BIOTROPICA 36(3): 297–317 2004

Forty Years of Tropical Forest Recovery from Agriculture: Structure and Floristics of Secondary and Old-growth Riparian Forests in the Dominican Republic[1]

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ABSTRACT

Interest in tropical secondary forests has grown as large areas of agriculture have been abandoned in recent decades; yet, there are few long-term studies of post-agriculture vegetation recovery in the tropics. In this study, we compared the vegetation structure and floristic composition of old-growth and 40-year-old secondary riparian forests in the Cordillera Central, Dominican Republic. Canopy height and stem density of woody plants were similar between forest types, but basal area of trees was 27 percent lower in secondary forests. Introduced tree species comprised 20 percent of the basal area and dominated the understory of secondary forests. Life-form diversity was higher in old-growth forests as arborescent ferns, the palm species, and epiphytic bromeliads, orchids, and bryophytes were much more abundant. The number of species of epiphytic orchids and bromeliads, ground ferns, and herbaceous plants was also significantly higher in old-growth forests. The species density of woody plants and vines, however, was comparable between forest types, and vine abundance was significantly higher in secondary forests. The high importance of introduced tree species and the delayed recovery of several plant life-forms have important implications for the conservation of plant diversity in secondary forests in the tropics. The robust regeneration of woody structure despite the long land tenure (*ca* 60 yr) by farmers is probably due to the nutrient-rich alluvial soils and low-intensity agriculture. This study revealed the potential for the rapid recovery of woody plant diversity and structure in fertile secondary forests adjacent to mature forest seed sources and the more delayed recovery of nonwoody plant diversity and abundance.

RESUMEN

El interés por los bosques tropicales secundarios ha crecido debido a que grandes extensiones de áreas agrícolas han sido abandonadas en las últimas décadas. Aun así, en los trópicos hay pocos estudios a largo plazo sobre la recuperación de la vegetación de zonas agrícolas abandonadas. En nuestro estudio, comparamos la estructura de la vegetación y la composición florística de bosques ribereños maduros y bosques de 40 años de edad en la Cordillera Central de República Dominicana. La altura del dosel y la densidad de tallos de plantas leñosas fueron similares en los distintos tipos de bosque, pero el área basal de los árboles fue 27 por ciento más baja en los bosques secundarios. Las especies arbóreas introducidas representaron 20 por ciento del área basal y dominaron el sotobosque de los bosques secundarios. La diversidad de formas de vida fue más alta en los bosques maduros, debido a que los helechos arborescentes, las palmas, bromelias, orquídeas, y musgos epífítos fueron mucho más abundantes. El numero de especies de orquídeas y bromelias epifítas, helechos de tierra y de plantas herbáceas fue significativamente más alta en los bosques maduros. Sin embargo, el números de especies leñosas y de bejucos fue comparable en los dos tipos de bosque, mientras que la abundancia de bejucos fue significativamente mayor en los bosques secundarios. La gran importancia de las especies arbóreas exóticas y la lenta recuperación de varias formas de vida vegetal, llevan implicaciones importantes para la conservación de la diversidad de plantas en bosques tropicales secundarios. La regeneración vigorosa de la estructura leñosa, a pesar de la larga ocupación de estas tierras por los granjeros (*ca* 60 años) se debe, probablemente, a la riqueza de nutrientes del suelo en los terrenos aluviales y a la agricultura de baja intensidad que se practicaba en la zona. Este estudio demuestra el potencial para una recuperación rápida de la diversidad y estructura de la vegetación leñosa en bosques secundarios fértiles que colindan con fuentes de semilla ubicadas en bosques maduros, y la recuperación más lenta de la diversidad y abundancia de plantas no leñosas.

Key words: *Dominican Republic; epiphytes; invasive species; old-growth forest; riparian forest; secondary forest; species diversity; succession; vines; tropical montane forest.*

Secondary forests in the tropics have received increased attention in recent years as their value in conserving biological diversity has been recognized (Chazdon 1998). An improved ecological understanding of secondary forests is sought, both for timber management (Wadsworth 1983, Finegan 1992) and biodiversity conservation (Guariguata *et*

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[1] Received 8 July 2003; revision accepted 10 February 2004.

al. 1997, Foster *et al.* 1999). Their importance in tropical landscapes, however, is not new; in most tropical countries, secondary forest have comprised larger areas than primary forest for decades (Gomez-Pompa & Vázquez-Yánes 1974). Yet, fundamental aspects of tropical forest succession following agriculture remain poorly understood (Finegan 1996, Foster *et al.* 1999), in part because most studies of tropical secondary forests have been confined to the first few decades of vegetation recovery.

Studies of later successional phases are needed to address issues central to the recovery of plant diversity and composition in tropical secondary forests, as clear patterns may only emerge over extended periods of time (Brown & Lugo 1990, Laurance & Bierregaard 1997). In particular, do protected areas of primary forests in the tropics act as effective sources of native plant species for the recolonization of abandoned lands? The expansion of plant populations through the recolonization of abandoned areas may be important for the medium- to long-term persistence of plant species found in smaller preserves of primary forest (Thebaud & Strasberg 1997). Does the high diversity of life-forms that typify mature tropical forests recover along the same trajectory as species richness? This question remains unanswered, as systematic assessments of plant life-form diversity in later stages of succession have rarely been carried out in tropical secondary forests. Such studies are particularly needed in the tropics where non-arboreal life-forms can often account for a substantial percentage of total species richness (Gentry & Dobson 1987).

Likewise, addressing these questions in a post-agricultural context is essential as farming and pasturing can affect forest regeneration rates and pathways by depleting the soil resources far in excess of natural disturbance (Aide & Cavelier 1994, McDowell 2001) and can reduce recruitment of primary forest species (Duncan & Chapman 1999). Furthermore, unlike natural disturbances, which may increase species richness (Molino & Sabatier 2001), post-agricultural forests may be species-poor due to the influence of introduced species, isolation from propagule sources, the loss of residual seeds and sprouts of forest species, and the potential disruption of pollinator and seed dispersal vectors (Nason *et al.* 1997).

We describe the floristic composition and structure of 40-year-old secondary forests and upstream old-growth forest in the riparian zone of two rivers in the Cordillera Central mountain range of the Dominican Republic. To date, there have been no studies of forest recovery in this region. We examined the variation in structure and composition, vascular plant species richness, and life-form variation within and between secondary and old-growth forests. Assuming dispersal limitation of isolated rare species and because of the lengthy tenure of agriculture (*ca* 60 yr), we expected species richness to be lower in the secondary forests. Following 40 years of forest recovery, we expected tree size structure to be similar in old-growth and secondary forests. We hypothesized, however, that the abundance and diversity of some plant life-forms (*e.g.,* epiphytes) would remain lower in the post-agricultural forests even after 40 years of recovery.

METHODS

Study area.—The study was conducted in riparian forests on the northeastern slopes of the Cordillera Central in Armando Bermudez National Park, Dominican Republic (Fig. 1). The natural vegetation in the area is classified as subtropical lower montane wet forest (Hartshorn *et al.* 1981) in the elevational range of our study (1100–1360 m elev.). Annual rainfall and temperature average 1860 mm and 19°C, respectively (INDRHI 2000). The area experiences a three-month dry season during the winter when monthly rainfall averages 80 mm (INDRHI 2000). The entire study was located on well drained, flat alluvial terraces in a fairly narrow floodplain (150–300 m wide). No formal soil classification has been conducted in the region, but soil analyses were performed as part of the present study. Soils in secondary forests did not differ systematically from old-growth forests in any major soil nutrient parameter (NO_3, P, K, Ca, and Mg), and pH averaged 5.4 for secondary forests and 5.5 for old-growth forests. Likewise, no consistent differences were evident in texture (all were coarse, sandy loams), soil organic matter, and bulk density between forest types. The natural disturbance regime in these floodplain forests includes treefall gaps of varying size created by windstorms, as well as catastrophic floods, both associated with intense hurricanes. The frequency and severity of the flood regime are undocumented, although large, destructive floods capable of felling large trees have occurred at least twice in the last 25 years during Hurricanes David in 1979 and George in 1998. No evidence of fire was apparent despite its widespread recurrence on nearby slopes and ridges (P. H. Martin, pers. obs.).

Secondary and old-growth vegetation were sampled along two rivers, Río Guanos and Río Ta-

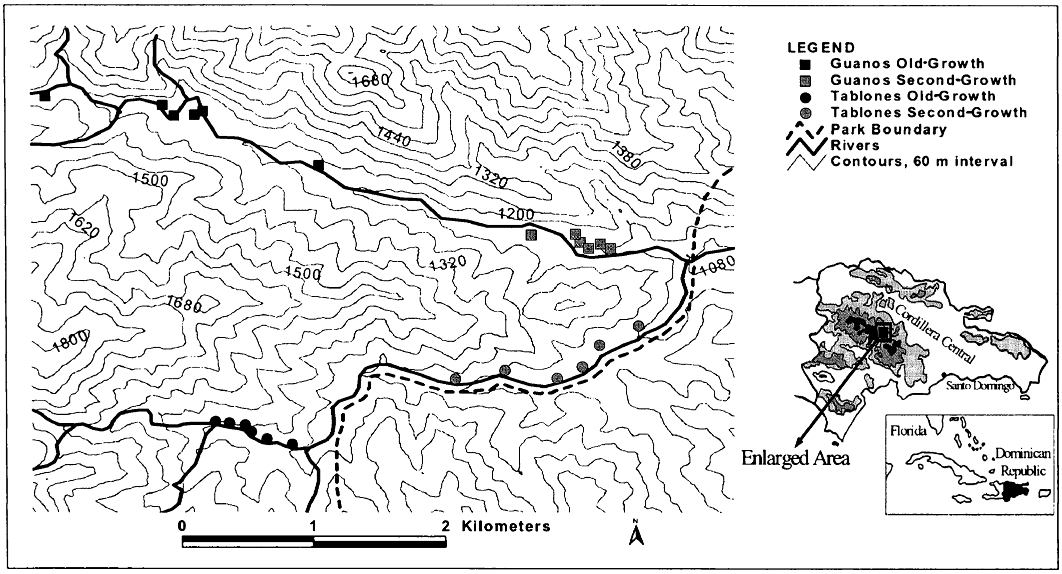

FIGURE 1. Map of the eastern entrance to Parque Nacional Armando Bermudez, Dominican Republic, and locations of secondary and old-growth forest plots.

blones, near the northeastern entrance to Bermudez National Park. Portions of the lower floodplain along both rivers now inside the park boundary were cleared for agriculture *ca* 1900 when the valley was settled (Dirección Nacional de Parques 1997). When the park was created in 1956, the settlers in these cleared riparian areas were relocated and natural regeneration began. No upland forests were similarly cleared and then abandoned; hence, only secondary riparian forests were available for study. For consistency, only old-growth riparian forests were used for comparisons in this analysis. Upstream old-growth riparian forests were never cleared as further settlement upstream was halted in 1923 when the area was first put under conservation protection (Dirección Nacional de Parques 1997). Because of this pattern of land clearance, all old-growth plots were necessarily located upstream from the secondary forests (Fig. 1). This site configuration was not ideal, but because there was only a modest elevation gradient across our sites, we do not think that this was sufficient to cause differences in composition between forest types. A recent multivariate analysis of vegetation composition across the larger elevation gradient did not find a difference within this elevational zone (P. H. Martin, pers. obs.). There were no other differences in local environmental factors (slope angle, aspect, or soils) among our sites.

