A Floristic Study of the White-Sand Forests of Peru

Author(s): Paul V. A. Fine, Roosevelt García-Villacorta, Nigel C. A. Pitman, Italo Mesones, and Steven W. Kembel

Source: Annals of the Missouri Botanical Garden, 97(3):283-305. 2010.
Published By: Missouri Botanical Garden
DOI: http://dx.doi.org/10.3417/2008068
URL: http://www.bioone.org/doi/full/10.3417/2008068

Volume 97
Number 3
2010

Annals
of the
Missouri
Botanical
Garden

A FLORISTIC STUDY OF THE WHITE-SAND FORESTS OF PERU[1]

Paul V. A. Fine,[2,8] *Roosevelt García-Villacorta,*[3,4] *Nigel C. A. Pitman,*[5] *Italo Mesones,*[6] *and Steven W. Kembel*[7]

Abstract

Tropical forests occurring on white-sand soils have a unique structure and are famous for their endemism. Yet, no comprehensive floristic study has ever been undertaken in white-sand forests in the western Amazon. Here, we present the results of floristic inventories from 16 plots in seven sites from the Peruvian Amazon to investigate diversity, species composition, and endemism in white-sand forests. We compare our results to a large data set from terra firme forests from more fertile soils in the same region. We found that white-sand forest plots have extremely low average species diversity (41.5 species per 0.1-ha plot) and that white-sand plots have significantly different species composition from terra firme plots. We classify 114 species as endemic to white sand, with another 21 species that can be considered facultative specialists or cryptic endemics. These endemics and specialists are extremely dominant, accounting for more than 83% of the total number of stems surveyed in white-sand forest plots. We place our results in the context of the role of environmental heterogeneity influencing patterns of species diversity and the conservation of Amazonian forests.

Key words: Amazon, beta-diversity, caatinga, edaphic specialization, endemic species, habitat specialists, heath forests, tropical tree diversity, varillal.

---

[1] This paper is dedicated to the memory of Alwyn H. Gentry, whose work inspired this study. We thank the Dirección General de Areas Naturales Protegidas y Fauna Silvestre–INRENA, which provided necessary permits for study, collection, and exportation of specimens; D. Del Castillo, L. Campos, E. Rengifo, and S. Tello of the Instituto de Investigaciones de la Amazonía Peruana (IIAP) for logistical support and permission to work in and around the Estación Allpahuayo and the Centro de Investigación Jenaro Herrera; the communities of Tierra Blanca, Tamshiyacu, and Jeberos for permission to work near their villages; S. Irazuzta, Don Meneleo of Jeberos, and F. Vacalla for field assistance; H. Mogollón, N. Dávila, M. Ríos, J. Guevara, M. Ahuite, D. Cardenas, P. Núñez V., and E. Valderrama for their extensive work establishing plots and identifying plants in the non-white-sand plots described in this paper; C. Bode for help with the figures; and S. Brewer and C. Vriesendorp for advice regarding analyses. We thank P.D. Coley for advice during all stages of this project. J. Álvarez Alonso has continually offered guidance and helped us to visit many of the field sites. This research was supported by grants DEB 02069196 (co-principal investigator P.D. Coley) and OISE 0402061 to P.V.A.F. by the National Science Foundation. N.C.A.P.'s work was supported by a National Science Foundation International Research Fellowship (INT-0107368) and the Field Museum's Rapid Biological Inventories program, with support from the Gordon and Betty Moore Foundation.

[2] Department of Integrative Biology, University of California, Berkeley, California 94720, U.S.A.

[3] Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, Michigan 48109, U.S.A.

[4] Facultad de Ciencias Biológicas, Universidad Nacional de la Amazonía Peruana, Iquitos, Peru.

[5] Center for Tropical Conservation, Nicholas School of the Environment and Earth Sciences, Box 90381, Duke University, Durham, North Carolina 27708, U.S.A.

[6] Facultad de Ciencias Forestales, Universidad Nacional de la Amazonía Peruana, Iquitos, Peru.

[7] Department of Integrative Biology, University of California, Berkeley, California 94720, U.S.A. Current address: Center for Ecology & Evolutionary Biology, 335 Pacific Hall, 5289 University of Oregon, Eugene, Oregon 97403-5289, U.S.A.

[8] Author for correspondence: paulfine@berkeley.edu.

doi: 10.3417/2008068

ANN. MISSOURI BOT. GARD. 97: 283–305. PUBLISHED ON 10 OCTOBER 2010.

The observation that white-sand soils in the Amazon basin support distinctive forest formations has long been noted (Spruce, 1908). White-sand forests have a shorter canopy, a brighter understory, and often a thicker layer of humus than the archetypal rainforest that is found on other terra firme soils (Anderson, 1981; Medina & Cuevas, 1989). In addition, white-sand forests are reputed to harbor many edaphic endemic plants (Ducke & Black, 1953; Anderson, 1981; Gentry, 1986). White-sand soils cover approximately 3% of the Amazon Basin and are most common in the Rio Negro Basin of Venezuela and Brazil as well as in the Guianas (ter Steege et al., 2000). However, small patches of white sand occur as far west as the Andes in Peru, contributing to the mosaic of heterogenous habitats found in the western Amazon (Tuomisto et al., 1995; Fine et al., 2005). Gentry (1981, 1986) hypothesized that edaphic specialization plays a major role in the overall extraordinarily high diversity of the Amazon Basin, and as one example he cited the low overlap in species composition between white-sand and other terra firme forest types near Iquitos, Peru.

Despite the attention white-sand forests have received in Peru as the cause célèbre for edaphic specialization, very few floristic studies of white-sand forests in Peru have been published, and all have been near Iquitos. For example, Gentry (1986) published only the species richness numbers from a comparison of three 0.1-ha white-sand transects with transects from other soil types. Most other studies have generally focused on one plant clade (Melastomataceae or Burseraceae or Pteridophyta) in the region and whether their species composition patterns correlate with many different environmental variables (including but not limited to white sand) (Tuomisto et al., 1995, 2003; Ruokolainen et al., 1997; Ruokolainen & Tuomisto, 1998; Tuomisto & Poulsen, 2000; Fine et al., 2005). Ruokolainen and Tuomisto (1998) inventoried all trees in three white-sand plots (ca. 0.1 ha) and published the plot data as an appendix. The most detailed published survey of white-sand plants from Peru was published by García-Villacorta et al. (2003), in which they attempted to classify different types of white-sand forest using species composition, canopy height, and soil drainage in the Allpahuayo-Mishana National Reserve near Iquitos.

Here, we present floristic data on seven geographically separated white-sand forests in Peru in order to extend available information on its white-sand flora. The objectives of the present contribution are to provide preliminary answers to the following questions: (1) How diverse are the white-sand forests of Peru? What are the most common species? Are Peruvian white-sand forests separated by hundreds of kilometers similar in composition to one another? (2) How much overlap in species composition is there between Peruvian white-sand and non-white-sand forest plots? How many white-sand species are endemic to white-sand forests? (3) How do Peruvian white-sand forests compare to other white-sand forests described from Colombia, Venezuela, Brazil, and the Guianas?

Methods

WHITE-SAND FOREST INVENTORIES

From 2001 to 2004, we conducted inventories of 16 white-sand (WS) forest plots in seven geographical locations in the state of Loreto, Peru (Table 1, Fig. 1). Because WS forests are structurally so much smaller than terra firme (TF) forests, it was necessary to modify standard sampling methods developed for TF forests to obtain representative samples of WS forests. Most inventories of TF rainforests in the past few decades have been conducted at the scale of 1 ha, with a minimum DBH cutoff of 10 cm. This protocol allows researchers to sample all of the reproductive trees of the midcanopy and canopy and most of the understory tree species. In WS forests, trees grow very slowly yet reach reproductive size with trunks smaller than 10 cm DBH (and in the extremely stunted forests, the great majority of individuals will never approach 10 cm DBH), thus a smaller cutoff is necessary to sample all reproductive adults. Another discrepancy is that some WS patches are smaller than 1 ha. To overcome these limitations, we sampled WS forests in two different ways, trying to sample comparable numbers of individuals as the TF plots. For varillales (García-Villacorta et al., 2003) (also known as caatinga forest [Anderson, 1981] or tall caatinga [Coomes & Grubb, 1996]), which consisted of forests with canopies at approximately 10–20 m ($N = 13$), 0.1-ha plots were used with DBH cutoffs of 5 cm to obtain a sample of approximately 300 individuals per plot. Three of the WS plots (WS 6, 10, and 15 in Fig. 1) were located in chamizal (or caatinga scrub [Anderson, 1981]) and consisted of stunted forest, with 99% of the trees less than 10 m tall and most around 5 m in height. To obtain a representative sample in these forests, we surveyed plots of 10 × 25 m (0.025 ha) and inventoried all stems larger than 2.5 cm DBH.

Representatives of all species encountered were collected at each site, and voucher specimens are deposited in the Field Museum of Natural History Herbarium in Chicago, Illinois (F), and the Herbario Amazonense (AMAZ) at the Universidad Nacional de la Amazonía Peruana in Iquitos, Peru (see Appendix 1

Table 1. The sites listed in Figure 1, with the plot codes for each site, the coordinates, habitat, and collectors.

Site	Plot code	Lat DD	Lon DD	Collectors[1]
Apayacu	TF 1	−3.11667	−72.71250	N. Pitman, I. Mesones, M. Ríos
Buenavista	TF 2	−4.83444	−72.39028	N. Pitman, R. García, H. Beltran, C. Vriesendorp
Curacinha	TF 3	−5.05139	−72.72833	N. Pitman, R. García, H. Beltran, C. Vriesendorp
Curaray	TF 4	−2.37869	−74.09147	N. Pitman, R. García, H. Mogollón, P. Nuñez
Ingano Llacta	TF 5	−1.86953	−74.66778	N. Pitman, R. García, H. Mogollón, P. Nuñez
Maronal	TF 6	−2.96564	−72.12786	N. Pitman, I. Mesones, M. Ríos
Nauta	TF 7	−4.44274	−73.61083	M. Ahuite, E. Valderrama
Orosa	TF 8	−3.62464	−72.24269	M. Ríos, N. Dávila
PV7.polvorin	TF 9	−0.88463	−75.21472	N. Pitman, R. García, H. Mogollón, P. Nuñez
PV7.terrace	TF 10	−0.87516	−75.20561	N. Pitman, R. García, H. Mogollón, P. Nuñez
Quebrado Blanco 1	TF 11	−4.35911	−73.15894	M. Ríos, N. Dávila
Quebrado Blanco 2	TF 12	−4.35928	−73.15728	M. Ríos, N. Dávila
Sabalillo	TF 13	−3.33533	−72.31111	E. Valderrama, M. Ahuite
San Jose	TF 14	−2.51064	−73.66072	M. Ríos, N. Dávila
Santa Maria	TF 15	−1.41603	−74.61650	N. Pitman, R. García, H. Mogollón, P. Nuñez
Santa Teresa	TF 16	−2.82572	−73.56350	M. Ríos, N. Dávila
Vencedores	TF 17	−1.13729	−75.01842	N. Pitman, R. García, H. Mogollón, P. Nuñez
Yaguas	TF 18	−2.86486	−71.41503	M. Ríos, N. Dávila
Allpahuayo-Mishana	WS 1	−3.95611	−73.42861	I. Mesones (P. Fine, R. García)
Allpahuayo-Mishana	WS 2	−3.95056	−73.40000	I. Mesones (P. Fine, R. García)
Allpahuayo-Mishana	WS 3	−3.94778	−73.41167	I. Mesones (P. Fine, R. García)
Allpahuayo-Mishana	WS 4	−3.94167	−73.43889	I. Mesones (P. Fine, R. García)
Upper Nanay (chamizal)	WS 5	−3.74083	−74.12222	P. Fine, I. Mesones (R. García)
Upper Nanay	WS 6	−3.74139	−74.13278	P. Fine, I. Mesones (R. García)
Jeberos	WS 7	−5.30000	−76.26667	P. Fine, I. Mesones (R. García)
Jenaro Herrera	WS 8	−4.85000	−73.60000	P. Fine, I. Mesones, R. García
Jenaro Herrera	WS 9	−4.85000	−73.60000	P. Fine, I. Mesones, R. García
Jenaro Herrera (chamizal)	WS 10	−4.85000	−73.60000	P. Fine, I. Mesones, R. García
Morona	WS 11	−4.26667	−77.23333	P. Fine, I. Mesones (R. García)
Morona	WS 12	−4.26667	−77.23333	P. Fine, I. Mesones (R. García)
Tamshiyacu	WS 13	−3.98333	−73.06667	P. Fine, I. Mesones (R. García)
Tamshiyacu	WS 14	−3.98333	−73.06667	P. Fine, I. Mesones (R. García)
Tamshiyacu (chamizal)	WS 15	−3.98333	−73.06667	P. Fine, I. Mesones (R. García)
Matsés	WS 16	−5.85500	−73.75400	P. Fine, N. Dávila, I. Mesones

[1] Persons in parentheses checked over the collected material, but were not present during field collection. All white-sand collections were ultimately determined by P. Fine, R. García, and I. Mesones, and all non-white-sand collections were ultimately determined by N. Pitman.

for collection numbers). Voucher specimens were identified by comparing them to specimens from the above two herbaria and the Missouri Botanical Garden (MO). A very few specimens were also identified at the New York Botanical Garden (NY). Specimens that were unable to be matched were left as "morphospecies" and are presented with their genus name and morphospecies number (or if genus is unknown, the family and morphospecies number; see Appendix 1).

