1996). Harvesting techniques and patterns that do not consider the ecological processes that underpin existing timber species distributions and abundances will substantively increase the risk of commercial extinction of many of the species that currently

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[4] URL: ⟨www.fao.org⟩

provide Guyana with a competitive advantage in the sawnwood market.

Conservation and protection.—Analysis of community (life history) characteristics and diversity on this spatial scale may help to define protected areas in Guyana (ter Steege et al. 2000*c*) and other countries, where such data exists. Standing diversity alone may be insufficient to make correct choices if the processes that maintain diversity are poorly understood. Assessing diversity by botanical collections alone may also lead to incorrect choices (Nelson et al. 1990, ter Steege et al. 2000*a*). Interestingly, the forests that seem least important for preservation from an alpha-diversity viewpoint may indeed be the most characteristic of Guyana, given the relatively large proportion of trees in these areas that are locally abundant, but have restricted distributions (ter Steege 1998*a,* ter Steege et al. 2000*a*). These forests may experience the most drastic change to poorly designed logging practices due to character convergence among tree species locked in a competitive environment that is not driven by frequent disturbance. As this area is also in the heart of the forestry concession belt of Guyana, quick action to preserve a vestige of these forests is urgently needed.

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APPENDIX

A table presenting the species enumerated in the National Forest Inventory of Guyana and their characteristics is available in ESA's Electronic Data Archive: *Ecological Archives* E082-037.