Interviews with local residents indicated that low-intensity agriculture, supplemented with introduced fruit trees, coffee, and small-scale animal husbandry, was the previous land use in these secondary forest areas. Farms were small, on the order of 1 to 2 ha. Fields were occasionally burned with light surface fires and were rarely, if ever, plowed. The locations of secondary forests were identified with the help of local guides and verified with aerial photographs taken in 1966 in which the boundary between intact forest and regenerating areas is clearly visible. Old-growth forests were further verified by the absence of stumps and cultivated species (*e.g.,* fruit trees or coffee).

Vegetation sampling.—Twelve circular 0.1 ha plots (six per forest type) were located on each river at random distances along transects running parallel to the rivers. Within each plot, we measured all live woody vegetation in three size classes: (1) trees (stems ≥10 cm DBH), (2) saplings (stems ≥1.4 m tall and <10 cm DBH), and (3) seedlings (stems ≥0.50 m tall and <1.4 m tall). Saplings and seedlings were measured in a nested strip plot 1 m wide and 17 m long running north–south along the plot's diameter. In this nested strip plot, the presence and species of ground ferns and herbaceous plants were also noted. To estimate canopy height, three dominant trees in each plot were measured using a Vertex Hypsometer (Haglöf, Sweden). These trees were selected to represent the maximum height of the contiguous canopy; emergent individuals above the canopy (which were rare) were not measured. Woody stems were classified by life-form as canopy tree, treelet (midstory species), shrub, palm, arborescent fern, hemiepiphyte, and liana. All species were identified by common name in the field with the aid a local expert (Francisco Peralta, Dominican Park Service) and type specimens were identified to species at the Dominican National Botanical Garden in Santo Domingo, where voucher specimens were deposited in the herbarium. Fortunately, the taxonomy of the region has been well studied (Hager & Zanoni 1993). Nomenclature follows Liogier (1982).

We employed a semiquantitative approach to estimate the abundance of vines (the term "vine" as used here includes both herbaceous climber species and woody lianas) and various epiphyte taxa, because casual observations suggested differences between forest types. We used an ocular method described by McCune and Lesica (1992), suitable when species richness is moderate. We initially surveyed the epiphytic and vine community across forests, gathering as many species as possible from standing and downed trees until the accumulation of new species leveled off. We found the species counts low enough to make ocular sampling feasible and our survey was very similar to the Dominican Park Service's epiphyte and vine species list (Dirección Nacional de Parques 1997). The annual precipitation at our site is considered "quite dry" for vascular epiphyte habitat, and typically only orchids and bromeliads are found at such moisture levels (Gentry & Dobson 1987), easing identification efforts. Once the species were learned, all epiphytes and vines growing on each tree were identified to species (except ferns, lycopods, and bryophytes, which were identified by groups) and categorized into abundance classes. For epiphytes (except bryophytes), the following abundance classes were used: low (1–5 individuals), intermediate (6–10), and high (>10). For vines and bryophytes on individual trees, we measured percent cover on that tree (both crown and trunk) using the following abundance classes: low (≤15% cover), intermediate (>15 and ≤30% cover) and high (>30% cover). The bounds for these abundance classes were developed based on observations of epiphyte and vine abundance in the field (*e.g.,* one vine species infrequently covered much more than 30 percent of a tree). The field crew worked together carefully to develop consistent estimates for classifying abundance. Quality assurance procedures are described in McCune *et al.* (1997). While not previously applied to vascular epiphytes and vines, these methods have been closely documented for reproducibility on lichen and bryophytes (McCune *et al.* 1997).

DATA ANALYSIS.—For forest structure, we computed means and variation separately for old-growth and secondary forest types on each of the two rivers. As the total number of species comprising the plant community was not estimated with rarefaction techniques (*e.g.* species-individual curves), species counts are referred to as species density (no. of species per unit area) rather than species richness. We calculated an importance value index (IVI) for trees as the average of relative density, frequency, and basal area, and used relative density and frequency for IVI calculations of saplings and seedlings. For epiphytes and vines, a different approach was used to calculate importance values because estimates of abundance for these groups were categorical. Dominance was calculated as the percentage of all trees sampled that had a high abundance class (as defined above) of a given epiphyte or vine species; density was calculated as the percentage of trees with a given species present on it in any amount; and frequency was calculated as the percentage of plots with a given species present in any abundance on any tree.

Floristic similarity of all life-forms that were identified to species (woody plants, woody and herbaceous vines, epiphytes, herbs, and ground ferns) was compared between and within forest types using Jaccard's similarity index (Mueller-Dombois & Ellenberg 1974). Additional comparisons of woody species similarity were made using the modified Sørenson's quantitative index (Bray & Curtis 1957), which compares the relative abundance of shared species. Tree composition was also compared using Ellenberg's quantitative index, which compares species similarity on a relative basal area basis (Mueller-Dombois & Ellenberg 1974).

Statistically significant differences in structure, life-form, and species density counts were detected using a nested ANOVA, with the 0.1 ha plots nested within their respective site as replicates. Analyses were performed using SAS (SAS 2003). Data transformations were made when necessary to conform all analyses to the assumptions of the general linear model (Neter *et al.* 1996). Differences in tree size-class distributions were detected using pairwise comparisons controlled at a family error rate of $\alpha = 0.05$ (Schwarz *et al.* 2001). Statistical significance was set at $\alpha < 0.05$.

TABLE 1. *Dominance, density, and species counts in 40-year-old secondary and old-growth riparian forests in the Cordillera Central, Dominican Republic. For woody plants, dominance is expressed as basal area (m^2/ha) and density as stems/ha. Pooled groups are all life-forms of that size class. For vines and epiphytes, percentages were calculated as the number of trees with a high abundance of each habit group (dominance) and as the number of trees with each habit group present (density). Species counts are tallies of each new species sampled in random samples of each forest type (12 0.1 ha plots per type). Significant differences (from a nested ANOVA; $\alpha <$ 0.05) between forest types are indicated by bold-faced values.*

	Dominance		Density		Species Counts		
Life-form	Old-growth	Secondary	Old-growth	Secondary	Old-growth	Secondary	All Sites
Trees (pooled)	**35.2**	**25.6**	685	596	46	38	59
Dicot canopy trees	31.4	25.4	**488**	**575**	41	34	54
Arborescent ferns	**1.3**	**0.1**	**43**	**3**	4	3	4
Palm	**2.7**	**0.3**	**154**	**18**	1	1	1
Saplings (pooled)	—	—	15,343	11,863	44	43	63
Treelets	—	—	**10,613**	**5011**	17	18	25
Seedlings (pooled)	—	—	15,736	13,677	45	40	64
Total woody spp.	**35.2**	**26.1**	**42,377**	**31,147**	67	61	92
Bromeliads	**18%**	**4%**	**64%**	**39%**	**10**	**6**	10
Orchids	**8%**	**<1%**	**34%**	**6%**	**30**	**9**	31
Moss	**8%**	**<1%**	**40%**	**30%**	—	—	—
Epiphytic ferns and lycopods	5%	1%	34%	24%	—	—	—
Other epiphytes	**3%**	**<1%**	**15%**	**4%**	**20**	**10**	20
Vines	**9%**	**21%**	**31%**	**49%**	29	34	35
Ground ferns	—	—	—	—	**28**	**21**	32
Herbs	—	—	—	—	**29**	**16**	34
Total spp.					**213**	**157**	254

RESULTS

FOREST STRUCTURE.—Densities of woody species for all the canopy tree, sapling, and seedling size classes were not significantly different between secondary and old-growth forests (Table 1). Basal area of trees was significantly higher in old-growth forests ($P <$ 0.02); secondary forests had 27 percent less basal area on average. Introduced species represented a high proportion of tree abundance in secondary forests, comprising 23.9 percent of the basal area for the Guanos forest and 15.6 percent for the Tablones forest. Introduced species were completely absent from old-growth forests. All forests exhibited the reverse-J-shaped tree diameter distribution (Fig. 2), but some density differences were evident, particularly in the smaller diameter classes. Secondary forests had a significantly higher ($P < 0.009$) stem percentage (22%) in the second smallest diameter class (20–29.9 cm DBH) than old-growth forests (13%), while old-growth forests had a significantly higher ($P < 0.037$) number of moderately large individuals (60–69.9 cm DBH). Quadratic mean diameter was not significantly different between forest types, 26.5 cm in old-growth forests and 23.4 cm in secondary forests ($P = 0.11$). Mean canopy height was only marginally greater in old-growth forests, 27.3 versus 24.6 m.

Life-form composition differed significantly between forest types. Old-growth forests had a significantly higher density ($P < 0.011$) and basal area ($P < 0.00$) of arborescent ferns (*Cyathea* spp. and *Alsophila* sp.) and a significantly higher density ($P < 0.032$) and basal area ($P < 0.033$) of the park's sole palm species, *Prestoea montana* (R. Graham) Nichols. Secondary forests had a significantly higher relative abundance (RA) of stems of dicotyledonous canopy trees ($P < 0.01$; Fig. 3a), whereas old-growth forests had a higher RA of palms ($P < 0.04$) and arborescent ferns ($P < 0.01$). For the sapling size class (Fig. 3b), the relative abundance of dicotyledonous canopy trees was also significantly higher in secondary forests ($P < 0.01$) as was the abundance of the palm species ($P < 0.016$), although the RA of the palm was still low in secondary forests (3%). Treelet species dominated both understory size classes in the old-growth forests. Sapling-sized treelet species were found in significantly higher densities in old-growth forests ($P < 0.01$), averaging 1.1 treelets/m^2 versus 0.5/m^2 in secondary forests. For the seedling size classes (Fig. 3c), the abundance of seedling-sized canopy tree species remained significantly higher in the secondary forests ($P < 0.001$), whereas seedling-sized treelet species were significantly more abundant in the old-growth forests ($P < 0.01$). There was no

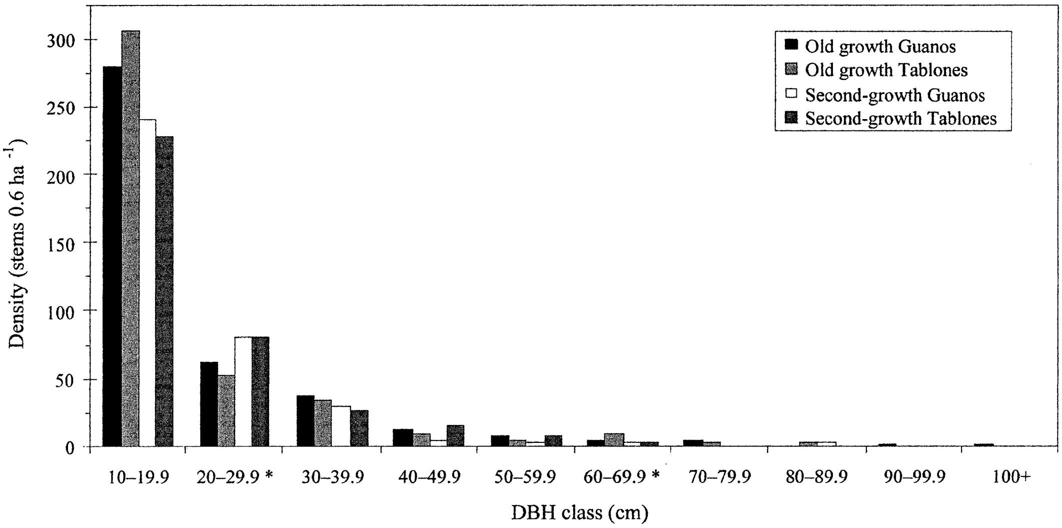

FIGURE 2. Diameter distribution of stems ≥10 cm DBH in two 40-year-old secondary and two old-growth riparian forests in the Cordillera Central, Dominican Republic. An asterisk denotes a significant forest type effect for DBH class.

significant variation in life-form composition within forest type in any size classes, except for tree-sized palms, which were significantly more abundant in old-growth Tablones than old-growth Guanos.