COMPARING WS PLOTS TO OTHER TF PLOTS

Pitman and colleagues provided data for 18 plots from Loreto, Peru (Fig. 1, Table 1; Pitman et al., 2008). These plots are 1-ha tree inventories (10 cm DBH) of 18 TF sites, and none of them sample WS forests. Although still a work in progress, these plots allow for a reasonable comparison of species overlap between WS and other non-WS TF soil types. These TF plots contained 1750 species and morphospecies out of 10,867 individuals and averaged 251.7 species per plot.

Two similarity matrices were constructed to compare the 34 plots. The first, $\beta_{sim} = a'_i / a'_i + \min(b'_i, c'_i)$, where a' is the number of species in common between two plots, b' is the species only in the neighboring plot, c' is the species only in the focal plot, and min means one chooses the smaller of the two numbers in parentheses (Lennon et al., 2001). This equation includes only the presence/absence

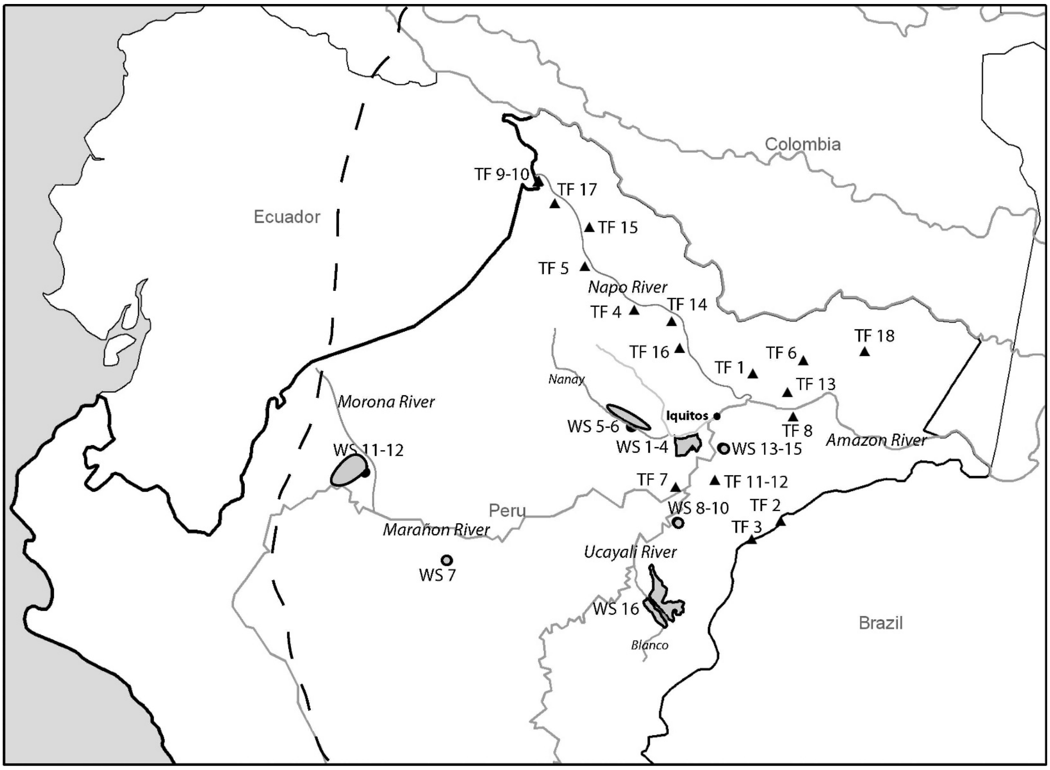

Figure 1. A map showing the locations of the white-sand plots (gray shapes, labeled WS 1 to 16) and the terra firme plots (triangles, labeled TF 1 to 18) in northeastern Peru. Rivers are labeled in italics. Dashed line approximates the limit of the Amazonian lowlands (less than 500 m above sea level). White-sand areas depicted on this map are all of those known in the Department of Loreto, Peru, and are drawn to approximate their extent on the landscape (modified from Vriesendorp et al., 2006), with the exception of WS 1 to 4, which details the boundaries of the Allpahuayo-Mishana National Reserve (of which approximately 25% of its area is covered by white-sand forests). See Table 1 for names and coordinates of all plots.

data and is a modified Sorenson's index that takes into account the differences in diversity between plots with the aim to decrease the influence that any local species richness has on dissimilarity. The second index that we used is the Steinhaus similarity index. It is calculated as: between plots A and B $= 2\ \Sigma\ \min (n^A, n^B) / \Sigma\ (n^A + n^B)$ where one chooses the smaller number of overlapping individuals between plot A and B, doubles that number, and divides by the total number of individuals in the two plots (Potts et al., 2002). Because WS plots are generally composed of a small number of fairly dominant species relative to TF plots, the Steinhaus index is likely to more accurately reflect similarity and differences between all of the plots, especially if the same species dominate different WS plots.

To compare WS plots to each other and to the non-WS plots, we collated all plot lists into a single data file. Both the second and third authors have collected specimens in the field and identified specimens from both databases in the herbarium (see Table 1), and thus it is highly unlikely that more than a very few TF morphospecies are the same as "named" WS species or WS morphospecies.

To quantify the spatial component of beta diversity, we tested whether sites that were closer together in space were more similar in terms of their species composition using Mantel tests (Mantel, 1967). We calculated the geographical distance between all sites and tested whether the two measures of species compositional dissimilarity mentioned above were correlated with the spatial distances separating sites. The Mantel test compares the observed correlation between these measures of dissimilarity with a null model based on randomization of dissimilarities among sites. We used 999 randomizations for each test. A significant result indicates that the two distance measures are more correlated than expected by chance. Both β_{sim} and the Steinhaus index were converted to their dissimilarity form for these analyses (Legendre & Legendre, 1998). These analyses were repeated for all sites and separately for WS and TF plots.

Nonmetric multidimensional scaling (NMS) ordinations were used to visualize the overall similarity in

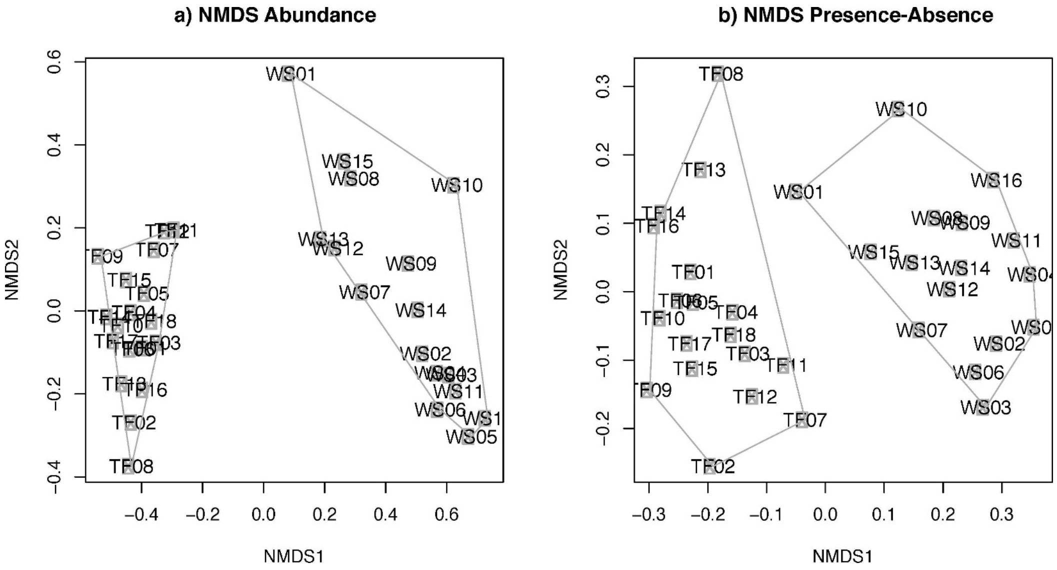

Figure 2. Nonmetric multidimensional scaling (NMDS) ordinations for (A) dissimilarity as measured by the species abundance data (Steinhaus) and (B) dissimilarity as measured by the species presence/absence data (β_{sim}). In both panels, WS and TF plots group into two distinct clusters.

species composition among all sites. We performed NMS ordinations separately on each of the two intersite dissimilarity matrices (β_{sim} and the Steinhaus index) using the vegan package (Oksanen et al., 2007) in the R statistical computing language (R Development Core Team, 2008). Both ordinations converged on a stable two-dimensional solution within 100 iterations. We also conducted a multi-response permutation procedure (MRPP) test to determine whether species composition differed more among habitat types than expected by chance (Mielke & Berry, 2001). The MRPP test compares the ratio of within- and among-habitat similarity to the ratio expected under a null model of 999 randomizations of site assignments to habitats.

RESULTS

DIVERSITY AND ABUNDANCE OF INDIVIDUALS IN WS FORESTS

We encountered 3631 individual trees in the 16 WS plots and separated them into 221 species and morphospecies (Appendix 1). The 13 varillal plots contained an average of 222 individuals from 41.5 species (range, 26 to 71). The three chamizal plots contained an average of 248 individuals from 14.3 species (range, 9 to 22). Even though chamizal plots were structurally very different in appearance than varillal plots, with canopies less than half the height of varillal plots, chamizal plots were not compositionally distinct from varillal plots, and the chamizal plots did not cluster together in either ordination (Fig. 2). One clear example of close similarity of a varillal and a chamizal plot was at the Upper Nanay site, where all but one of the 12 species encountered in the chamizal plot was also present in the nearby varillal plot.

The most common species overall was *Pachira brevipes* (A. Robyns) W. S. Alverson (Malvaceae), accounting for 606 individuals, an incredible 17% of all stems encountered. The top 10 species in the WS plots were all very common, accounting for more than 49% of the total individuals. Clusiaceae was the most important family in the WS plots; 890 individuals (24.5% of total) from seven species were encountered (Table 2). When considering the top 10 most common species from each of the seven sites, 17 of these occur in more than one site, and eight of them occur three times on the top 10 lists in different WS sites (Table 3).

SIMILARITY COMPARISONS WITHIN AND AMONG WS AND TF PLOTS

Measures of similarity between a given WS plot and another WS plot averaged close to 20%—whether measured by presence/absence or by species-abundance statistics, very similar to the average similarity measures between a given TF plot and another TF plot (Table 4). Yet, similarity between any given WS and TF plot averaged at 9% with presence/absence and 2% with abundance data (Table 4). The NMS ordinations clearly separated WS and TF plots into two distinct groups in terms of their species

Table 2. The top 12 families in importance in the 16 white-sand plots, the number of species in each family, the number of individuals encountered, and the percentage of the total stems overall.