In general, the epiphyte community was dominated by drought-resistant bromeliads of the genus *Tillandsia.* Epiphyte abundance, in terms of dominance and density as defined above, was much higher in old-growth forests. In particular, Bromeliaceae epiphytes were significantly more abundant in old-growth plots ($P < 0.016$), present in a high abundance on 18 percent of trees in old-growth plots compared to only 4 percent with high abundance in secondary plots. Orchidaceae epiphytes were also significantly more abundant in old-growth plots in all abundance classes (Table 1). Epiphytes of the Orchidaceae family were present in all abundance classes on 34 percent of old-growth trees compared to only 6 percent in secondary plots ($P < 0.000$). Similarly, both moss and the strangler group (a single species, *Oreopanax capitatus* [Jacq.] Dcne. & Pl.) occurred with a significantly higher percentage on trees in old-growth plots. Moss was present in the high abundance class on 8 percent of trees in old-growth plots compared to less than 1 percent of trees in secondary plots ($P < 0.02$). The strangler species was also present on significantly more trees ($P < 0.033$) in old-growth forests (6%). In contrast, vines (including both herbaceous climbers and woody lianas) were significantly more abundant in secondary forests. This difference was most pronounced in the high abundance class in which secondary forests had vines in high abundance on 13 percent of trees compared to only 6 percent in old-growth forests ($P < 0.006$). In general, 49 percent of trees in secondary forests had vines present in some abundance compared to 31 percent for old-growth forests ($P < 0.018$). Most of the vine species were herbaceous in growth form; woody lianas were uncommon (Appendix 1). The frequency and abundance of epiphytic ferns, lycopods, foliose lichen (*Usnea* sp.), and parasitic mistletoes were not significantly different between old-growth and secondary forests.

DIVERSITY AND COMPOSITIONAL PATTERNS.—A total of 86 woody plant species, 54 with DBH ≥10 cm, were encountered across all the plots (2.4 ha); seven of these were introduced species (Appendix 1). Tallying all taxonomic groups identified to species, the old-growth sites had 213 species, while the secondary forests had 157 species (Table 1). Woody species comprised 32 percent of the vascular species in old-growth forests compared to 39 percent in the secondary forests. Introduced species were 12 percent of the woody species in secondary forests. Mean forest type and site-level comparisons indicated that the number of tree species was comparable between secondary and old-growth forests; however, when only native tree species were com-

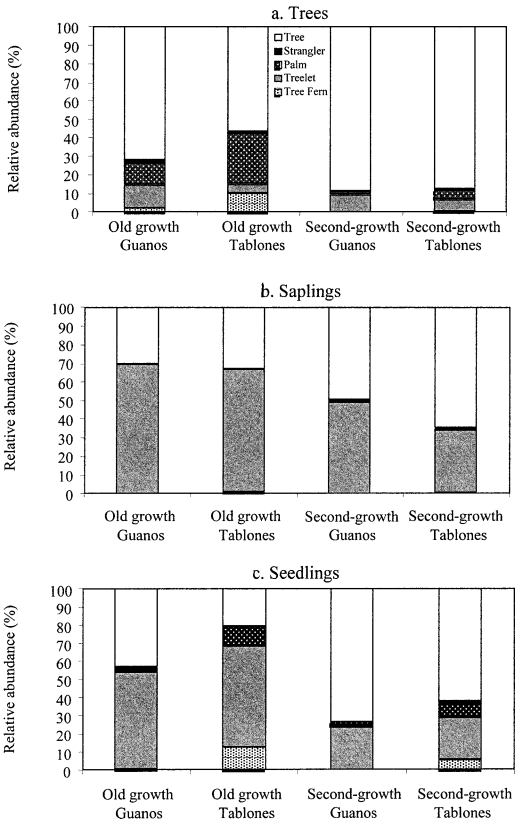

FIGURE 3. Life-form composition of woody stems in terms of relative stem abundance sampled in two 40-year-old secondary and two old-growth riparian forests in the Cordillera Central, Dominican Republic.

pared, the mean number of tree species per plot was significantly lower in secondary plots ($P <$ 0.007). There were 25 treelet species sampled in all forests, 27 percent of the total woody species. Despite a much higher density in old-growth forests, treelet species density was very similar between forest types. Ground ferns and herbaceous plants both made important contributions to the species numbers of each forest type, comprising 13 and 14 percent, respectively, of total old-growth plant species and 13 and 10 percent of secondary forests. Overall, ferns, herbs, and woody species confined to the understory comprised 35 percent of total species in both forest types.

Comparisons of floristic similarity (Jaccard's index) for all plant life-forms were lower between old-growth and secondary forests (45–55%; $\bar{x}$ = 51%) than within forest type (61% and 79%; Table 2), as expected. Floristic similarity of canopy trees weighted for abundance (Sørenson's index) was lower for comparisons between old-growth and second-growth forests (32–49%) than within forest types (49% and 58%), and second-growth forests were more similar in composition to one another than were old-growth forests. Similarity values were higher when weighted for basal area (Ellenberg's index). Again, the species composition within the two secondary forests had a higher similarity value (81%) than within old-growth forests (62%), and these values were higher than the comparisons between forest types (33–58%). Surprisingly, mean floristic similarity between secondary and old-growth forests was higher for trees (39%) than for comparisons of canopy tree species in the sapling (35%) and seedling (30%) size classes. Introduced species appeared to play an important role in this dissimilarity; when only native canopy tree species were compared, mean similarity values of saplings and seedlings between forest types were higher (42 and 36%, respectively).

Two of the dominant tree species, *Tabebuia berterii* (DC) Britton and *Ocotea leucoxylon* (Sw.) Mez, exhibited similar abundance in old-growth and secondary forests (Fig. 4a). The canopy tree *Meliosma impressa* Krug & Urb. was much more abundant in both old-growth forests. Introduced species comprised an average of 29 percent IVI in secondary forests, largely associated with two species, *Syzygium jambos* (L.) Alst. and *Inga vera* Willd. (native to lower elevations of Hispaniola but introduced locally as a nitrogen-fixing shade tree). The endemic pine *Pinus occidentalis* was also important in both secondary forests where it attained large sizes as an emergent. The pattern of relative dominance among tree species was similar between old-growth and second-growth forests, with the five most dominant tree species constituting 59–66 percent of the total IVI in each of the four forests.

Shifts in the composition of the smaller size classes were suggestive of successional trends. Two canopy tree species, *O. leucoxylon*, and *Prunus occidentalis* Swartz, were abundant in the sapling size classes in all forests (Fig. 4b), suggesting these species are late-successional dominants. All of the trees that dominate the canopy of the old-growth forests appeared as saplings in the secondary forests, with the exception of *M. impressa* and the arborescent ferns. Three of the canopy dominants in old-growth (*P. montana*, *Sloanea ilicifolia* Urb., and *T. berterii*) were more abundant as saplings in the secondary forests than in the old-growth forests, suggesting these species are mid-successional. Introduced tree species, especially *S. jambos*, continued to be important in the sapling layer of the second-

TABLE 2. *Jaccard's percent similarity of all life-forms combined, Sørenson's quantitative index (abundance) of woody plants (all size classes), vines and epiphytes, and Ellenberg's quantitative index (basal area) of trees sampled in two 40-year-old secondary and two old-growth riparian forests in the Cordillera Central, Dominican Republic.*

Jaccard's Percent Similarity			
All life-forms	Old-growth Guanos	Secondary Guanos	Secondary Tablones
Old-growth Tablones	0.61	0.45	0.52
Old-growth Guanos	—	0.52	0.55
Secondary Guanos	—	—	0.79
Sørenson's quantitative index (abundance)			
All trees			
Old-growth Tablones	0.49	0.32	0.39
Old-growth Guanos	—	0.35	0.49
Secondary Guanos	—	—	0.58
Treelets			
Old-growth Tablones	0.45	0.34	0.52
Old-growth Guanos	—	0.23	0.24
Secondary Guanos	—	—	0.40
Vines			
Old-growth Tablones	0.41	0.55	0.57
Old-growth Guanos	—	0.49	0.39
Secondary Guanos	—	—	0.47
Epiphytes			
Old-growth Tablones	0.60	0.30	0.40
Old-growth Guanos	—	0.35	0.46
Secondary Guanos	—	—	0.53
Ellenberg's quantitative index (basal area)			
All trees			
Old-growth Tablones	0.62	0.33	0.47
Old-growth Guanos	—	0.48	0.58
Secondary Guanos	—	—	0.81

ary forests, comprising a combined 31 percent of sapling IVI. Some treelet species were dominant in the sapling layer of both old-growth and secondary forests, particularly *Psychotria berteriana* DC. (28% and 30% RA, respectively) and *Gomidesia lindeniana* Berg. (14 and 8% RA, respectively), while *Myrica splendens* (Sw.) DC. and *Alophyllus crassinervis* Radlk. were abundant in old-growth forests (27 and 8% RA) but scarce in secondary forests (2 and 1% RA). Four introduced species of the genus *Citrus* were abundant treelets in the secondary forests (24% RA). There were no striking compositional shifts between saplings and seedling size classes (Fig. 4c), as the IVI of the dominant species remained similar; however, two shade tolerant tree species, *O. leucoxylon* and *S. jambos*, notably increased in importance from the sapling size class to the seedling size class in the secondary forest along the Río Tablones.

EPIPHYTES AND VINES.—Overall, 61 species of vascular epiphytes and 35 species of vines were encountered across all plots (2.4 ha; Table 1). These tallies were very similar to the Dominican Park Service species list (Dirección Nacional de Parques 1997). The species counts of all vascular epiphytes and vines combined were significantly higher in old-growth forests ($P < 0.000$). Vascular epiphyte species density averaged 46 spp./0.6 ha in old-growth forests, while the secondary forests averaged only 19 spp./0.6 ha. Vascular epiphytes comprised 29 percent of the total species of old-growth forests compared to 17 percent for secondary forests. Mean counts of Orchidaceae and Bromeliaceae species were significantly higher in old-growth forests ($P < 0.000$ and $P < 0.001$, respectively). In contrast, species counts of vines were similar between forest types. The number of species of vascular epiphytes at our site was fairly high given the comparatively low annual precipitation (Gentry & Dobson 1987, Benzing 1990, Nieder *et al.* 2001). Frequent cloud formation in this high elevation forest is the most likely explanation.

Comparing composition between forest types

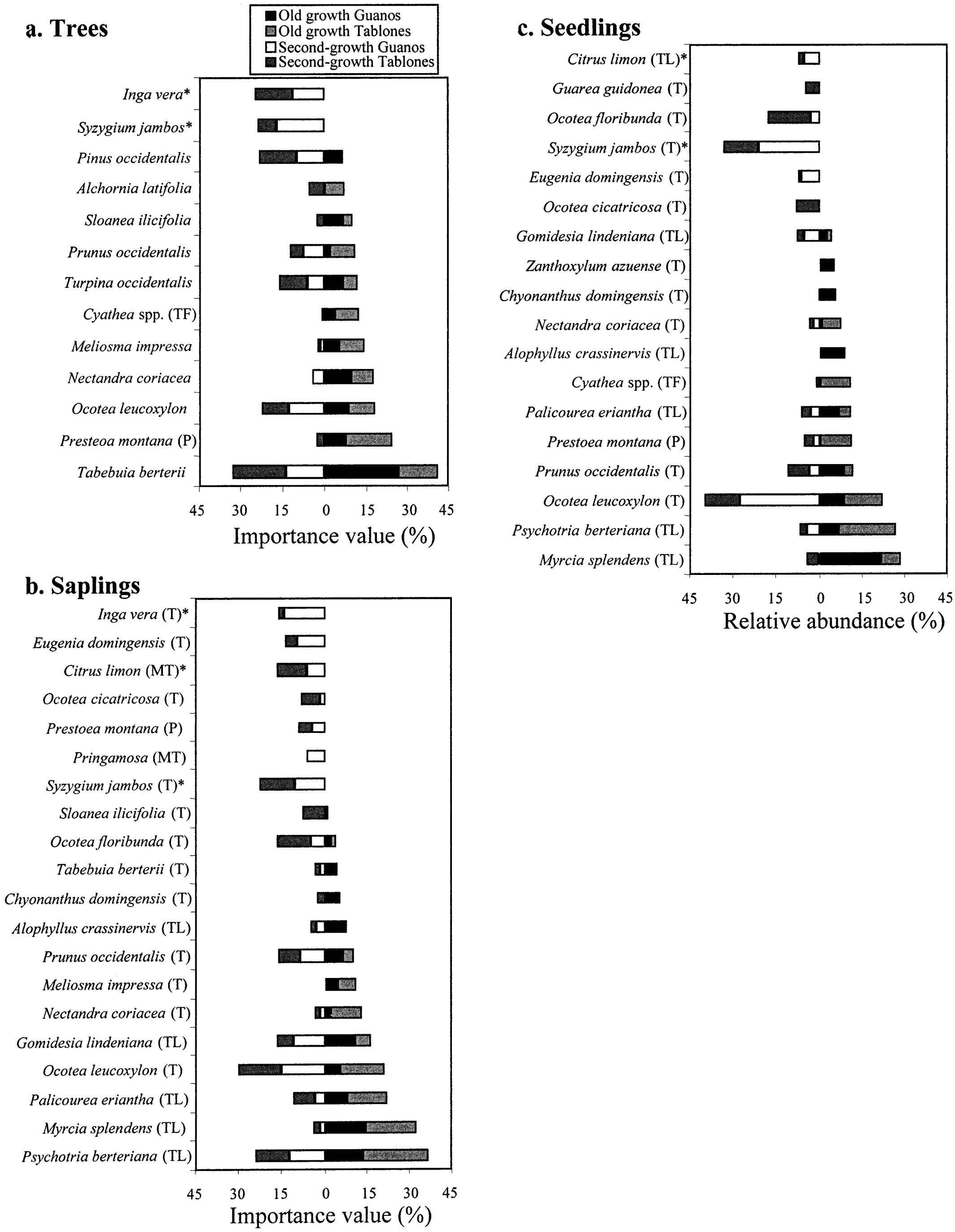

FIGURE 4. Dominant woody species (comprising a minimum of 5% of the importance value index in at least one forest type) by size class in two 40-year-old secondary and two old-growth riparian forests in the Cordillera Central, Dominican Republic. Life-form codes are as follows: (T) = canopy tree, (TL) = treelet, (P) = palm, and (TF) = aborescent fern. An asterisk denotes introduced species.

using Sørenson's index, bromeliads as a group had the highest floristic similarity ($\bar{x}$ = 59%), as the same six species of bromeliads recolonized both secondary forests; the bromeliad community of the two old-growth sites was also floristically highly similar (80%). Although vines were much more abundant in secondary forests, floristic similarity was also high for vines within and between the old-growth and the secondary forests (Table 2). In contrast, between-forest type similarity was notably low for Orchidaceae, ranging from 9 to 29 percent ($\bar{x}$ = 18%), with a similarity of 39 percent for within-forest type comparisons.

Among the vines, *Manetia domingensis* Sprengel had the highest IVI in all forests, with a range of 17 to 28 percent IVI ($\bar{x}$ = 24%; Table 3). In general, the same six species of vines (*ca* 25% of all vine species) comprised 52–84 percent IVI in all four forests ($\bar{x}$ = 59%). For bromeliads, the same three species of *Tillandsia* were ranked the most important in all forests. Without exception, *Tillandsia compressa* Bert. Ex Schult was the most important bromeliad, comprising a range of 16 to 56 percent IVI ($\bar{x}$ = 29%). Comparing between forest types, this species was more important in secondary forests ($\bar{x}$ = 42%) than old-growth forests ($\bar{x}$ = 21%). Some other bromeliad species were either notably more important in old-growth forests (*Vriesea sintenisii* [Baker] Smith & Pitt, *Tillandsia useoides* L.) or absent from secondary forests altogether (*Catopsis nitida* [Hooker] Griseb.). For orchids, two species accounted for most of the floristic similarity between forest types, *Stelis domingensis* Cogn. and *Quisqueya fuertesii* Dod. To a lesser degree, *Pleurothallis domingensis* Cogn. and *Lycaste barringthoniae* (Smith) Lindley were also important in both forest types. The old-growth forests had many other orchid species that were absent from secondary forests (Appendix 1).

DISCUSSION

Our study demonstrated that the structure of woody vegetation in secondary tropical riparian forests can approach old-growth characteristics in canopy height, tree stem density, and size distributions within 40 years, even after decades of prior low-intensity agriculture. In practice, clearing for agriculture is the major anthropogenic disturbance in these riparian forests, as the vast majority of these forests in the Dominican Republic were converted to agriculture decades earlier (Hartshorn *et al.* 1981); thus, the regeneration pattern of this study provides an informative example for understanding future natural regeneration of Hispaniolan riparian forests.

There are no published studies of secondary forests in Hispaniola for comparison, but other research in the Neotropics has reported rapid vegetation recolonization when prior land use had been light (2–3 yr of pasturing or agriculture in Eastern Amazonia; Uhl 1987, Uhl *et al.* 1988), and the basal area of secondary forests can approach or equal old-growth in 20 to 40 yrs after natural disturbances (Knight 1975, Worbes 1997) or in post-pasture forests (Snedaker 1970, Scott 1977, Lugo 1992, Aide *et al.* 1996, Guariguata *et al.* 1997, Foster *et al.* 1999). Our results, however, are in contrast to these findings; basal area was 27 percent lower in our secondary forest forests. Saldarriaga *et al.* (1988), who studied a long chronosequence of post-slash-and-burn secondary forests in Western Amazonia, likewise found secondary forests with 30 percent lower basal area than old growth after 40 years; they maintained that full structural recovery could take up to 200 years despite the short tenure of agriculture (2–3 yr) at their study sites, perhaps due to the very poor soils in that region. Guariguata *et al.* (1997) hypothesized that differences in soil fertility are responsible for contrasting regional recovery rates, although the idiosyncrasies of each site probably account for some differences as well. In our study, it is not clear why basal area was lower in secondary forests when the soils remained fertile and other measures of woody structure were similar between forest types. Perhaps the extended length of land use slowed the recovery of basal area by eliminating most remnant trees, stump sprouts, and buried seeds. Indeed, remnant vegetation can play a critical role in forest recovery, promoting rapid increases in species richness, tree density, and aboveground biomass (Guariguata & Ostertag 2001). Guariguata *et al.* (1997) found that remnant trees were important to the recovery of basal area in their secondary forests of Costa Rica.

In terms of structural and life-form complexity, our second-growth forests were clearly simpler than the old-growth forests. Denslow (1996) noted that this was a common feature in very young secondary forests in the tropics, and our study suggests that this condition can persist for decades. In particular, treelet species were more abundant in the understory of old-growth forests, and these species contribute to greater canopy stratification, a condition commonly noted in mature tropical forests (Golley 1983). The arborescent ferns *Cyathea* spp. and *Alsophila* sp., the hemiepiphyte strangler *O. capitatus*, and the palm species *P. montana*, were also much more abundant in old-growth forests, as was true of this palm species in Puerto Rico (Aide *et al.* 1996). Life-form complexity of woody species in secondary forests has not been widely studied in the tropics, although Guariguata *et al.* (1997) and Svenning (1998) also found canopy palms comparatively more abundant in old-growth forests (suggesting this is a common pattern). Guariguata *et al.* (1997) also noted higher abundances of treelets in old-growth forests. The higher abundance of treelets in old-growth forests may have important implications for regeneration by reducing forest floor light levels and accelerating succession to very shade tolerant species.

The most striking life-form difference between our forest types was the abundance of epiphytes and vines. Most types of epiphytes were markedly more abundant in the old-growth forests while vines were more abundant in the secondary forests. While there are few similar studies in the tropics, the pattern of reduced abundance of epiphytes in tropical secondary forests has been documented elsewhere (Hietz-Seifert *et al.* 1996, Hietz 1998). Köhler (2002) found a seven-fold lower biomass of epiphytic bryophytes in a 40-year-old secondary forest compared to an adjacent old-growth forest in montane Costa Rica. Conversely, the high abundance of vines in secondary forests has been well documented (Ewel 1983, Hegarty & Caballé 1991, Laurance 1997), and vines have been found to dominate very young secondary forests in the tropics (Uhl *et al.* 1988). The long persistence of a high abundance of vines observed in our study is one of the few reported for tropical secondary forests. DeWalt *et al.* (2000) also found high densities of lianas in a chronosequence of Panamanian forests even after 40 years, with liana density declining only after 70 years of succession.