Family[1]	No. of species	No. of individuals	% of total individuals
Clusiaceae (CVB)	7	890	24.5
Malvaceae (s.l.) (CV)	3	613	16.9
Fabaceae (CVB)	30	484	13.3
Arecaceae (CV)	7	175	4.8
Sapotaceae (CVB)	13	168	4.6
Rubiaceae (B)	13	162	4.4
Sapindaceae	5	139	3.8
Elaeocarpaceae (C)	4	135	3.7
Annonaceae	14	87	2.4
Myrtaceae (VB)	11	82	2.3
Euphorbiaceae (CVB)	7	78	2.1
Lauraceae (CV)	18	66	1.8
All others (35)	88	571	15.7

[1] C, V, and B in parentheses indicate whether the family was on a list of top 12 families in white-sand forest in Colombia (C), Venezuela (V), or the top six in Brazil (B) (Caquetá, Colombia, Duivenvoorden et al., 2001; La Esmerelda, Venezuela, Coomes & Grubb, 1996; Manaus, Brazil, Anderson, 1981).

composition, regardless of the index used to measure similarity among sites (β_{sim} and Steinhaus index) (Fig. 2), a result further supported by the highly significant differences in species composition among habitats detected by the MRPP tests (β_{sim}: $A = 0.06989$, $P < 0.0001$; Steinhaus: $A = 0.08853$, $P < 0.0001$).

PATTERNS OF ENDEMISM IN WS FORESTS

Of the 221 species in the WS data set, 141 do not occur in the TF data set (64%) and 80 of them (36%) do. However, it would be premature to label all of the species that do not occur in the TF data set as WS endemics, since the 18 TF plots are likely such a poor sample of all of the non-WS habitats in the western Amazon. Therefore, we compared our WS list to the published Ecuadorian flora (*Catalogue of the Vascular Plants of Ecuador*, Jørgensen & Léon-Yánez, 1999). WS forests had never been reported in Ecuador at the time of publication of this flora (a few WS areas in Ecuador have been found near the Peruvian border in the Cordillera del Condor in the past few years; D. Neill, pers. comm.), thus if a species from our WS list appears in the *Catalogue of Ecuador*, it should not be considered a WS endemic. We found 81 of the 221 WS species also occurred in Ecuador (36%). Defined in this way, the number of WS endemics (species that do not occur in either the TF data set or the *Catalogue of Ecuador*) becomes 114 species (52% of the total).

There are an additional 21 species that we propose should be classified as "facultative specialists" or "cryptic endemics." Eleven of these 21 are species that also do not occur in the *Catalogue of Ecuador* and occur more commonly in WS than in TF plots and also are found in fewer than four total plots in TF. We speculate that this group of species has source populations in WS forests and sink populations in TF forests. The other 10 species occur in multiple WS plots, are represented by more than 10 individuals in the WS data set, are represented by one or zero individuals in the TF data set, and also occur in the *Catalogue of Ecuador*. We speculate that this group of species may include cryptic species or are otherwise genetically distinct from populations that occur in Ecuador. Three of these species (discussed below) are listed in the *Catalogue of Ecuador* but according to its text do not occur in the Amazon Basin, and thus the taxa found in our WS data set are likely to be new species. Taken together, the WS endemics and "facultative specialists" account for 135 of the 221 species (61%) found in the WS plots, and 3110 individuals (83% of the total).

Spatial distance was correlated with species compositional similarity with both the presence/absence and abundance data when all plots were analyzed with Mantel tests (β_{sim}: 73.8% of variation in original data explained by NMDS, $P < 0.001$; Steinhaus: 71.4% of variation in original data explained by NMDS, $P < 0.001$). This is not surprising, given that in general, WS and TF plots were not evenly distributed throughout the region, and indeed many of the plots of the same soil type were located within a few hundred meters of one another (Fig. 1). When correlating just the TF plots with spatial distance, Mantel tests using both the presence/absence and abundance data yielded significant correlations ($P < 0.015$ and 0.006, respectively). However, Mantel tests of the WS plots with spatial distance were only significant when using the abundance data ($P < 0.023$). The Mantel test within WS plots using the presence/absence data was not significant, indicating no correlation between species composition similarity and spatial distance.

DISCUSSION

PATTERNS OF DIVERSITY IN WS FORESTS

WS plots in Peru contain a low species diversity compared to other TF forest plots. We found only 221 species out of 3631 individuals occurring in the WS plots. Moreover, our average plot diversity was 36.4

species per plot, an extremely low number for lowland Amazonia. For comparison, Gentry's plots from Loreto (the same area as Fig. 1) were also 0.1 ha (but included all stems greater than 2.5 DBH as well as shrubs); these plots contained an average of 172.7 species (range, 114 to 210 species) (Gentry, 1988; Phillips & Miller, 2002).

Low diversity for WS plots has been reported in eastern and central Amazonia, with Anderson (1981) estimating 25 species at 10 cm DBH per hectare near Manaus, Brazil. In Venezuela, a 0.1-ha transect of WS forest had 35 species of 5 cm DBH (same DBH cutoff and plot size as our study) (Coomes & Grubb, 1996). In Guyana, 62 species per hectare of 10 cm DBH trees has been reported (ter Steege et al., 2000). Previous reports from near Iquitos claimed plot-level diversity totals of more than 100 species for WS forest plots (Gentry, 1986; Ruokolainen & Tuomisto, 1998; Phillips & Miller, 2002). We believe that this discrepancy results from their plots covering more than one type of soil, as Gentry (1986) used narrow 500-m belt transects, and Ruokolainen and Tuomisto (1998) report percent sand in their soil analyses at only 80% from their "white-sand" plots near Iquitos, and their species list lacks many of the dominant species from our WS data set. Preliminary soil texture data from our WS plots indicate consistent values of $> 95\%$ sand (Fine, unpublished data).

DOMINANCE PATTERNS IN PERUVIAN AMAZONIA

WS plots in Peru often have substantial overlap in species composition (Table 3), and this pattern holds whether one compares adjacent plots in the same WS forest, or WS forests as far apart as Jeberos and Allpahuayo-Mishana (Figs. 1, 2). Moreover, out of the 40 species that appear on the 10 most common species list for each of the seven sites, 17 of them occur more than once, and eight of them occur three times on the top 10 lists in different WS sites (Table 3). These 17 species dominate the WS forest plots, accounting for an amazing 62.4% of all individuals (Table 3). WS plots are thus dominated by a cadre of species, and this dominance is likely the main factor driving the pattern of low plot-level diversity.

Pitman et al. (2001) found a remarkable similarity of species composition between Yasuní and Manu, forests more than 2000 km apart. There were 42 species that were common in both forests (stem densities of over one individual per hectare). He extrapolated this pattern as evidence that forests found on fertile clay soils throughout the western Amazon were predictable and dominated by an oligarchy of relatively common species. Pitman et al. (2001) further predicted that the oligarchic taxa from western Amazonian clay forests would not be common in forests of other soil types (indeed, only two of the most common 42 species from Yasuní and Manu even occur in our WS data set), and they concluded that: "… the oligarchic taxa will vary from region to region, and in cases of environmental heterogeneity from patch to patch, but the patches themselves may be largely homogeneous in composition and structure." In many ways, the WS data match Pitman et al.'s expectation: WS forests have similar species composition across Peru, and each WS patch harbors low diversity forests dominated by a small number of species. Yet the WS oligarchy differs in one important respect from the patterns reported in western Amazonian clay forests (Pitman et al., 2001). Unlike clay forest plots, the common species in WS plots are not as predictable from site to site. For example, only one species, *Pachira brevipes*, was collected at all seven WS sites. In many of these sites, *P. brevipes* was the most common tree, or at least in the top 10 most common (Table 3), but in some sites, it was collected only a few times. Of the 17 species highlighted in Table 3, 13 occur in both the western and eastern WS sites (Fig. 1) and four occur only in eastern sites.

The results of the Mantel tests indicate significant patterns of correlation between spatial distance and species abundance data, yet no significant pattern with spatial distance and compositional similarity with the species presence/absence data. In other words, dominant species in one plot were more likely to be dominant in nearby WS plots, while the overall species composition among all of the WS plots had no spatial correlation. This lack of spatial correlation is consistent with the idea that WS flora may be largely composed of species that are wind or bird dispersed, with wide-ranging dispersal capabilities (Macedo & Prance, 1978, but see ter Steege et al., 2006). Moreover, that many of the common species do not occur in every WS site is likely due to the island-like nature of WS forests in Peru. In contrast to the clay soils that are found at Manu, Yasuní, and the intervening lowland forests near the Andean foothills between these two sites, WS soils are rare in the western Amazon and are scattered across the region in noncontiguous patches (Fig. 1). Even though many of the WS-dominant species are good dispersers (and indeed 13/17 of them have arrived in both western and eastern WS patches), not all of them have had the good fortune to arrive at all sites. In addition, given that many of these habitat islands are small, those species that have arrived later may have a difficult time gaining a foothold. WS forests are different than TF forests in the fact that one often finds large patches composed of a single species (Fine, pers. obs.), a

Table 3. The top 10 species for each of the seven white-sand forest locations shown in Figure 1. Species in boldface occur in the top 10 list for more than one site.

Morona, WS 11 to 12		
Arecaceae	***Euterpe catinga***	**41**
Fabaceae	***Tachigali paniculata***	**35**
Siparunaceae	***Siparuna guianensis***	**28**
Sapotaceae	***Chrysophyllum sanguinolentum*** **subsp.** ***sanguinolentum***	**17**
Fabaceae	***Macrolobium microcalyx***	**17**
Sapindaceae	***Matayba inelegans***	**16**
Myristicaceae	*Virola calophylla*	12
Humiriaceae	*Sacoglottis ceratocarpa*	12
Annonaceae	*Oxandra asbeckii*	9
Euphorbiaceae	***Hevea guianensis***	**9**
Jeberos, WS 7		
Fabaceae	***Parkia igneiflora***	**31**
Icacinaceae	*Emmotum floribundum*	26
Sapotaceae	***Chrysophyllum sanguinolentum*** **subsp.** ***sanguinolentum***	**25**
Apocynaceae	*Macoubea sprucei*	16
Aquifoliaceae	***Ilex*** **sp. indet., cf.** ***nayana***	**14**
Euphorbiaceae	***Hevea guianensis***	**14**
Sapindaceae	***Matayba inelegans***	**14**
Clusiaceae	***Tovomita calophyllophylla***	**13**
Sapotaceae	*Pouteria lucumifolia*	11
Sapotaceae	*Pouteria cuspidata* subsp. *cuspidata*	11
Jenaro Herrera, WS 8 to 10		
Clusiaceae	***Caraipa tereticaulis***	**164**
Clusiaceae	***Haploclathra cordata***	**77**
Clusiaceae	*Calophyllum brasiliense*	70
Myrtaceae	*Marlierea caudata*	26
Rubiaceae	***Platycarpum orinocense***	**26**
Burseraceae	*Protium subserratum*	25
Annonaceae	*Bocageopsis canescens*	25
Sapindaceae	***Cupania diphylla***	**19**
Siparunaceae	***Siparuna guianensis***	**19**
Clusiaceae	***Tovomita calophyllophylla***	**17**
Tamshiyacu, WS 13 to 15		
Clusiaceae	***Caraipa utilis***	**209**
Clusiaceae	***Haploclathra cordata***	**125**
Malvaceae	***Pachira brevipes***	**92**
Clusiaceae	***Caraipa tereticaulis***	**33**
Sapindaceae	***Matayba inelegans***	**21**
Rubiaceae	***Platycarpum orinocense***	**21**
Fabaceae	***Tachigali paniculata***	**11**
Clusiaceae	***Tovomita calophyllophylla***	**11**
Fabaceae	*Macrolobium* sp. indet. B	11
Elaeocarpaceae	***Sloanea*** **sp. indet., cf.** ***robusta***	**11**
Upper Nanay, WS 5 to 6		
Malvaceae	***Pachira brevipes***	**96**
Clusiaceae	***Caraipa utilis***	**73**
Elaeocarpaceae	***Sloanea*** **sp. indet., cf.** ***robusta***	**68**
Fabaceae	***Dicymbe uaiparuensis***	**58**
Sapindaceae	***Cupania diphylla***	**37**
Rubiaceae	*Ferdinandusa chlorantha*	23
Arecaceae	*Mauritiella armata*	17
Fabaceae	***Macrolobium microcalyx***	**13**
Araliaceae	*Dendropanax palustris*	12
Fabaceae	*Dimorphandra macrostachya* subsp. *glabrifolia*	12

Table 3. Continued.