In comparison, studies in temperate secondary forests have found that vines can dominate regrowth even after 40 years of succession and rapidly recolonize post-agricultural sites (Fike & Niering 1999). Perhaps the low abundance of epiphytes in our secondary forests resulted in part from this phenomenon, as abundant vines may suppress epiphytes by increasing shade and occupying colonization sites. Most vascular epiphytes have long-range seed dispersal (Gentry & Dobson 1987), but their sensitivity to low atmospheric humidity makes them unlikely candidates to successfully colonize open or thinly revegetated areas (Hietz-Seifert *et al.* 1996, Corlett & Turner 1997, Hietz 1998). Moreover, vascular epiphytes, particularly wind-dispersed taxa like bromeliads and orchids, tend to colonize new forests in a clumped pattern as they colonize adjacent trees more rapidly (Madison 1979), and substantial time may be needed to build up reproductive capacity to counter high mortality rates of both juvenile and adult epiphytes (Benzing 1990). Hence, while the woody biomass of secondary forests in the tropics may rapidly recuperate in fertile sites, it appears that the recovery of structural and life-form complexity may be comparatively slow.

Counts of woody plant species (species density) in our secondary forests approached old-growth values in all size classes. Other investigators have reported similar recoveries in 40 years or less in post-slash-and-burn (Saldarriaga *et al.* 1988) and post-pasture tropical secondary forests (Lugo 1992, Aide *et al.* 1996). The similar number of tree species between forest types in our study does contrast with some secondary forests characterized by species-poor canopies of long-lived species (Lang & Knight 1983, Guariguata *et al.* 1997), although these secondary forests were only *ca* 20 years old when studied. Some older secondary forests were found to have low species richness as well, attributable to degraded soils and high local diversity of trees (Pinard *et al.* 1996, Corlett & Turner 1997), and the short-term results of Uhl *et al.* (1988) in Eastern Amazonia corroborated this view. Dispersal limitation may be expected to influence species richness in secondary forests when large areas are abandoned (Thebaud & Strasberg 1997); however, in our study, the extent of clearing was modest, limited by the terrain, and rare species are not numerous in the island flora of Hispaniola (Liogier 1982). In sum, the number of tree species in our post-agricultural, riparian forests quickly approached species numbers in old-growth riparian forests. It would appear that tropical regions, which have poor soils and high local diversity of trees in old-growth forests, are more vulnerable to lowered species richness in a human-altered landscape (Bawa & Seidler 1998).

The percentage of total vascular plant species confined to the understory (treelets, shrubs, ferns, and herbs) was high in both forest types and comparable to other Neotropical forests (Gentry & Emmons 1987). Absolute species counts, however, were considerably higher in our old-growth forests, which had 35 percent more understory species than secondary forests; treelet species numbers, however, were similar and comprised 27–32 percent of the total woody plant species in both forest types. Treelets can comprise a substantial portion of the total

TABLE 3. *Importance value indexes (IVI) of epiphytes and vine species in 40-year-old secondary and old-growth riparian forests in the Cordillera Central, Dominican Republic. Dominance was calculated as the percentage of all trees per forest type with a high abundance class of a given species. Density was calculated as the percentage of all trees per forest type with a given species present. Frequency was calculated as the percentage of plots with a given species found on at least one tree. Importance values are the average of relative dominance, density, and frequency.*

Old-growth Forests	Dominance (%)	Relative Dominance (%)	Density (%)	Relative Density (%)	Frequency	Relative Frequency (%)	IVI (%)
Vines							
Manetia domingensis	1.7	27.8	10.6	18.4	0.75	13.0	20
Mikania barahonensis	0.7	11.9	3.3	5.7	0.58	10.1	9
Senecio lucens	0.7	11.9	3.0	5.1	0.50	8.7	9
Mikania sp.	0.2	3.4	2.4	4.1	0.75	13.0	7
Passiflora sexflora	0.2	3.4	3.2	5.5	0.67	11.6	7
Ipomoea furcyensis	0.3	5.4	2.8	4.8	0.58	10.1	7
Arthrostilidium sarmentosum	0.1	1.7	4.6	7.9	0.58	10.1	7
Odontadenia polyneura	0.3	5.5	4.0	6.9	0.34	5.8	6
Misc. (21 spp.)	1.8	29.0	24.0	41.5	1.00	17.4	29
	6	100	58	100	5.75	100	100
Bromeliaceae							
Tillandsia selleana	3.2	36.6	25.9	22.1	0.83	12.8	24
T. compressa	1.4	15.6	31.2	26.6	1.00	15.4	19
T. caribaea	1.3	15.3	20.1	17.1	1.00	15.4	16
T. compacta	1.0	10.8	15.2	13.0	1.00	15.4	13
Vriesea sintenisii	1.0	11.5	11.7	10.0	0.92	14.1	12
T. useoides	0.6	6.5	5.8	4.9	0.83	12.8	8
Misc. (4 spp.)	0.3	3.8	7.3	6.2	0.92	14.1	8
	9	100	117	100	6.50	100	100
Orchidaceae							
Stelis domingensis	1.1	20.6	8.1	20.9	0.83	13.5	18
Quisqueya fuertesii	0.8	15.1	4.3	11.1	1.00	16.2	14
Lycaste barringthoniae	0.7	12.4	6.4	16.5	0.75	12.1	14
Dichaea glausa	0.8	14.5	6.0	15.5	0.67	10.8	14
Pleurothallis domingensis	0.6	10.2	3.7	9.7	0.75	12.1	11
Tricopilia fragans	0.6	10.9	2.0	5.2	0.42	6.8	8
Jacquiniella teretifolia	0.2	2.7	2.0	5.0	0.42	6.8	5
Isochilis linearis	0.2	3.2	1.5	3.8	0.33	5.4	4
Misc. (22 spp.)	0.7	11.8	5.9	15.2	1.00	16.2	14
	5.6	100	39.9	100	6.17	100	100
Secondary Forests	Dominance (%)	Relative Dominance (%)	Density (%)	Relative Density (%)	Frequency	Relative Frequency (%)	IVI (%)
Vines							
Manetia domingensis	6.4	29.1	25.2	31.4	1.00	20.0	27
Odontadenia polyneura	3.2	14.3	13.7	17.1	0.75	15.0	15
Ipomoea furcyensis	3.1	14.0	7.4	9.2	0.83	16.7	13
Rajania marginata	1.0	4.7	5.4	6.7	0.58	11.7	8
Passiflora sexflora	0.4	1.7	4.6	5.7	0.58	11.7	6
Smilax habanensis	1.1	5.0	3.6	4.5	0.25	5.0	5
Misc. (28 spp.)	6.9	31.3	20.5	25.5	1.00	20.0	26
	22	100	80	100	5.00	100	100
Bromeliaceae							
Tillandsia compressa	1.0	42.4	20.1	37.2	0.92	26.2	35
T. selleana	0.6	26.2	16.3	30.1	0.67	19.0	25
T. caribaea	0.4	15.7	9.9	18.2	0.92	26.2	20
T. compacta	0.2	10.5	2.7	4.9	0.42	11.9	9
T. useoides	0.1	5.2	4.1	7.7	0.33	9.5	7
Vriesea sintenisii	0.0	0.0	1.0	1.9	0.25	7.1	3
	2	100	54	100	3.50	100	100

TABLE 3. *Continued.*

Secondary Forests Vines	Dominance (%)	Relative Dominance (%)	Density (%)	Relative Density (%)	Frequency	Relative Frequency (%)	IVI (%)
Orchidaceae							
Quisqueya fuertesii	0.3	100.0	1.6	42.3	41.7	22.7	55
Lycaste barringthoniae	0.0	0.0	0.8	19.8	0.42	22.9	14
Pleurothallis domingensis	0.0	0.0	0.3	6.6	0.33	18.0	8
Stelis domingensis	0.0	0.0	0.4	10.1	0.17	9.1	6
Jacquiniella teretifolia	0.0	0.0	0.2	6.6	0.17	9.1	5
Misc. (4 spp.)	0.0	0.0	0.6	14.6	0.33	18.2	11
	0	100	4	100	1.83	100	100

woody species of mature tropical forests (62% on mainland Panama; Hubbell & Foster 1986) and therefore, if sensitive to human disturbance, may account for major reductions in woody species richness of tropical secondary forests. This issue has not been addressed directly in the literature, but Lieberman *et al.* (1985) suggested that treelets turn over more rapidly than other groups of trees because of damage from falling trees and limbs, perhaps making them better adapted to dynamic processes. Denslow (1996), however, noted that they are slower to recover from forest clearing than canopy trees. Our results support this view, showing a slower recovery of treelet stem densities if not species richness in secondary forests.

In general, species counts of most nonwoody life-forms were significantly lower in our secondary forests. We emphasize that our counts of epiphyte and herb species are most likely underestimates because they were not conducted on a year-round basis and because an exhaustive survey of the epiphyte community was not performed; hence, our observations of species numbers are most appropriate for comparative purposes within this study. Nevertheless, it appears that these groups—vascular epiphytes, herbaceous plants, and ground ferns—have a smaller suite of species adapted to rapidly colonize deforested areas than do woody species. To our knowledge, this pattern has not been previously documented in the tropics. In temperate secondary forests, herb abundance and diversity may not recover to old-growth levels even after long periods (25–87 yr) of regeneration from cutting or agriculture (Duffy & Meier 1992, Stover & Marks 1998, Singleton *et al.* 2001). Likewise, patterns of higher epiphyte diversity in old-growth forests have been documented by several studies in temperate forests in which species richness of epiphytic mosses and lichens was notably higher in old-growth than second-growth forests (Hietz 1998). Epiphyte abundance and diversity have been strongly correlated with increasing tree size (Benzing 1990, Hietz & Hietz-Seifert 1995, Hietz-Seifert *et al.* 1996, Zotz & Buche 2000); thus, a higher abundance of very large trees in old-growth forests may provide more habitat for epiphytes both in this study and in general. Changes in the canopy environment associated with larger, older trees, such as increased canopy soil and moss mat accumulation, may explain why such mature trees are essential for the successful colonization of many vascular epiphyte species.