Allpahuayo-Mishana, WS 1 to 4		
Malvaceae	***Pachira brevipes***	**271**
Clusiaceae	***Caraipa utilis***	**53**
Fabaceae	***Dicymbe uaiparuensis***	**48**
Araliaceae	*Dendropanax umbellatus*	30
Arecaceae	***Euterpe catinga***	**26**
Fabaceae	*Tachigali ptychophysca*	22
Sapotaceae	***Chrysophyllum sanguinolentum*** **subsp.** ***sanguinolentum***	**22**
Fabaceae	***Parkia igneiflora***	**21**
Elaeocarpaceae	***Sloanea*** **sp. indet., cf.** ***robusta***	**20**
Rubiaceae	*Pagamea guianensis*	17
Matsés, WS 16		
Malvaceae	***Pachira brevipes***	**131**
Arecaceae	***Euterpe catinga***	**50**
Burseraceae	*Protium heptaphyllum* subsp. *ulei*	18
Rubiaceae	***Platycarpum orinocense***	**15**
Malphigiaceae	*Byrsonima laevigata*	14
Elaeocarpaceae	***Sloanea*** **sp. indet., cf.** ***robusta***	**13**
Chrysobalanaceae	*Licania* sp. indet. A	12
Aquifoliaceae	***Ilex*** **sp. indet., cf.** ***nayana***	**8**
Three tied at 6		

pattern at odds with the high-diversity TF forests that exhibit density-dependent spatial patterns (Wills et al., 2006). In TF forests, common species that occur at high densities are thought to suffer disproportionately high attacks from natural enemies, giving rare species an advantage. WS forests have lower rates of herbivory than TF forests near Iquitos (Fine et al., 2006). Thus, unlike TF forests, rare species (including recent arrivals) may not gain any such advantage in WS forests, and thus potential oligarchs may not be able to quickly increase their local abundance in new WS sites, even if they do happen to get dispersed there.

OVERLAP IN SPECIES COMPOSITION BETWEEN WS AND NON-WS FOREST PLOTS

WS and TF plots are distinctive from one another. This is reflected in the fact that there are local names for WS forests in every Amazonian country in which they are found (Anderson, 1981). But, how distinctive are they? This question has no clear answer because, as far as we know, no one has formalized a standard vocabulary or statistical methods for rigorously defining similarity between communities of different species compositions (Koleff et al., 2003; Jost, 2007). The amount of similarity between the WS and TF plots that we report depends on which index we use to estimate it. Most WS-TF comparisons so far have used the Jaccard index and have reported similarities of 0.10 to 0.20 (Ruokolainen & Tuomisto, 1998; Duivenvoorden et al., 2001).

Table 4. Average similarity between plots of a similar soil type and plots of divergent soil types using both presence/absence (β_{sim}) and species abundance (Steinhaus) statistics.

Comparisons	Presence/Absence	Species abundance
WS-WS	0.23	0.16
TF-TF	0.20	0.19
WS-TF	0.09*	0.02*

* Asterisks indicate significant differences with $P < 0.0001$ with multi-response permutation procedure tests.

Tuomisto et al. (1995) suggest that the Peruvian Amazon is composed of more than 100 different "biotopes," each harboring unique plant species compositions that closely track environmental variables. If the biotope model properly depicts Amazonian forest diversity patterns, one would predict that each plot would have low overlap in species composition, and that different suites of species would dominate each plot. While we find that WS plots are indeed quite different from one another (Fig. 2), the dominant species at the seven sites were composed of a suite of 17 species that were found across many WS sites (Table 3). We should also emphasize that our plots were chosen to include all of the different kinds of WS forest, including both varillales and chamizales, well-drained and poorly drained areas, etc. (cf. García-Villacorta et al., 2003). Our results, together with the results of Pitman et al. (2001), thus paint a much broader picture of western Amazonian tree habitats. WS forest, heralded as the most distinctive TF forest type in the Amazon (Anderson, 1981;

Gentry, 1986), still contains a substantial number of species that also occur in more fertile soils. Therefore, we conclude that although WS forests are certainly "distinctive" from forests on more fertile soils, they are distinctive because of their low diversity and the composition of their dominant species rather than just because of their overall species compositions.

PATTERNS OF ENDEMISM IN WS FORESTS

Our preliminary conclusion is that a little more than half of the 221 species are WS endemics. These 114 species do not occur in the TF plots nor do they occur in the *Catalogue of Ecuador*. We believe that this is a fair estimate, although it does include 33 morphospecies that may or may not be new species (Appendix 1). Some of these morphospecies may be species for which we did not find a match in the herbarium but are distributed in lowland Amazonia in TF forests, but not where Pitman and colleagues set up plots (Fig. 1). Yet many of these 33 morphospecies are likely to be new species. It is important to stress how few plant collections have been made in any WS forests in Peru, especially in WS forests distant from Iquitos. For example, three of the dominant Clusiaceae species in our WS plots were described only within the past two decades (Vásquez, 1991, 1993; García-Villacorta & Hammel, 2004). One of the collections from our inventories in Jeberos yielded a new genus for Peru (*Hortia* Vand., Rutaceae) (Brako & Zarucchi, 1993).

In addition, there could be quite a few cryptic species that are hidden in the data set, artificially inflating the overlap between forest types. In a study of the match between taxonomic criteria and molecular sequence divergence in the genus *Inga* Mill. (Fabaceae), Dexter et al. (2010) found several morphologically similar but molecularly divergent taxa that had previously been lumped together, after which further study yielded other morphological but previously overlooked characters, resulting in the discovery of new cryptic *Inga* species. Along these lines, there are three species on our list that we suggest should be investigated for cryptic diversity and whose clades should be subjected to a molecular phylogenetic analysis: *Ferdinandusa chlorantha* (Wedd.) Standl. (Rubiaceae), *Euterpe catinga* Wallace (Arecaceae), and *Dendropanax umbellatus* (Ruiz & Pav.) Decne. & Planch. (Araliaceae). The latter two species are potential WS endemics that did not occur in any TF plots, and the former occurred in one TF plot (two individuals). What is most intriguing about these three species is that the *Catalogue of Ecuador* reports them as being absent from Amazonian lowland forests. *Ferdinandusa chlorantha* and *E. catinga* are reported only from high elevations in the Andes (1000–1500 m), while *D. umbellatus* is reported to occur on the Pacific coast, on the other side of the Andes.

COMPARING PERUVIAN WS FORESTS TO THOSE IN EASTERN AMAZONIA

Ten out of the 12 most common families from Peruvian WS forests appear in lists of the most important families in WS forests farther east from published sources in Colombia, Brazil, and Venezuela (Table 2). One family in particular, the Clusiaceae, dominates WS forests throughout the Amazon. Unlike the Fabaceae, which dominates everywhere in Amazonia (Gentry, 1988), the Clusiaceae family does not appear in the top 12 families for Peruvian non-WS plots, suggesting that there is something about WS substrate that encourages high populations of Clusiaceae trees.

To be able to examine the similarity of Peruvian WS plots to WS plots in eastern and central Amazonia and the Guianas, one needs to compare complete species lists, but as far as we know, there is not a single published account of any plot-level species list of WS forests in eastern Amazonia or the Guianas. There is a published checklist of the plants of the Guianas (including Guyana, Suriname, and French Guiana) (Boggan et al., 1997) as well as a comparison of three florulas within Guyana with central French Guiana and the Reserva Ducke of Manaus, Brazil (Clarke et al., 2001). Although the checklist of Boggan et al. (1997) does not list edaphic associations of its species, it is interesting to note that 78 (35%) of the species in our WS lists occur in this checklist, almost as many species that occur in the *Catalogue of Ecuador* (81 species, 36% of the total), even though the Guianas are more than 2000 km from Peru. Thirty-one of these 78 species are classified as WS endemics or facultative specialists here. One assumes that many of these species occur in sandy soil habitats in the Guianas, but this assumption will have to be tested with future inventory work. In addition, most of our herbarium comparisons were undertaken at F and MO, which have extensive western Amazonian tree collections, but do not have nearly as many collections from WS forest areas in central and eastern Amazonia. It is entirely possible that many WS species (and likely also some of the unnamed morphospecies) are shared between Peruvian WS forests and WS forests farther east. Indeed, species from our WS list like *Mauritia carana* Wallace (Arecaceae) have been reported from WS forests in Colombia, Brazil, and Venezuela (Anderson, 1981; Coomes & Grubb, 1996; Duivenvoorden et al., 2001). On the other hand, even within the Rio Negro, WS forests have been reported to be compositionally extremely dissimilar (Anderson, 1981). Thus, the characterization of the South American WS flora remains an avenue of exciting future research.

CONSERVATION OF AMAZONIAN FORESTS: THE FOCUS OF FUTURE BOTANICAL RESEARCH EFFORTS

Articles reporting the results of current botanical research in the Amazon often conclude by recommending that investigators increase the number of tree inventories (ter Steege et al., 2003). While accumulating more data on uncollected regions is certainly a laudable goal, more attention needs to be paid to understanding the diversity of tree plots that have already been inventoried. Too many of these trees languish as unidentified morphospecies, or just as tragic, dubiously named species from genera and families with no current taxonomic specialist (i.e., Nyctaginaceae). How can we compare vast networks of plots across an entire continent when we have little idea of the identities of the tree species?

Are similar-appearing species cryptic habitat specialists or local endemics? Or are some morphologically distinct taxa exhibiting phenotypic plasticity? These last questions can only be answered with systematic monographs coupled with molecular phylogenetic and population genetic studies, yet only a handful of tropical tree groups are currently the focus of any active research program in any laboratory. To solve this problem, we believe that research on the systematics and floristics of Amazonian plants ought to receive a very high priority for funding.

CONSERVATION IMPORTANCE OF WS FORESTS

Despite being species-poor, we believe WS forests should be given high conservation priority. First, the species recorded in WS forests are often edaphic and geographic endemics, found nowhere else in the world. In the past 20 years, biologists working in WS forests near Iquitos have discovered many animal and plant species new to science (Vásquez, 1991, 1993; Alvarez & Whitney, 2003; García-Villacorta & Hammel, 2004). These species have not been registered outside of WS forests, and many are only found in Peru. Using the current data set as a point of comparison, we compared our species list to a published comparative checklist of various florulas including three areas from Guyana and one from Brazil (the Ducke Reserve near Manaus), which all included WS forest habitats (Clarke et al., 2001). Of the 135 species that we classified in this study as WS endemics, cryptic endemics, and facultative WS specialists, 41 do not occur in this checklist, and thus may be restricted to only western Amazonian WS areas, underscoring their rarity. Moreover, in Peru, WS habitats are even less common in the landscape than they are farther east in South America. Currently, there are only nine known patches of WS forest in the lowland Peruvian Amazon, representing less than 1% of lowland Peruvian rainforest (Fig. 1). These nine WS patches are isolated from one another and similar habitats in Colombia, Venezuela, and Brazil, and this scattered distribution likely reinforces not only the endemism but also the vulnerability of Peru's WS flora and fauna. For example, fewer than 25 individuals are known of the newly described gnatcatcher *Polioptila clementsi* and all occur in two WS forest patches in and near the Reserva Nacional Allpahuayo-Mishana (Whitney & Alvarez, 2005). At present, only two areas in Peru that harbor WS forests enjoy any legal conservation status, the Reserva Nacional Allpahuayo-Mishana (58,069 ha) and the Reserva Nacional Matsés (420,635 ha) (Vriensendorp et al., 2006).

Finally, WS forests are extremely fragile. These soils have some of the lowest nutrient availabilities recorded anywhere, mineral nutrients reside within living organisms, and roots and fungi quickly capture any decomposing nutrients. If the trees are cleared in a WS forest, nutrients leach rapidly through the sand, and the soil fertility quickly degrades. Using these forests for extractive or agricultural activity is counterproductive economically, because more resources are expended in clearing the forests than could ever be recuperated from agricultural or logging enterprises.

CONCLUSIONS

We now have a preliminary database with which we can describe the tree flora of the Peruvian WS forests. WS forests are different from other Amazonian forests on TF, mostly due to their very low plot-level diversity and dominance by a set of 17 species that account for a majority of all individuals. We expected the WS flora to be composed of mostly WS specialists because WS is so extremely nutrient poor relative to all other TF soils in the Amazon. On one hand, our prediction was fulfilled, as most individuals encountered in WS plots belong to species that are endemic to WS forests, or at least much more common in WS plots than TF plots ("facultative WS specialists"). On the other hand, it was surprising that so many different species of trees common in other more fertile soil types were encountered in the WS plots. While their numbers could possibly be inflated due to cryptic diversity, it seems fair to estimate that almost half of the total number of species that we encountered in all WS plots were due to species more common on other soil types. We speculate that many species possess traits that allow for survival in WS soil, but very few species possess traits that allow them to become dominant, for example, traits that promote long-term growth or performance in nutrient-starved soils including leaf longevity, nutrient use efficiency, high levels of defense against natural enemies (Fine et al., 2004, 2006), and for lineages like *Dicymbe* Spruce ex Benth. (Fabaceae) among others, association with ectomycorrhyzae (Singer & Araujo, 1979; McGuire, 2007). This phenomenon results in the pattern that we find of extremely low overlap in species composition between TF and WS plots of species that are common in WS, along with substantial overlap between TF and WS plots of species that are rare in WS plots but present in TF plots.

Literature Cited

Alvarez, J. & B. Whitney. 2003. New distributional records of birds from white-sand forests of the northern Peruvian Amazon, with implications for biogeography of northern South America. Condor 105: 552–566.

Anderson, A. 1981. White-sand vegetation of Brazilian Amazonia. Biotropica 13: 199–210.

Boggan, J., V. Funk, C. Kelloff, M. Hoff, G. Cremers & C. Feuillet. 1997. Checklist of the Plants of the Guianas (Guyana, Surinam, French Guiana). Biological Diversity of the Guianas Program, Smithsonian Institution, Washington, D.C.

Brako, L. & J. L. Zarucchi. 1993. Catalogue of the Flowering Plants and Gymnosperms of Peru. Monogr. Syst. Bot. Missouri Bot. Gard. 45.

Clarke, H. D., V. A. Funk & T. Hollowell. 2001. Using checklists and collecting data to investigate plant diversity: A comparative checklist of the plant diversity of the Iwokrama forest, Guyana. Sida, Bot. Misc. 21: 1–86.

Coomes, D. A. & P. J. Grubb. 1996. Amazonian caatinga and related communities at La Esmeralda, Venezuela: Forest structure, physiognomy and floristics, and control by soil factors. Vegetatio 122: 167–191.

Dexter, K. G., T. D. Pennington & C. W. Cunningham. 2010. Using DNA to assess errors in tropical tree identifications: How often are ecologists wrong and does it matter? Ecol. Monogr. 80(2): 267–286.

Ducke, A. & G. A. Black. 1953. Phytogeographic notes on the Brazilian Amazon. Anais Acad. Brasil. Ci. 25: 1–46.

Duivenvoorden, J. F., H. Balslev, J. Cavelier, C. Grandez, H. Tuomisto & R. Valencia. 2001. Evaluación de recursos vegetales no maderables en la Amazonía noroccidental. IBED, Universiteit van Amsterdam, Amsterdam.

Fine, P. V. A., I. Mesones & P. D. Coley. 2004. Herbivores promote habitat specialization by trees in Amazonian forests. Science 305: 663–665.

———, D. C. Daly, G. Villa, I. Mesones & K. M. Cameron. 2005. The contribution of edaphic heterogeneity to the evolution and diversity of Burseraceae trees in the western Amazon. Evolution 59: 1464–1478.

———, Z. J. Miller, I. Mesones, S. Irazuzta, H. M. Appel, M. H. H. Stevens, I. Saaksjarvi, J. C. Schultz & P. D. Coley. 2006. The growth-defense trade-off and habitat specialization by plants in Amazonian forests. Ecology 87: S150–S162.

García-Villacorta, R., M. Ahuite & M. Olórtegui. 2003. Clasificación de bosques sobre arena blanca de la zona reservada Allpahuayo-Mishana. Folia Amazónica 14: 11–31.

——— & B. E. Hammel. 2004. A noteworthy new species of *Tovomita* (Clusiaceae) from Amazonian white-sand forests of Peru and Colombia. Brittonia 56: 132–135.

Gentry, A. H. 1981. Distributional patterns and an additional species of the *Passiflora vitifolia* complex: Amazonian species diversity due to edaphically differentiated communities. Pl. Syst. Evol. 137: 95–105.

———. 1986. Endemism in tropical versus temperate plant communities. Pp. 153–181 *in* M. E. Soulé (editor), Conservation Biology: The Science of Scarcity and Diversity. Sinauer Associates, Sunderland, Massachusetts.

———. 1988. Patterns of plant community diversity and floristic composition on environmental and geographical gradients. Ann. Missouri Bot. Gard. 75: 1–34.

Jørgensen, P. & S. Léon-Yánez (editors). 1999. Catalogue of the Vascular Plants of Ecuador. Monogr. Syst. Bot. Missouri Bot. Gard. 75.

Jost, L. 2007. Partitioning diversity into independent alpha and beta components. Ecology 88: 2427–2439.

Koleff, P., K. J. Gaston & J. J. Lennon. 2003. Measuring beta diversity for presence-absence data. J. Anim. Ecol. 72: 367–382.

Legendre, P. & L. Legendre. 1998. Numerical Ecology, 2nd ed. (English). Elsevier, Amsterdam.

Lennon, J. J., P. Koleff, J. Greenwood & K. J. Gaston. 2001. The geographical structure of British bird distributions: Diversity, spatial turnover and scale. J. Anim. Ecol. 70: 966–979.

Macedo, M. & G. T. Prance. 1978. Notes on the vegetation of Amazonia II. The dispersal of plants in Amazonian white sand campinas: The campinas as functional islands. Brittonia 30: 203–215.

Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. Cancer Res. 27: 209–220.

McGuire, K. L. 2007. Common ectomycorrhizal networks may maintain monodominance in a tropical rain forest. Ecology 88: 567–574.

Medina, E. & E. Cuevas. 1989. Patterns of nutrient accumulation and release in Amazonian forests of the upper Rio Negro basin. Pp. 217–240 *in* J. Proctor (editor), Mineral Nutrients in Tropical Forest and Savanna Ecosystems. Blackwell Scientific, Oxford.

Mielke Jr., P. W. & K. J. Berry. 2001. Permutation Methods: A Distance Function Approach. Springer-Verlag, New York.

Oksanen, J., R. Kindt, P. Legendre, B. O'Hara & M. H. H. Stevens. 2007. vegan: Community Ecology Package. R package version 1.88. <http://vegan.r-forge.r-project.org/>, accessed 11 May 2010.

Phillips, O. & J. S. Miller. 2002. Global Patterns of Plant Diversity: Alwyn H. Gentry's Forest Transect Data Set. Monogr. Syst. Bot. Missouri Bot. Gard. 89.

Pitman, N. C. A., H. Mogollón, N. Dávila, M. Ríos, R. García-Villacorta, J. Guevara, M. Ahuite, M. Aulestia, D. Cardenas, C. E. Cerón, P.-A. Loizeau, D. Neill, P. Núñez, W. A. Palacios, O. L. Phillips, R. Spichiger, E. Valderrama & R. Vásquez-Martínez. 2008. Tree community change across 700 km of lowland Amazonian forest from the Andean foothills to Brazil. Biotropica 40: 525–535.

———, J. W. Terborgh, M. R. Silman, P. Nuñez, D. A. Neill, C. E. Cerón, W. A. Palacios & M. Aulestia. 2001. Dominance and distribution of tree species in upper Amazonian terra firme forests. Ecology 82: 2101–2117.

Potts, M. D., P. S. Ashton, L. S. Kaufman & J. B. Plotkin. 2002. Habitat patterns in tropical rain forests: A comparison of 105 plots in northwest Borneo. Ecology 83: 2782–2797.

R Development Core Team. 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>, accessed 6 May 2010.

Ruokolainen, K., A. Linna & H. Tuomisto. 1997. Use of Melastomataceae and pteridophytes for revealing phytogeographical patterns in Amazonian rain forests. J. Trop. Ecol. 13: 243–256.

——— & H. Tuomisto. 1998. Vegetación natural de la zona de Iquitos. Pp. 253–365 *in* R. Kalliola & S. Flores (editors), Geoecologia y Desarrollo Amazonico: Estudio Integrado en la Zona de Iquitos, Peru. University of Turku Press, Turku.

Singer, R. & I. Araujo I. 1979. Litter decomposition and ectomycorrhiza in Amazonian forest I. A comparison of litter decomposition and ectomycorrhizal basidiomycetes in latosol-terra-firme forest and white podzol campinarana. Acta Amazonica 9: 25–41.

Spruce, R. 1908. Notes of a Botanist in the Amazon and Andes. MacMillan, London.

ter Steege, H., R. Lilwah, R. Ek, T. van Andel, P. van der Hout, R. Thomas, J. van Essen & I. Ramdass. 2000. Diversity at different scales: A comparison of large-scale forest inventories and smaller plots. Pp. 117–130 *in* H. ter Steege (editor), Plant Diversity in Guyana, with Recommendations for a National Protected Area Strategy. Tropenbos, Wageningen, Netherlands.

———, N. C. A. Pitman, O. L. Phillips, J. Chave, D. Sabatier, A. Duque, J.-F. Molino, M.-F. Prévost, R. Spichiger, H. Castellanos, P. von Hildebrand & R. Vásquez. 2006. Continental-scale patterns of canopy tree composition and function across Amazonia. Nature 443: 444–447.

———, N. Pitman, D. Sabatier, H. Castellanos, P. Van Der Hout, D. C. Daly, M. Silveira, O. L. Phillips, R. Vásquez-Martinez, T. Van Andel, J. Duivenvoorden, A. de Oliveira, R. Ek, R. Lilwah, R. Thomas, J. Van Essen, C. Baider, P. Maas, S. Mori, J. W. Terborgh, P. Nuñez, H. Mogollón & W. Morawetz. 2003. A spatial model of tree alpha-diversity and tree density for the Amazon. Biodivers. & Conservation 12: 2255–2277.

Tuomisto, H. & A. D. Poulsen. 2000. Pteridophyte diversity and species composition in four Amazonian rain forests. J. Veg. Sci. 11: 383–396.

———, K. Ruokolainen, R. Kalliola, A. Linna, W. Danjoy & Z. Rodriguez. 1995. Dissecting Amazonian biodiversity. Science 269: 63–66.

———, ——— & M. Yli-Halla. 2003. Dispersal, environment, and floristic variation of Western Amazonian forests. Science 299: 241–244.

Vásquez, M. R. 1991. *Caraipa* (Guttiferae) del Peru. Ann. Missouri Bot. Gard. 78: 1002–1008.

———. 1993. Una nueva *Haploclathra* (Clusiaceae) de la Amazonia Peruana. Novon 3: 499–501.

Vriensendorp, C., N. Pitman, J. I. Rojas Moscoso, B. A. Pawlak & L. Rivera Chavez. 2006. Perú: Matsés. Rapid Biological Inventories Report 16. The Field Museum, Chicago.

Whitney, B. M. & J. Alvarez A. 2005. A new species of gnatcatcher from white-sand forests of northern Amazonian Peru with revision of the *Polioptila guianensis* complex. Wilson Bull. 117: 113–210.