The compositional similarity of canopy trees between our secondary and old-growth forests was notable, as virtually all studies of post-agricultural recovery in tropical forests have found a slow recovery of species composition to preclearing characteristics (Chazdon 2003). In general, the slow recovery of species composition in secondary forests is often attributed to inadequate dispersal of late-successional species (Whitmore 1991, Ingle 2003), which are often large-seeded species. Indeed, many large-seeded species that persist in older forests of Puerto Rico are rare or absent in adjacent secondary forests, including the palm species found in this study (Aide *et al.* 2000). Our study suggests that the recovery of floristic similarity in secondary stands in tropical riparian forests may be an exception to this pattern. Here, the compositional similarity of canopy trees was largely due to the importance of *T. berterii*, and to a lesser extent, *O. leucoxylon*, in both forest types. *Tabebuia* is a common floodplain forest genus in the Caribbean (Borhidi 1996, Francis & Lowe 2000) and the Amazon (Worbes 1997), and the *Ocotea* genus is common in late-successional Neotropical forests (Aide *et al.* 1996, Gregory *et al.* 2001). Despite the importance of *T. berterii* in all forests, it was not abundant in regeneration size classes, suggesting that it may be disturbance-dependent. This pattern is similar to

Puerto Rico where the congener *Tabebuia heterophylla* dominates recently abandoned pastures and secondary forests at higher elevations (Lugo 1992, Aide *et al.* 1996). The floristic evidence suggests that the Guanos River has been influenced by natural disturbance more recently than the Tablones River, given the comparatively high percentages of *P. occidentalis* and *T. berterii* in the tree size class of the old-growth forests along the Guanos River. The pine is a classic early-successional species, requiring high light levels, and both species comprise the vast majority of seedlings currently colonizing the large openings made by flooding associated with Hurricane George in 1998 (P. H. Martin, pers. obs.). *Tabebuia* vigorously stump sprouts at our sites (P. H. Martin, pers. obs.), another advantage in a disturbance-prone ecosystem. Thickets of the tall grass *Gynerium sagittatum* also form in recently disturbed areas along the river's banks. Riparian forests in general are frequently disturbed by flooding (Walter 1974, Salo *et al.* 1986, Perry 1994). Our site's frequent exposure to hurricanes and floods may have indirectly selected for a greater resilience to deforestation than in some tropical forests. Frequent disturbance is a likely reason for the high similarity of canopy tree species between forest types; indeed, all of the tree species dominant in the old-growth forest have appeared in high numbers in the canopy of at least one of our secondary forest plots.

The high abundance of introduced tree species in our secondary forests is a clear legacy of prior agriculture. The influence of introduced species in tropical secondary forests has not yet received much attention. While introduced plants are rare in undisturbed tropical forests, they can become invasive and dominant in human-disturbed tropical forests (Fine 2002). Laurance (1997) noted that nonnative herbs and vines are far more likely to proliferate in disturbed tropical forest remnants. Studies in Puerto Rico (Lugo 1992, 2004; Aide *et al.* 1996, Chinea 2002) noted the prominence of introduced species in secondary forests, which comprised a high percentage of all species in secondary forests (with *S. jambos* dominating in some cases). *Syzygium jambos* has been reported as an invasive species in other areas of the tropics (Borhidi 1996, Di Stefano *et al.* 1998, Fine 2002); however, the high incidence of introduced species found in Caribbean secondary forests was not found in secondary forests of Costa Rica and Panama (Guariguata *et al.* 1997, Denslow & Guzman 2000), suggesting that the trend described here may be more typical of island ecosystems (which often have high numbers of introduced species). Nevertheless, the high shade tolerance of *S. jambos* and its abundant regeneration suggest that it is entrenched in our secondary forests; the same is true for other shade tolerant introduced species, such as *Citrus* spp. These introduced species may play a detrimental role in the recovery of species richness for native plants in secondary forests and have cascading effects on fauna (Cruz 1987), as other studies have emphasized the highly inhibitory role that nonnative plants can have on the successful recolonization of abandoned areas by native vegetation (MacDonald *et al.* 1991, Fike & Niering 1999). These introduced species will ensure that the human influence on forest composition will likely persist for decades to come.

The recovery of woody structure and tree species richness in this study is encouraging for the prospect of biodiversity conservation in tropical secondary forests; however, adequate reservoirs of regional biodiversity are necessary if similar recoveries of tropical forest are to occur in other areas. Given the importance of nonwoody life-forms to total species richness, conservation plans should include these groups. Secondary forests will require lengthy periods of protection if the populations of nonwoody plants are to recover along with woody species. Additional studies on the recovery of life-form diversity, including nonwoody plants, in older secondary forests are needed to determine how long this process may take. Our findings also highlight the need to consider introduced plants in the management of tropical secondary forests (Lugo 2004).

ACKNOWLEDGMENTS

We thank F. Peralta, P. Martinez, E. Raposo, J. Demers, E. Grant, J. Cramer, G. Newman, and J. LeBoyer for their help with fieldwork. We gratefully acknowledge the logistical support provided by Dr. R. Lora and the support of the Dominican Park Service. This research was supported by an Andrew W. Mellon Ecosystem Research Program grant administered by the Nature Conservancy. P. Marks, T. Whitlow, and two reviewers provided helpful comments on earlier drafts of the manuscript.

LITERATURE CITED

Aide, T. M., and J. Cavelier. 1994. Barriers to lowland tropical forest restoration in the Sierra Nevada de Santa Maria, Colombia. Rest. Ecol. 2: 219–229.

———, J. K. Zimmerman, L. Herrera, M. Rosario, and H. Marcano. 1996. Forest recovery in abandoned cattle pastures along an elevational gradient in northeastern Puerto Rico. Biotropica 28: 537–548.

———, ———, J. B. Pascarella, L. Rivera L. and H. Marcano-Vega. 2000. Forest regeneration in a chronosequence of tropical abandoned pastures: Implications for restoration ecology. Rest. Ecol. 8: 328–338.

Bawa, K. S., and R. Seidler. 1998. Natural forest management and conservation of biodiversity in tropical forests. Conserv. Biol. 12: 46–55.

Benzing, D. H. 1990. Vascular epiphytes: General biology and related biota. Cambridge University Press, Cambridge, England.

Borhidi, A. 1996. Phytogeography and vegetation ecology of Cuba, 2nd edition. Akadémiai Kiadó, Budapest, Hungary.

Bray, J. R., and J. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. 27: 326–349.

Brown, S., and A. E. Lugo. 1990. Tropical secondary forests. J. Trop. Ecol. 6: 1–32.

Chazdon, R. L. 1998. Tropical forests—Log 'em or leave 'em? Science 281: 1295–1296.

———. 2003. Tropical forest recovery: legacies of human impact and natural disturbances. Perspect. Plant Ecol. Evol. Syst. 6: 51–71.

Chinea, J. D. 2002. Tropical forest succession on abandoned farms in the Humacao Municipality of eastern Puerto Rico. For. Ecol. Manage. 167: 195–207.

Corlett, R. T., and I. M. Turner. 1997. Long-term survival in tropical forest remnants in Singapore and Hong Kong. *In* W. F. Laurance and R. O. Bierregaard (Eds.). Tropical forest remnants: Ecology, management, and conservation of fragmented communities, pp. 333–345. University of Chicago Press, Chicago, Illinois.

Cruz, A. 1987. Avian community organization in a mahogany plantation on a Neotropical island. Caribb. J. Sci. 23: 286–296.

Denslow, J. S. 1996. Functional group diversity and responses to disturbance. *In* G. H. Orians, R. Dirzo and J. H. Cushman (Eds.). Biodiversity and ecosystem processes in tropical forests, pp. 127–151. Springer–Verlag, Heidelberg, Germany.

———, and G. S. Guzman. 2000. Variation in stand structure, light and seedling abundance across a tropical moist forest chronosequence, Panama. J. Veg. Sci. 11: 201–212.

DeWalt, S. J., S. A. Schnitzer, and J. S. Denslow. 2000. Density and diversity of lianas along a chronosequence in a central Panamanian tropical forest. J. Trop. Ecol. 16: 1–19.

Dirección Nacional de Parques. 1997. Plan de manejo y conservacion del parque nacional Armando Bermudez. Estudies y Disenos en Ingenieria Hiraulica, S.A., Santo Domingo, Dominican Republic.

Di Stefano, J. F., L. A. Fournier, J. Carranza, W. Marin, and A. Mora. 1998. Potencial invasor de *Syzygium jambos* (Myrtaceae) en fragmentos boscosos: El caso de Cuidad Colon, Costa Rica. Rev. Biol. Trop. 46: 567–573.

Duffy, D. C., and A. J. Meier. 1992. Do Appalachian herbaceous understories ever recover from clearcutting? Conserv. Biology 6: 196–201.

Duncan, R. S., and C. A. Chapman. 1999. Seed dispersal and potential forest succession in abandoned agriculture in tropical Africa. Ecol. Appl. 9: 998–1008.

Ewel, J. J. 1983. Succession. *In* F. B. Golley (Ed.). Tropical rain forest ecosystems, pp. 217–223. Elsevier Scientific, Amsterdam, The Netherlands.

Fike, J., and W. A. Niering. 1999. Four decades of old field vegetation development and the role of *Celastrus orbiculatus* in the northeastern United States. J. Veg. Sci. 10: 483–492.

Fine, P. V. A. 2002. The invasibility of tropical forests by exotic plants. J. Trop. Ecol. 18: 687–705.

Finegan, B. 1992. The management potential of Neotropical secondary lowland rain-forest. For. Ecol. Manage. 47: 295–321.

———. 1996. Pattern and process in Neotropical secondary rainforests: The first 100 years of succession. Trends Ecol. Evol. 11: 119–124.

Foster, D. R., M. Fluet, and E. R. Boose. 1999. Human or natural disturbance: Landscape-scale dynamics of the tropical forest of Puerto Rico. Ecol. Appl. 9: 555–572.

Francis, J. K., and C. A. Lowe. 2000. Bioecologia de Arboles Nativos y Exoticos de Puerto Rico y las Indias Occidentalis. U.S. For. Serv. Gen. Tech. Rep. IITF-15, Río Piedras, Puerto Rico.

Gentry, A. H., and C. H. Dobson. 1987. Diversity and biogeography of Neotropical vascular epiphytes. Ann. Mo. Bot. Gard. 74: 205–233.

———, and L. H. Emmons. 1987. Geographical variation in fertility, phenology, and composition of the understory of neotropical forests. Biotropica 19: 216–227.

Golley, F. B. 1983. Tropical rain forest ecosystems. Elsevier Scientific, Amsterdam, The Netherlands.

Gomez-Pompa, A., and C. Vázquez-Yánes. 1974. Studies on secondary succession of tropical lowlands: The life-cycle of secondary species. *In* Proceedings of the First International Congress of Ecology, pp. 336–342. The Hague, The Netherlands.

Gregory, S., G. S. Gilbert, K. E. Harms, D. N. Hamill, and S. P. Hubbell. 2001. Effects of seedling size, El Niño drought, seedling density, and distance to nearest conspecific adult on 6-year survival of *Ocotea whitei seedlings* in Panamá. Oecologia 127: 509–516.

Guariguata, M. R., R. L. Chazdon, J. S. Denslow, J. M. Dupuy, and L. Anderson. 1997. Structure and floristics of secondary and old-growth forest stands in lowland Costa Rica. Plant Ecol. 132: 107–120.