Wills, C., K. E. Harms, R. Condit, D. King, J. Thompson, F. He, H. C. Muller-Landau, P. Ashton, E. Losos, L. Comita, S. Hubbell, J. LaFrankie, S. Bunyavejchewin, H. S. Dattaraja, S. Davies, S. Esufali, R. Foster, N. Gunatilleke, S. Gunatilleke, P. Hall, A. Itoh, R. John, S. Kiratiprayoon, S. L. de Lao, M. Massa, C. Nath, M. N. S. Noor, A. R. Kassim, R. Sukumar, H. S. Suresh, I.-F. Sun, S. Tan, T. Yamakura & J. Zimmerman. 2006. Nonrandom processes maintain diversity in tropical forests. Science 311: 527–531.

APPENDIX 1. An alphabetical list by family of all of the species and morphospecies collected in the white-sand plots, with authorities and voucher numbers.

Family[1]	Genus	Species	Authority[2]	Collection numbers from WS[3,4]	No. of WS plot occurrences, no. of TF plot occurrences, and presence in the *Catalogue of Ecuador* (0 = no, 1 = yes)[5]*
Anacardiaceae	*Anacardium*	sp. indet., cf. *giganteum*	J. Hancock ex Engl.	PF750/IM45	3, 3, 0 facultative specialist
Anacardiaceae	*Tapirira*	*guianensis*	Aubl.	IM25/IM52/PF744/PF865	5, 14, 1 TF
Annonaceae	*Anaxagorea*	*brevipes*	Benth.	PF767/PF777	1, 0, 1 TF
Annonaceae	*Anaxagorea*	*manausensis*	Timmerman	IM13	1, 0, 0 WS endemic
Annonaceae	*Annona*	sp. indet., cf. *montana*	Macfad.	PF557	1, 4, 1 TF
Annonaceae	*Bocageopsis*	*canescens*	(Spruce ex Benth.) R. E. Fr.	IM6/PF643/PF566PF/913	5, 0. 0 WS endemic*
Annonaceae	*Diclinanona*	*tesmannii*	Diels	IM30/PF558/PF896	3, 3, 0 TF
Annonaceae	*Duguetia*	*trunciflora*	Maas & A. H. Gentry	IM70	1, 0, 0 WS endemic
Annonaceae	*Guatteria*	*decurrens*	R. E. Fr.	PF456/PF1027	2, 2, 1 TF
Annonaceae	*Guatteria*	*maypurensis*	Kunth	PF792	1, 0, 0 WS endemic
Annonaceae	*Guatteria*	*megalophylla*	Diels	PF596/PF611	2, 7, 1 TF
Annonaceae	*Guatteria*	*schomburgkiana*	Mart.	PF510	1, 9, 0 TF
Annonaceae	*Oxandra*	*asbeckii*	(Pulle) R. E. Fr.	PF550/PF598/PF645/PF723/PF763/PF890	6, 0, 0 WS endemic
Annonaceae	*Ruizodendron*	*ovale*	(Ruiz & Pav.) R. E. Fr.	PF711	2, 3, 1 TF
Annonaceae	*Xylopia*	sp. indet., aff. *calophylla*	R. E. Fr.	PF809	1, 0, 0 WS endemic
Annonaceae	*Xylopia*	*benthamii*	R. E. Fr.	PF655	1, 2, 0 TF
Apocynaceae	*Aspidosperma*	*pichonianum*	Woodson	IM11/IM59/IM64/IM80/PF460/PF463/PF489/PF516/PF520/PF586/PF640/PF785	7, 0, 0 WS endemic*
Apocynaceae	*Aspidosperma*	*schultesii*	Woodson	IM34/IM85/PF565/PF609	3, 3, 0 facultative specialist
Apocynaceae	*Lacmellea*	*lactescens*	(Kuhlm.) Markgr.	IM29/IM115	2, 0, 1 TF
Apocynaceae	*Macoubea*	*sprucei*	(Müll. Arg.) Markgr.	PF458/PF497/PF721/PF801/PF862	5, 0, 0 WS endemic
Apocynaceae	*Parahancornia*	*peruviana*	Monach.	PF562/PF728	3, 7, 0 TF
Aquifoliaceae	*Ilex*	sp. indet., cf. *nayana*	Cuatrec.	IM150/PF468/PF850/PF850a/PF874/ND1093	5, 0, 0 WS endemic*

Appendix 1. Continued.

Family[1]	Genus	Species	Authority[2]	Collection numbers from WS[3,4]	No. of WS plot occurrences, no. of TF plot occurrences, and presence in the *Catalogue of Ecuador* (0 = no, 1 = yes)[5]*
Araliaceae	*Dendropanax*	*palustris*	(Ducke) Harms	PF1008/PF1023/PF1025	2, 0, 0 WS endemic*
Araliaceae	*Dendropanax*	*umbellatus*	(Ruiz & Pav.) Decne. & Planch.	IM77/IM89/IM121/PF816	4, 0, 1 cryptic endemic*
Araliaceae	*Schefflera*	*dichotoma*	Fiaschi & Frodin	IM24/PF882	2, 0, 0 WS endemic
Arecaceae	*Attalea*	sp. indet. A	[Kunth]	PF841	2, 0, 0 WS Endemic
Arecaceae	*Euterpe*	*catinga*	Wallace	PF840	4, 0, 1 cryptic endemic
Arecaceae	*Mauritia*	*carana*	Wallace	PF photos	2, 0, 0 WS endemic
Arecaceae	*Mauritia*	*flexuosa*	L. f.	PF photos	1, 0, 1 TF
Arecaceae	*Mauritiella*	*aculeata*	(Kunth) Burret	PF1043	4, 0, 0 WS endemic
Arecaceae	*Mauritiella*	*armata*	(Mart.) Burret	PF1011	1, 0, 1 TF
Arecaceae	*Oenocarpus*	*bataua*	Mart.	PF842	4, 12, 1 TF
Bignoniaceae	*Jacaranda*	*macrocarpa*	Bureau & K. Schum.	IM62/PF895	2, 3, 0 TF
Bignoniaceae	*Tabebuia*	*serratifolia*	(Vahl) G. Nicholson	IM98/IM144/PF608/PF1033	5, 2, 1 TF
Burseraceae	*Protium*	*heptaphyllum* subsp. *ulei*	(Swart) Daly	PF57/ND1098	2, 0, 0 WS endemic
Burseraceae	*Protium*	*laxiflorum*	Engl.	PF482/PF486/PF589	2, 0, 0 WS endemic
Burseraceae	*Protium*	*opacum*	Swart	PF745	1, 5, 1 TF
Burseraceae	*Protium*	sp. indet., cf. *rubrum*	Cuatrec.	PF919	1, 0, 0 WS endemic
Burseraceae	*Protium*	sp. indet., aff. *subserratum*[6]	(Engl.) Engl.	PF833	2, 0, 0 WS endemic
Burseraceae	*Protium*	*subserratum*	(Engl.) Engl.	PF579/PF642/PF864	6, 0, 0 WS endemic
Burseraceae	*Trattinnickia*	*burserifolia*	Mart.	PF509	1, 0, 0 WS endemic
Caryocaraceae	*Anthodiscus*	sp. indet., cf. *amazonicus*	Gleason & A. C. Sm.	PF459	1, 0, 1 TF
Celastraceae	*Maytenus*	*macrocarpa*	(Ruiz & Pav.) Briq.	PF475	1, 0, 1 TF
Chrysobalanaceae	*Couepia*	*parillo*	DC.	IM107/IM110	1, 3, 1 TF
Chrysobalanaceae	*Couepia*	*racemosa*	Benth. ex Hook. f.	PF509/PF766	2, 4, 0 TF

Appendix 1. Continued.

Family[1]	Genus	Species	Authority[2]	Collection numbers from WS[3,4]	No. of WS plot occurrences, no. of TF plot occurrences, and presence in the *Catalogue of Ecuador* (0 = no, 1 = yes)[5]*
Chrysobalanaceae	*Couepia*	*williamsii*	J. F. Macbr.	IM8	1, 3, 0 TF
Chrysobalanaceae	*Licania*	sp. indet., cf. *apetala*	(E. Mey.) Fritsch	PF813	1, 4, 1 TF
Chrysobalanaceae	*Licania*	*intrapetiolaris*	Spruce ex Hook. f.	IM145/IM146/PF551/PF570/PF718/PF861	5, 0, 0 WS endemic
Chrysobalanaceae	*Licania*	*lata*	J. F. Macbr.	IM152/PF575/PF873	3, 0, 1 WS endemic
Clusiaceae	*Calophyllum*	*brasiliense*	Cambess.	IM138/PF553/PF779/PF855	6, 1, 1 cryptic endemic
Clusiaceae	*Caraipa*	*tereticaulis*	Tul.	IM134/PF628/PF639/PF925/PF1005	5, 0, 0 WS endemic*
Clusiaceae	*Caraipa*	*utilis*	Vásquez	IM124/IM125/1M131/PF747/PF794/PF807/PF815/PF852/PF885/PF1001/PF1006/PF1012	9, 0, 0 WS endemic*
Clusiaceae	*Chrysochlamys*	sp. indet. A	[Poepp. & Endl.]	IM12	1, 0, 0 WS endemic
Clusiaceae	*Haploclathra*	*cordata*	Vásquez	IM56/PF627/PF857	5, 0, 0 WS endemic*
Clusiaceae	*Tovomita*	*calophyllophylla*	García-Villacorta & Hammel	IM148/PF469/PF472/PF474/PF499/PF504/PF587/PF712/PF775/PF869	8, 0, 0 WS endemic*
Clusiaceae	*Tovomita*	*laurina*	Planch. & Triana	IM19	1, 0, 0 WS endemic*
Combretaceae	*Buchenavia*	*parvifolia*	Ducke	ND1092	1, 2, 1 TF
Combretaceae	*Buchenavia*	*reticulata*	Eichler	PF754	1, 3, 1 TF
Cyathaceae	*Cyathea*	sp. indet. A	[Sm.]	PF1007	1, 0, 0 WS endemic
Elaeocarpaceae	*Sloanea*	*floribunda*	Spruce ex Benth.	IM9/PF652/PF799/PF1029	4, 0, 0 WS endemic
Elaeocarpaceae	*Sloanea*	*latifolia*	(Rich.) K. Schum.	PF795	1, 3, 0 TF
Elaeocarpaceae	*Sloanea*	*laxiflora*	Spruce ex Benth.	IM136/PF584/PF626/PF644	4, 0, 0 WS endemic
Elaeocarpaceae	*Sloanea*	sp. indet., cf. *robusta*	Uittien	IM51/IM128/PF926/PF1022/PF1038	6, 1, 1 cryptic endemic*
Erythroxylaceae	*Erythroxylum*	*kapplerianum*	Peyr.	IM143/PF619/PF804	3, 0, 0 WS endemic
Euphorbiaceae	*Amanoa*	sp. indet. A	[Aubl.]	IM44/IM63	1, 0, 0 WS endemic
Euphorbiaceae	*Hevea*	*guianensis*	Aubl.	IM137/PF464/PF498/PF514/PF559/PF706/PF863/PF927	10, 11, 1 TF
Euphorbiaceae	*Mabea*	*subsessilis*	Pax & K. Hoffm.	IM38/PF612/PF716	3, 0, 0 WS endemic
Euphorbiaceae	*Micrandra*	*elata*	(Didr.) Müll. Arg.	IM2/IM57	2, 0, 0 WS endemic
Euphorbiaceae	*Micrandra*	*spruceana*	(Baill.) R. E. Schult.	PF732/PF736/PF918	3, 4, 0 TF
Euphorbiaceae	*Nealchornea*	*yapurensis*	Huber	PF653	1, 15, 1 TF

Appendix 1. Continued.