———, and R. Ostertag. 2001. Neotropical secondary forest succession: Changes in structural and functional characteristics. For. Ecol. Manage. 148: 185–206.

Hager, J., and T. A. Zanoni. 1993. La vegetacion natural de la Republica Dominicana: Una nueva clasificacion. Moscosoa 7: 39–81.

Hartshorn, G., G. Antonini, R. DuBois, D. Harcharik, S. Heckadon, H. Newton, C. Quesada, J. Shores, and G. Staples. 1981. The Dominican Republic, country environmental profile: A field study. JRB Associates, McLean, Virginia.

Hegarty, E. E., and G. Caballé. 1991. Distribution and abundance of vines in forest communities. *In* F. E. Putz and H. A. Mooney (Eds.). The biology of vines, pp. 313–336. Cambridge University Press, Cambridge, England.

Hietz, P. 1998. Diversity and conservation of epiphytes in a changing environment. IUPAC 70: 2114–2125.

———, and U. Hietz-Seifert. 1995. Structure and ecology of epiphyte communities of a cloud forest in central Veracruz, Mexico. J. Veg. Sci. 6: 719–728.

Hietz-Seifert, U., P. Hietz, and S. Guevara. 1996. Epiphyte vegetation and diversity on remnant trees after forest clearance in southern Veracruz, Mexico. Biol. Conserv. 75: 103–111.

Hubbell, S. P., and R. B. Foster. 1986. Commonness and rarity in a Neotropical forest: Implications for tropical tree conservation. *In* M. E. Soulé (Ed.). Conservation biology: The science of scarcity and diversity, pp. 205–231. Sinauer Associates, Sunderland, Massachusetts.

INDRHI (Instituto Nacional de Recursos Hidraulicos). 2000. Datos de la precipitación en Parque Nacional Armando Bermudez, 1983–1999. Santo Domingo, Dominican Republic.

Ingle, N. 2003. Seed dispersal by wind, birds, and bats between Philippine montane rainforest and successional vegetation. Oecologia 134: 251–261.

Knight, D. H. 1975. A phytosociological analysis of species-rich tropical forest on Barro Colorado Island, Panama. Ecol. Monogr. 45: 259–284.

Köhler, L. 2002. The significance of epiphytes to water and nutrient fluxes in different successional stages of a montane rainforest in Costa Rica. Ph.D. dissertation. University of Goettingen, Goettingen, Germany.

Lang, G. E., and D. H. Knight. 1983. Tree growth, mortality, recruitment, and canopy gap formation during a 10-year period in a tropical moist forest. Ecology 64: 1075–1080.

Laurance, W. F. 1997. Hyper-disturbed parks: Edge-effects and the ecology of isolated rainforest reserves in tropical Australia. *In* W. F. Laurance and R. O. Bierregaard (Eds.). Tropical forest remnants: Ecology, management, and conservation of fragmented communities, pp. 71–83. University of Chicago Press, Chicago, Illinois.

———, and R. O. Bierregaard. 1997. Tropical forest remnants: ecology, management, and conservation of fragmented communities. University of Chicago Press, Chicago, Illinois.

Lieberman, D., M. Lieberman, G. S. Hartshorn, and R. Peralta. 1985. Growth rates and age–size relationships of tropical wet forest trees in Costa Rica. J. Trop. Ecol. 1: 97–109.

Liogier, A. H. 1982. La Flora de la Española. Universidad Central del Este, San Pedro de Macorís, Dominican Republic.

Lugo, A. E. 1992. Comparison of tropical tree plantations with secondary forests of similar age. Ecol. Monogr. 62: 1–41.

———. 2004. The outcome of alien tree invasions in Puerto Rico. Front. Ecol. Env. 2: 265–273.

MacDonald, I. A. W., C. Thebaud, W. A. Strahm, and D. Strasberg. 1991. Effects of alien plant invasions on native vegetation remnants on La Reunion. Environ. Conserv. 18: 51–61.

Madison, M. 1979. Distribution of epiphytes in a rubber plantation in Sarawak. Selbyana 5: 207–213.

McCune, B., J. Dey, J. Peck, D. Cassell, K. Heiman, S. Will-Wolf, and P. Neitlich. 1997. Repeatability of community data: Species density versus gradient scores in large-scale lichen studies. Bryologist 100: 40–46.

———, and P. Lesica. 1992. The trade-off between species capture and quantitative accuracy in ecological inventory of lichens and bryophytes in forests in Montana. Bryologist 95: 296–304.

McDowell, W. H. 2001. Hurricanes, people, and riparian zones: controls on nutrient losses from forested Caribbean watersheds. For. Ecol. Manage. 154: 443–451.

Molino, J. P., and D. Sabatier. 2001. Tree diversity in tropical rain forests: A validation of the intermediate disturbance hypothesis. Science 294: 1702–1704.

Mueller-Dombois, D., and H. Ellenberg. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, New York, New York.

Nason, J. D., P. R. Aldrich, and J. L. Hamrick. 1997. Dispersal and the dynamics of genetic structure in fragmented tropical tree populations. *In* W. F. Laurance and R. O. Bierregaard (Eds.). Tropical forest remnants: Ecology, management, and conservation of fragmented communities, pp. 304–320. University of Chicago Press, Chicago, Illinois.

Neter, J., M. H. Kutner, C. J. Nachtsheim, and W. Wasserman. 1996. Applied linear statistical models. 4th edition. WCB McGraw–Hill, Boston, Massachusetts.

Nieder, J., J. Prosper, and G. Michaloud. 2001. Epiphytes and their contribution to canopy diversity. Plant Ecol. 153: 51–63.

Perry, D. A. 1994. Forest ecosystems. Johns Hopkins University Press, Baltimore, Maryland.

Pinard, M., B. Howlett, and D. Davidson. 1996. Site conditions limit pioneer tree recruitment after logging of dipterocarp forests in Sabah, Malaysia. Biotropica 28: 2–12.

Saldarriaga, J. G., D. C. West, M. L. Tharp, and C. Uhl. 1988. Long-term chronosequence of forest succession in the Upper Río Negro of Colombia and Venezuela. J. Ecol. 76: 938–958.

Salo, J., R. Kalliola, and I. Hakkinen. 1986. River dynamics and the diversity of Amazon lowland forest. Nature 322: 254–258.

SAS. 2003. SAS system version 8. SAS Institute Inc., Cary, North Carolina.

Schwarz, P. A., T. J. Fahey, C. W. Martin, T. G. Siccama, and A. Bailey. 2001. Structure and composition of three northern hardwood–conifer forests with differing disturbance histories. For. Ecol. Manage. 144: 201–212.

Scott, G. 1977. The importance of old-field succession biomass increments to shifting cultivation. Gt. Plains–Rocky Mt. Geogr. J. 6: 318–327.

Singleton, R., S. Gardescu, P. L. Marks, and M. G. Geber. 2001. Forest herb colonization of postagricultural forests in central New York State, USA. J. Ecol. 89: 325–338

Snedaker, S. C. 1970. Ecological studies on tropical moist forest succession in eastern lowland Guatemala. Ph.D. dissertation. University of Florida, Gainesville, Florida.

Stover, M. A., and P. L. Marks. 1998. Successional vegetation on abandoned cultivated and pastured land in Tompkins County, New York. J. Torrey Bot. Soc. 125: 150–164.

Svenning, J. C. 1998. The effect of land-use on the local distribution of palm species in an Andean rain forest fragment in northwestern Ecuador. Biodiv. Conserv. 7: 1529–1537.

Thebaud, C., and D. Strasberg. 1997. Plant dispersal in fragmented landscapes: A field study of woody colonization in rainforest remnants in the Mascarene Archipelago. *In* W. F. Laurance and R. O. Bierregaard (Eds.). Tropical forest remnants: Ecology, management, and conservation of fragmented communities, pp. 321–332. University of Chicago Press, Chicago, Illinois.

Uhl, C. 1987. Factors controlling succession following slash-and-burn agriculture in Amazonia. J. Ecol. 75: 377–407.

———, R. Buschbacher, and E. A. S. Serrao. 1988. Abandoned pastures in Eastern Amazonia. I. Patterns of plant succession. J. Ecol. 76: 663–681.

Wadsworth, F. H. 1983. Production of usable wood from tropical forests. *In* F. B. Golley (Ed.). Tropical rain forest ecosystems, pp. 279–288. Elsevier Scientific, Amsterdam, The Netherlands.

Walter, J. M. 1974. Trees and alluvial forests of the Rhine. Bull. Soc. Hist. Nat., Colmar 55: 37–88.

Whitmore, T. C. 1991. Tropical rain forest dynamics and its implications for management. *In* A. Gómez-Pompa, T. C. Whitmore, and M. Hadley (Eds.). Rain forest regeneration and management, pp. 67–89. Parthenon Publishing,Lancaster, England.

Worbes, M. 1997. The forest ecosystem of the floodplain. *In* W. J. Junk (Ed.). The central Amazon floodplain: Ecology of a pulsing system. Ecological studies vol. 126, pp. 223–265. Springer–Verlag, Berlin, Germany.

Zotz, G., and M. Buche. 2000. The epiphytic filmy fern of a tropical lowland forest—Species occurrence and habitat preferences. Ecotropica 6: 203–206.

APPENDICE *Plant species encountered in 24 0.1 ha plots. * = Introduced species*

Family and species	Growth form
Acanthaceae	
Justicia alsinoides Leonard	Herb
Apiaceae	
Hydrocotyle hirsuta Sw.	Herb
H. pusilla A. Richard	Herb
Apocynaceae	
Odontadenia polyneura (Urb.) Woodson	Vine
Aquifoliaceae	
Ilex fuertesiana (Loes) Loes.	Tree
I. impressus Loes. & Ekm.	Tree
I. macfadyenii (Walp.) Rehder	Tree
I. microwrightioides Loes.	Tree
Araceae	
Anthurium scanders (Aubl.) Engler	Epiphyte
Araliaceae	
Didymopanax tremulus Krug & Urb.	
Oreopanax capitatus (Jacq.) Decne.	Tree
& Pl.	Tree
Asteraceae	
Ageratum conyzoides L.	Herb
Artemisia domingensis Urb.	Herb
Arthrostilidium sarmentosum	Vine
Begonia sp.	Herb
Chamissoa altisima	Vine
Conyza bonarienzis (L.) Crong.	Herb
Elephantophus mollis Kuntze	Herb
Eupatorium illitium Urb.	Treelet
E. odoratum L.	Treelet
E. puberulum Lam.	Treelet
Gnaphalium amecicanum Mill	Herb
G. domingense Lam.	Herb
G. eggersii Urb.	Herb
Hieracium gronovii L.	Herb
Lantanopsis hoffmannii Urb.	Herb
Mikania sp.	Vine
M. barahonensis Urb.	
M. lepidophora Urb.	Vine
Salmea scandens	Vine
Senecio constanzae Urb.	Vine
S. lucens (Poiret) Urb.	Herb
Vernonanthura buxifolia (Less.)	Vine
H. Robinson	Vine
Bignoniaceae	
Tabebuia berterii (DC) Britton	Tree
Brassicaceae	
Cardamine Africana L.	Herb
Bromeliaceae	
Catopsis nitida (Hooker) Griseb.	Epiphyte
Guzmania sp.	Epiphyte
Racinaea spiculose (Griseb)	Epiphyte
Tillandsia caribaea Smith	Epiphyte
T. compacta Griseb.	Epiphyte