Family[1]	Genus	Species	Authority[2]	Collection numbers from WS[3,4]	No. of WS plot occurrences, no. of TF plot occurrences, and presence in the *Catalogue of Ecuador* (0 = no, 1 = yes)[5]*
Euphorbiaceae	*Pera*	*bicolor*	(Klotzsch) Müll. Arg.	IM99/PF786/PF892	3, 0, 0 WS endemic
Fabaceae	*Abarema*	*auriculata*	(Benth.) Barneby & J. W. Grimes	IM147	1, 1, 0 TF
Fabaceae	*Calliandra*	*guildingii*	Benth.	PF845	1, 0, 1 TF
Fabaceae	*Dicymbe*	*uaiparuensis*	R. S. Cowan	IM94/IM119/PF624/PF1003/PF1034	6, 0, 0 WS endemic*
Fabaceae	*Dimorphandra*	*macrostachya* subsp. *glabrifolia*	(Ducke) M. F. Silva	PF1021	2, 0, 0 WS endemic
Fabaceae	*Dimorphandra*	*macrostachya* subsp. *macrostachya*	[Benth.]	PF616	1, 0, 0 WS endemic
Fabaceae	*Hymenolobium*	*nitidum*	Benth.	IM139	1, 1, 0 TF
Fabaceae	*Hymenolobium*	sp. indet. A	[Benth.]	PF577/PF632	2, 0, 0 WS endemic
Fabaceae	*Inga*	*heterophylla*	Willd.	PF515/PF519/PF522/PF940	2, 3, 1 TF
Fabaceae	*Inga*	*punctata*	Willd.	IM4/PF625/PF921	3, 5, 1 TF
Fabaceae	*Macrolobium*	*bifolium*	(Aubl.) Pers.	IM92/PF455/PF582/PF594/PF814/PF893	6, 0, 0 WS endemic
Fabaceae	*Macrolobium*	sp. indet., cf. *huberianum*	Ducke	PF637	1, 0, 0 WS endemic
Fabaceae	*Macrolobium*	*ischnocalyx*	Harms	PF710/PF751	1, 0, 1 TF
Fabaceae	*Macrolobium*	*limbatum* var. *limbatum*	[Spruce ex Benth.]	PF818	1, 0, 1 TF
Fabaceae	*Macrolobium*	*limbatum* var. *propinquun*	R. S. Cowan	IM22/PF583/PF603/PF910/PF912	5, 3, 0 facultative specialist
Fabaceae	*Macrolobium*	*microcalyx*	Ducke	IM82/IM122/PF623/PF701/PF870/PF1009	9, 4, 1 TF
Fabaceae	*Macrolobium*	sp. indet. A	[Schreb.]	PF631/PF634/PF752	3, 0, 0 WS endemic
Fabaceae	*Macrolobium*	sp. indet. B	[Schreb.]	PF588/PF654/PF924	3, 0, 0 WS endemic
Fabaceae	*Ormosia*	*coccinia*	(Aubl.) Jacks.	PF477/PF803	2, 0, 0 WS endemic
Fabaceae	*Parkia*	*igneiflora*	Ducke	IM66/IM95/IM127/PF453/PF868/PF1004	7, 5, 0 TF
Fabaceae	*Parkia*	*panurensis*	Benth. ex H. C. Hopkins	PF614/PF735	3, 7, 1 TF
Fabaceae	*Pentaclethra*	*macroloba*	(Willd.) Kuntze	IM60/IM151	2, 0, 0 WS endemic
Fabaceae	*Pterocarpus*	*rohrii*	Vahl	PF773	1, 1, 1 TF

APPENDIX 1. Continued.

Family[1]	Genus	Species	Authority[2]	Collection numbers from WS[3,4]	No. of WS plot occurrences, no. of TF plot occurrences, and presence in the *Catalogue of Ecuador* (0 = no, 1 = yes)[5]*
Fabaceae	*Swartzia*	*benthamiana* var. *benthamiana*	[Miq.]	IM27/PF556/PF720	6, 0, 1 cryptic endemic
Fabaceae	*Swartzia*	*cardiosperma*	Spruce ex Benth.	IM3	2, 1, 1 TF
Fabaceae	*Swartzia*	*pendula*	Spruce ex Benth.	PF730/PF787	2, 0, 0 WS endemic*
Fabaceae	*Tachigali*	*bracteosa*	(Harms) Zarucchi & Pipoly	IM20	1, 0, 0 WS endemic
Fabaceae	*Tachigali*	*paniculata*	Aubl.	IM40/PF470/PF467/PF527/PF585/PF715/PF721/PF762/PF765/PF811/PF881/PF889/PF916	6, 8, 1 TF
Fabaceae	*Tachigali*	*ptychophysca*	Spruce ex Benth.	IM1/IM36/PF899	2, 0, 0 WS endemic*
Fabaceae	*Taralea*	*oppositifolia*	Aubl.	PF757/PF805/PF941	3, 0, 0 WS endemic
Fabaceae	*Zygia*	*cauliflora*	(Willd.) Killip	PF705	1, 0, 0 WS endemic*
Humiriaceae	*Humiria*	*balsamifera*	Aubl.	PF742/PF871	3, 0, 0 WS endemic
Humiriaceae	*Sacoglottis*	*ceratocarpa*	Ducke	PF707/PF853/PF891	4, 1, 0 facultative specialist
Icacinaceae	*Discophora*	*guianensis*	Miers	PF561/PF648	2, 4, 1 TF
Icacinaceae	*Emmotum*	*floribundum*	R. A. Howard	IM68/IM96/IM100/IM103/IM141/IM149/PF353/PF476/PF650/PF788/PF806/PF1026	8, 0, 0 WS endemic*
Lauraceae	*Aniba*	*firmula*	(Nees & Mart.) Mez	IM37	1, 0, 0 WS endemic*
Lauraceae	*Endlicheria*	*bracteolata*	(Meisn.) C. K. Allen	PF800	1, 0, 0 WS endemic
Lauraceae	*Endlicheria*	*citriodora*	van der Werff	PF776	1, 0, 0 WS endemic
Lauraceae	*Licaria*	*brasiliensis*	(Nees) Kosterm.	PF708	1, 0, 0 WS endemic*
Lauraceae	*Licaria*	*cannella*	(Meisn.) Kosterm.	IM61/IM101/IM126	3, 8, 1 TF
Lauraceae	*Mezilaurus*	*opaca*	Kubitzki & van der Werff	PF782	1, 2, 0 TF
Lauraceae	*Ocotea*	*aciphylla*	(Nees) Mez	IM10/IM35/IM39/IM104/PF473/PF521/PF574/PF597/PF641/PF726/PF866/PF877/PF879/PF894	8, 9, 1 TF
Lauraceae	*Ocotea*	*argyrophylla*	Ducke	IM5/PF620/PF914	3, 6, 1 TF
Lauraceae	*Ocotea*	sp. indet., cf. *gardneri*	(Meisn.) Mez	PF703/PF741/PF756/PF759	2, 0, 0 WS endemic*
Lauraceae	*Ocotea*	*glomerata* subsp. *magnifica*	(O. C. Schmidt) Rohwer	PF746	1, 0, 0 WS endemic
Lauraceae	*Ocotea*	*myriantha*	(Meisn.) Mez	PF764	1, 4, 0 TF

APPENDIX 1. Continued.

Family[1]	Genus	Species	Authority[2]	Collection numbers from WS[3,4]	No. of WS plot occurrences, no. of TF plot occurrences, and presence in the *Catalogue of Ecuador* (0 = no, 1 = yes)[5]*
Lauraceae	*Ocotea*	*olivacea*	A. C. Sm.	IM49/IM113	2, 0, 1 TF
Lauraceae	*Ocotea*	sp. indet. A	[Aubl.]	IM53	1, 0, 0 WS endemic
Lauraceae	*Persea*	sp. indet., cf. *areolatocostae*	(C. K. Allen) van der Werff	PF511/PF604/PF719/PF810/PF819	4, 0, 0 WS endemic*
Lauraceae	*Rhodostemonodaphne*	sp. indet. A	[Rohwer & Kubitzki]	PF789	1, 0, 0 WS endemic
Lauraceae	Indet.	sp. indet. A		PF904	1, 0, 0 WS endemic
Lauraceae	Indet.	sp. indet. B		IM108	1, 0, 0 WS endemic
Lauraceae	Indet.	sp. indet. C		IM33	1, 0, 0 WS endemic
Linaceae	*Roucheria*	*punctata*	(Ducke) Ducke	PF646/PF740	3, 3, 1 TF
Linaceae	*Roucheria*	*schomburgkii*	Planch.	IM69/IM93/PF876	3, 2, 0 facultative specialist
Lissocarpaceae	*Lissocarpa*	*stenocarpa*	Steyerm.	IM78/IM106	2, 0, 0 WS endemic*
Malpighiaceae	*Byrsonima*	sp. indet., cf. *densa*	(Poir.) DC.	PF526	1, 0, 0 WS endemic
Malpighiaceae	*Byrsonima*	*laevigata*	(Poir.) DC.	PF500/PF524/ND1115	2, 0, 0 WS endemic*
Malpighiaceae	*Byrsonima*	*stipulina*	J. F. Macbr.	IM18/IM55/IM90/PF591	5, 2, 0 facultative specialist*
Malvaceae	*Apeiba*	sp. indet., cf. *membranacea*	Spruce ex Benth.	PF731/PF739	1, 0, 1 TF
Malvaceae	*Lueheopsis*	*althaeiflora*	(Spruce ex Benth.) Burret	IM50/PF630	2, 0, 0 WS endemic*
Malvaceae	*Pachira*	*brevipes*	(A. Robyns) W. S. Alverson	IM41/PF466/PF605/PF700/PF859/PF1002	13, 0, 0 WS endemic*
Melastomataceae	*Graffenrieda*	*limbata*	Triana	PF928	1, 0, 0 WS endemic*
Melastomataceae	*Miconia*	*klugii*	Gleason	PF571/PF793	2, 0, 0 WS endemic*
Melastomataceae	*Miconia*	sp. indet. A	[Ruiz & Pav.]	PF769	1, 0, 0 WS endemic
Meliaceae	*Guarea*	*vasquezii*	W. Palacios	PF704	2, 0, 0 WS endemic*
Meliaceae	*Trichilia*	*micrantha*	Benth.	PF552	1, 3, 1 TF
Meliaceae	*Trichilia*	*pallida*	Sw.	PF578/PF615	1, 5, 1 TF
Moraceae	*Brosimum*	*rubescens*	Taub.	IM21/PF485/PF595/PF722	4, 12, 1 TF
Moraceae	*Brosimum*	*utile*	(Kunth) Oken ex J. Presl	IM31/PF512/PF638/PF872	5, 10, 1 TF
Moraceae	*Ficus*	sp. indet. A	[L.]	PF783	1, 0, 0 WS endemic
Moraceae	*Helicostylis*	*scabra*	(J. F. Macbr.) C. C. Berg	IM16	1, 10, 1 TF

Appendix 1. Continued.

Family[1]	Genus	Species	Authority[2]	Collection numbers from WS[3,4]	No. of WS plot occurrences, no. of TF plot occurrences, and presence in the *Catalogue of Ecuador* (0 = no, 1 = yes)[5]*
Moraceae	*Pseudolmedia*	*rigida*	(Klotzsch & H. Karst.) Cuatrec.	PF481/PF567/PF622/PF886/PF909	3, 4, 1 TF
Myristicaceae	*Compsoneura*	*capitellata*	(A. DC.) Warb.	IM84/PF714	3, 9, 1 TF
Myristicaceae	*Iryanthera*	*laevis*	Markgr.	PF749	1, 12, 1 TF
Myristicaceae	*Iryanthera*	*paradoxa*	(Schwacke) Warb.	PF658	1, 0, 0 WS endemic
Myristicaceae	*Iryanthera*	*paraensis*	Huber	IM7	1, 12, 1 TF
Myristicaceae	*Iryanthera*	*ulei*	Warb.	PF610/PF651/PF900/PF901	3, 0, 1 TF
Myristicaceae	*Virola*	*calophylla*	(Spruce) Warb.	PF727	2, 11, 1 TF
Myristicaceae	*Virola*	*pavonis*	(A. DC.) A. C. Sm.	IM28/PF518/PF629/PF743/PF772/PF920/PF1030	7, 17, 1 TF
Myristicaceae	*Virola*	*surinamensis*	(Rol. ex Rottb.) Warb.	IM133	1, 0, 1 TF
Myrsinaceae	*Cybianthus*	*nanayensis*	(J. F. Macbr.) G. Agostini	PF798	1, 0, 0 WS endemic*
Myrsinaceae	*Cybianthus*	*peruvianus*	(A. DC.) Miq.	IM32/PF856	2, 1, 1 TF
Myrsinaceae	*Myrsine*	sp. indet. A	[L.]	ND1120	1, 0, 0 WS endemic
Myrsinaceae	*Stylogyne*	sp. indet. A	[A. DC.]	IM74/IM123/PF488/PF506/PF523/PF525	3, 0, 0 WS endemic
Myrtaceae	*Calyptranthes*	*bipennis*	O. Berg	PF903	1, 0, 1 TF
Myrtaceae	*Calyptranthes*	sp. indet. A	[Sw.]	PF734	1, 0, 0 WS endemic
Myrtaceae	*Eugenia*	*feijoi*	O. Berg	PF778/PF797/PF923	2, 6, 1 TF
Myrtaceae	*Eugenia*	*macrocalyx*	(Rusby) McVaugh	IM91/IM97/PF1020/PF1028/PF1041	3, 0, 1 cryptic endemic
Myrtaceae	*Eugenia*	sp. indet. A	[L.]	PF791	1, 0, 0 WS endemic
Myrtaceae	*Eugenia*	sp. indet. B	[L.]	PF606	1, 0, 0 WS endemic
Myrtaceae	*Marlierea*	*caudata*	McVaugh	IM15/PF589/PF581/PF802/PF858/PF884	6, 0, 0 WS endemic
Myrtaceae	*Marlierea*	sp. indet. A	[Cambess.]	IM23/PF593	2, 0, 0 WS endemic
Myrtaceae	*Myrcia*	sp. indet. A	[DC. ex Guill.]	PF943	2, 0, 0 WS endemic
Myrtaceae	Indet.	sp. indet. A		IM118	1, 0, 0 WS endemic
Myrtaceae	Indet.	sp. indet. B		IM81	1, 0, 0 WS endemic
Nyctaginaceae	*Neea*	*divaricata* cf.	Poepp. & Endl.	PF633/PF758/PF851/PF906/PF1035	7, 1, 1 cryptic endemic*
Nyctaginaceae	*Neea*	sp. indet., cf. *macrophylla*	Poepp. & Endl.	PF554	2, 1, 1 TF
Nyctaginaceae	*Neea*	sp. indet. A	[Ruiz & Pav.]	IM26/PF768	2, 0, 0 WS endemic

Appendix 1. Continued.

Family[1]	Genus	Species	Authority[2]	Collection numbers from WS[3,4]	No. of WS plot occurrences, no. of TF plot occurrences, and presence in the *Catalogue of Ecuador* (0 = no, 1 = yes)[5]*
Nyctaginaceae	*Neea*	sp. indet., cf. *verticillata*	Ruiz & Pav.	IM46/PF600/PF607	2, 1, 1 TF
Ochnaceae	*Godoya*	sp. indet. A	[Ruiz & Pav.]	PF647	1, 0, 0 WS endemic
Ochnaceae	*Ouratea*	sp. indet. A	[Aubl.]	PF880	1, 0, 0 WS endemic
Olacaceae	*Aptandra*	*tubicina*	(Poepp.) Benth. ex Miers	IM88	1, 2, 1 TF
Olacaceae	*Cathedra*	*acuminata*	(Benth.) Miers	IM105	1, 1, 1 TF
Olacaceae	*Dulacia*	*candida*	(Poepp.) Kuntze	PF601/PF657	2, 0, 1 TF
Picramniaceae	*Picramnia*	sp. indet. A	[Sw.]	PF887	1, 0, 0 WS endemic
Quiinaceae	*Quiina*	*amazonica*	A. C. Sm.	PF846	1, 2, 1 TF
Rosaceae	*Prunus*	*detrita*	J. F. Macbr.	PF878/PF1031	2, 0, 0 WS endemic*
Rubiaceae	*Alibertia*	*hispida*	Ducke	IM72	1, 0, 0 WS endemic
Rubiaceae	*Alibertia*	*myrciifolia*	K. Schum.	PF808	1, 5, 1 TF
Rubiaceae	*Chimarrhis*	sp. indet. A	[Jacq.]	IM48/PF713	2, 0, 0 WS endemic
Rubiaceae	*Ferdinandusa*	*chlorantha*	(Wedd.) Standl.	IM111/PF462/PF761/PF860/PF1010/PF1037	6, 1, 1 cryptic endemic*
Rubiaceae	*Ixora*	*ulei*	K. Krause	IM130	1, 0, 1 TF
Rubiaceae	*Pagamea*	sp. indet., cf. *acrensis*	Steyerm.	ND1094	1, 0, 0 WS endemic*
Rubiaceae	*Pagamea*	*coriacea*	Spruce ex Benth.	PF617/PF781/PF898	3, 0, 0 WS endemic*
Rubiaceae	*Pagamea*	*guianensis*	Aubl.	IM42	1, 2, 0 TF
Rubiaceae	*Platycarpum*	*orinocense*	Bonpl.	PF599/PF875	6, 0, 0 WS endemic*
Rubiaceae	*Remijia*	*pacimonica*	Standl.	IM135/PF568	5, 0, 0 WS endemic*
Rubiaceae	*Rudgea*	*lanceifolia*	Salisb.	IM129/PF748	2, 0, 0 WS endemic
Rubiaceae	*Simira*	*rubescens*	(Benth.) Bremek. ex Steyerm.	PF80/PF796/PF1014	2, 4, 1 TF
Rubiaceae	*Stachyarrhena*	*spicata*	Hook. f.	PF770/PF790	1, 0, 0 WS endemic*
Rutaceae	*Adiscanthus*	*fusciflorus*	Ducke	PF621	1, 0, 0 WS endemic
Rutaceae	*Hortia*	*vandelliana*	Groppo	PF490/PF493	1, 0, 0 WS endemic*
Salicaceae	*Casearia*	sp. indet., cf. *javitensis*	Kunth	PF494/PF917	2, 2, 1 TF
Salicaceae	*Lunania*	sp. indet. A	[Hook.]	IM109	1, 0, 0 WS endemic
Salicaceae	*Ryania*	*speciosa* var. *minor*	Monach.	PF755	1, 0, 1 TF

Appendix 1. Continued.

Family[1]	Genus	Species	Authority[2]	Collection numbers from WS[3,4]	No. of WS plot occurrences, no. of TF plot occurrences, and presence in the *Catalogue of Ecuador* (0 = no, 1 = yes)[5]*
Sapindaceae	*Cupania*	*diphylla*	Vahl	IM43/IM117/IM140/PF517/PF563/PF576/PF602/PF854/PF1013/PF1018/PF1040	8, 0, 0 WS endemic*
Sapindaceae	*Cupania*	sp. indet. A	[L.]	PF724/PF738	1, 0, 0 WS endemic
Sapindaceae	*Matayba*	*inelegans*	Spruce ex Radlk.	IM76/PF79/PF112/PF478/PF454/PF531/PF555/PF771/PF867/PF883	7, 2, 0 facultative specialist
Sapindaceae	*Matayba*	*purgans*	(Poepp.) Radlk.	PF774	1, 0, 0 WS endemic
Sapindaceae	*Matayba*	sp. indet. A	[Aubl.]	PF613/PF636/PF656	3, 0, 0 WS endemic
Sapotaceae	*Chrysophyllum*	*bombycinum*	T. D. Penn.	IM58	1, 0, 0 WS endemic*
Sapotaceae	*Chrysophyllum*	*manaosense*	(Aubrév.) T. D. Penn.	PF573/PF897/ND1095	3, 1, 1 TF
Sapotaceae	*Chrysophyllum*	*sanguinolentum* subsp. *sanguinolentum*	(Pierre) Baehni	IM65/IM75/IM120/IM132/PF452/PF492/PF1019	6, 6, 1 TF
Sapotaceae	*Chrysophyllum*	*sanguinolentum* subsp. *spurium*	(Ducke) T. D. Penn.	PF560/PF717/PF908	4, 0, 0 WS endemic
Sapotaceae	*Diploon*	*cuspidatum*	(Hoehne) Cronquist	ND1116	1, 2, 0 TF
Sapotaceae	*Micropholis*	*guyanensis* subsp. *guyanensis*	(A. DC.) Pierre	IM83/PF592/PF733/PF915	4, 3, 1 TF
Sapotaceae	*Micropholis*	*trunciflora*	Ducke	IM47	1, 0, 0 WS endemic
Sapotaceae	*Micropholis*	*venulosa*	(Mart. & Eichler) Pierre	IM67/PF487/PF572/PF580/PF649/PF753/PF888	8, 9, 1 TF
Sapotaceae	*Pouteria*	*cuspidata* subsp. *cuspidata*	(A. DC.) Baehni	IM86/IM116/IM142//PF465/PF480/PF496/PF508/PF729/PF737/PF1016/PF1036	7, 0, 0 WS endemic
Sapotaceae	*Pouteria*	*cuspidata* subsp. *dura*	(Eyma) T. D. Penn.	PF528/PF590	2, 2, 0 facultative specialist
Sapotaceae	*Pouteria*	*lucumifolia*	(Reissek ex Maxim.) T. D. Penn.	PF457/PF479/PF491/PF495/PF503/PF529/PF530/PF533/PF760	2, 2, 1 TF
Sapotaceae	*Pouteria*	*oblanceolata*	Pires	PF484/PF532/PF618/PF902	3, 2, 1 TF
Sapotaceae	*Pradosia*	*cochlearia*	(Lecomte) T. D. Penn.	PF907	1, 0, 0 WS endemic
Simaroubaceae	*Simaba*	sp. indet. A	[Aubl.]	IM54	1, 0, 0 WS endemic

Appendix 1. Continued.

Family[1]	Genus	Species	Authority[2]	Collection numbers from WS[3,4]	No. of WS plot occurrences, no. of TF plot occurrences, and presence in the *Catalogue of Ecuador* (0 = no, 1 = yes)[5]*
Siparunaceae	*Siparuna*	*guianensis*	Aubl.	PF564/PF635/PF702	5, 0, 1 cryptic endemic
Theaceae	*Ternstroemia*	*klugiana*	Kobuski	IM71/IM87/IM102/PF513/PF1024	4, 0, 0 WS endemic*
Urticaceae	*Pourouma*	*bicolor* subsp. *bicolor*	Mart.	PF709	1, 10, 1 TF
Urticaceae	*Pourouma*	*cecropiifolia*	Mart.	IM73/PF1032	2, 11, 1 TF
Urticaceae	*Pourouma*	*ovata*	Trécul	IM17	1, 4, 0 TF
Violaceae	*Gloeospermum*	sp. indet. A	[Triana & Planch.]	PF817	1, 0, 0 WS endemic

* Species with an asterisk are identified WS species that are not in the comparative checklist of Clarke et al. (2001) and are provisionally classified as restricted to western Amazonian WS forests.

[1] Family designations follow the 2009 update from the Angiosperm Phylogeny Group (<http://www.mobot.org/MOBOT/research/APweb/>).

[2] Authorities in brackets apply to the genus.

[3] For collection numbers, PF stands for Paul Fine, IM for Italo Mesones, and ND for Nallarett Dávila.

[4] All vouchers are deposited in AMAZ and F, and some of them are available online (search the database in <http://fm1.fieldmuseum.org/vrrc/>).

[5] Number of white-sand (WS) plots in which the species was encountered, followed by the number of terra firme (TF) plots in which the species was encountered, with a 0 or a 1 signifying whether or not the species is listed in the *Catalogue of the Vascular Plants of Ecuador* (see text). Following the string of numbers is our provisional classification for that species: either WS endemic, facultative specialist, cryptic endemic, or TF species. See text for details on how species were classified.

[6] This species is named and described in Daly, D. C. & P. V. A. Fine. A new Amazonian section of *Protium* (Burseraceae) including both edaphic specialist and generalist taxa studies in neotropical Burseraceae XVI. Syst. Bot. (in press).