APPENDICE *Continued*

Family and species	Growth form
T. compressa Bert. Ex Schult	Epiphyte
T. hotteana Urb.	Epiphyte
T. juncea	Epiphyte
T. useoides L.	Epiphyte
Vriesea sintenisii (Baker) Smith & Pitt	Epiphyte
Brunelliaceae	
Brunellia comocladifolia H & B.	Tree
Cactaceae	
Rhipsalis bacifera (J. S. Mill) Stearn	Epiphyte
Campanulaceae	
Lobelia cliffortiana L.	Herb
L. robusta Graham	Herb
Siphocampylus igneus (Urb.)	Herb
Clusiaceae	
Clusia clusiodes (Griseb) D'arcy	Tree
Convolvulaceae	
Ipomoea furcyensis Urb.	Vine
Cucurbitaceae	
Anacaona sphaerica Liogier	Vine
Cayaponia Americana (Lam.) Cogn.	Vine
Psiguria pedata (L.) R. A. Howard	Vine
Cyatheaceae	
Alsophilla abbottii (Maxon) Tryon	Tree Fern
Cyathea spp.	Tree Fern
Cyperaceae	
Cyperus flavus (Vahl) Nees	Herb
Uncinia hamata (Sw.) Urb.	Herb
Dioscoriaceae	
Dioscorea polygonoides	Vine
Rajania marginata R. Kunth	Vine
Elaeocarpaceae	
Sloanea ilicifolia Urb.	Tree
Ericaceae	
Lyonia buchii Urb.	
Vaccinum racemosum (Vahl.) Wilbur	Tree
& Letern	Vine
Euphorbiaceae	
Alchornia latifolia Sw.	Tree
Ditta maestrensis Borhidi	Tree
Pera bumelifolia Griseb.	Tree
Fabaceae	
Calopogonium galactioides	Vine
Canavalia nitida	Vine
Rhynchosia phasealoides	Vine
Rodophis lowdenii Judd.	Vine
Flacourtiaceae	
Lunania ekmanii Urb.	Tree
Garryaceae	
Garrya fadyenii (Hooker)	Tree

APPENDICE *Continued*

Family and species	Growth form
Gesneriaceae	
Trichantha domingensis (Urb.) Wieblee	Epiphyte
Iridaceae	
Sisyrinchium angustifolium P. Miller	Herb
S. micranthum Cav.	Herb
Lauraceae	
Beilschmiedia pendula (Sw.) Benth. & Hook.	Tree
Cinnamomum grisebachianum Mez.	Tree
Nectandra coriacea (Sw.) Griseb.	Tree
Ocotea floribunda (Sw.) Mez	Tree
O. foeniculacea Mez.	Tree
O. leucoxylon (Sw.) Mez.	Tree
O. wrightii (Meissn) Mez.	Tree
Persea oblongifolia Kopp.	Tree
Malpighiaceae	
Byrsonima lucida (Miller) L. C. Rich.	Tree
Stigmaphyllon angularium	Vine
S. emarginatum	Vine
Malvaceae	
Povonia spinifex	Vine
Melastomataceae	
Clidemia fuertesii Cogn.	Treelet
C. umbellata (Miller) L. O. Wms.	Treelet
Meriania involucrata (Desr.) Naud.	Tree
Miconia desportesii Urb.	Treelet
M. dodecandra (Desr.) Cogn.	Treelet
M. punctata (Desr.) DC.	Treelet
Meliaceae	
Guarea guidonea (L.) Sleumer	Tree
Mimosaceae	
* *Inga vera* Willd.	Tree
Moraceae	
Ficus velutina H. & B.	Tree
Myricaceae	
Myrcia deflexa (Poiret) DC.	Treelet
M. picardae Krug & Urb.	Treelet
M. splendens (Sw.) DC.	Treelet
Myrsinaceae	
Myrsine coriaceae (Sw.) R. Br	Tree
Wallenia apiculata Urb.	Tree
Myrtaceae	
Calyptranthes limoncillo Alain	Treelet
Eugenia domingensis Berg.	Tree
E. odorata Berg.	Treelet
Gomidesia lindeniana Berg.	Treelet
Pimenta racemosa var. hispaniolensis (Urb.) Landrum	Tree
* *Psidium guajava* L.	Treelet
* *Syzygium jambos* (L.) Alston	Tree
Oleaceae	
Chyonanthus domingensis Lam.	Tree

APPENDICE *Continued*

Family and species	Growth form
Onagraceae	
Fuchsia pringsheimii Urb.	Vine
Orchidaceae	
Anacheilum vespum (Vell.) Pabst. Mout. & Panto	Epiphyte
Cranichis diphylla Sw.	Epiphyte
Dichaea glausa (Sw.) Lindley	Epiphyte
D. glavea (Sw.) Lindley	
D. graminoides (Sw.) Lindley	Epiphyte
D. morrisii Fawcett & Rendle	Epiphyte
D. swartzii (C. Schueinf.) Garay	Epiphyte
& Sweet	Epiphyte
D. tricocarpa (Sw.) Lindley	Epiphyte
Dilomilis montana (Sw.) Summeh	Epiphyte
Elleanthus cephalotus Garay & Sweet	Epiphyte
Eneyclia isochila (Rchbif) D. Dod	Epiphyte
Isochilis linearis (Jacq.) Schltr.	Epiphyte
Jacquiniella teretifolia (Sw.) Britt & Wilson	Epiphyte
Lycaste barringthoniae (Smith) Lindley	Epiphyte
Malaxis unifolia Michaux	Epiphyte
Maxillaria conferta (Griseb) Schweinf.	Epiphyte
M. conforta (C. Schw.) Griseb.	Epiphyte
M. refuscens Lindley	Epiphyte
Oncidium compressicaule (Sw.) Lindley	Epiphyte
O. cf. *variegatum* (Sw.) Lindley	Epiphyte
Pleurothallis domingensis Cogn.	Epiphyte
P. oblongifolia Lindley	Epiphyte
P. ruscifolia (Jacq.) R. BR	Epiphyte
Prescottia stachyoides Lindley	Epiphyte
Psilochilis macrophyllus	Epiphyte
Quisqueya fuertesii Dad.	Epiphyte
Spiranthes torta (Thumb) Garay & Sweet	Epiphyte
Stelis domingensis Cogn.	Epiphyte
Tolumnia tuerekheimii	Epiphyte
Tricopilia fragans (Lindl) Rchb. f.	Epiphyte
Xylobium palmifolium (Sw.) Benth	Epiphyte
Palmae	
Prestoea montana (Graham) Nichols	Palm
Papaveraceae	
Bocconia frutescens L.	Small shrub
Parmeliaceae	
Usnea sp.	Epiphyte
Passifloraceae	
Passiflora rubra	Vine
P. sexflora A. Juss	Vine
Phytolaccaceae	
Phytolaccai cosandra L.	Herb
Piperaceae	
Peperomia acuminata Ruiz & Pavon	Epiphyte
P. alata Ruiz & Pav	Epiphyte
P. eggersii V. D. C.	Herb
P. glabella (Sw.) A. Dietr.	Herb
P. hernandifolia (Vahl.) A. Dietr.	Vine

APPENDICE *Continued*

Family and species	Growth form
P. cf. *montazoana* Trelease	Epiphyte
P. quadrifolia (L.) H. B. K.	Herb
P. tetraphylla (S. Forst.) Hook & Ar.	Epiphyte
P. uniquiculata Trel.	Herb
Piper aduncum L.	Treelet
P. alamago L.	Tree
P. rugosum Lam.	Treelet
Poaceae	
Decsgampsia domingensis Hitch. & Ekm	
Gynerium sagittatum (Aubl.) Beauv.	Herb
Homolepis glutinosa (Sw.) Zuleaga	Herb
& Soderstrom	Herb
Panicum xalapense H. B. K.	Herb
Polygalaceae	
Polygala fuertesii (Urb.) Blake	Tree
Ranunculaceae	
Clematis sp.	Vine
C. dioica L.	Vine
Ranunculus cubensis Griseb.	Herb
Rubiaceae	
Chione seminervis Urb. & Ekm.	Tree
Guettarda pungens Urb.	Tree
Manettia domingensis Sprengel.	Vine
Palicourea eriantha DC.	Treelet
Psychotria berteriana DC.	Treelet
Rondeletia ochracea Urb.	Tree
Scolosanthus sp.	Small shrub
Rutaceae	
* *Citrus aurantium* L.	Tree
* *C. limeta* L.	
* C. *limon* (L.) Burm. F.	Treelet
* *C. sinensis* Pers.	Treelet
Zanthoxylum azuense (Urb. & Ekm.)	Tree
Jiménez	Tree
Sabiaceae	
Meliosma impressa Krug & Urb.	Tree
Sapindaceae	
Alophyllus crassinervis Radlk	Treelet
Cupania americana L.	Tree
Serjania sinuata Schum.	Vine
Sapotaceae	
Chrysophyllum oliviforme L.	
Sideroxylon cubense (Griseb.) T.	Tree
Pennintong	Tree
S. obovatum Lam.	Tree
Selaginellaceae	
Selaginella sp.	Epiphyte
Smilacaceae	
Smilax habanensis Jacq.	Vine

APPENDICE *Continued*

Family and species	Growth form
Solanaceae	
Cestrum azuense Urb. & Ekm.	Small shrub
C. inclusum Urb.	Small shrub
C. mononeurum Urb. & Ekm.	Small shrub
C. tuerckheimii O. E. Sch.	Treelet
Solanum americanum Miller	Herb
S. crotonoides Lam.	Treelet
S. nudum Humb. & Bonpl. Ex Dunal	Treelet
S. virgatum	Vine
Staphyllaceae	
Turpina occidentalis (Sw.) G. Don.	Tree
Symplocaceae	
Symplocos domingensis Urb.	Tree
Theaceae	
Laplacea portoricensis (Krug & Urb.) Dryer	Tree
Ulmaceae	
Trema micrantha (L.) Blume	Treelet
Urticaceae	
Gyrotaenia myriocarpa Griseb.	Tree
Pilea herniarioides (Sw.) Lindll	Herb
Verbenaceae	
Citharexyluym caudatum L.	Tree
C. fruticosum L.	Tree
Viscaceae & Loranthaceae	
Arceuthobium bicarinatum Urb.	Mistletoe
Dendropemon palvifolius (Sw.) Steud	Mistletoe
D. pycrophyllus	Mistletoe
Dendrophthora sp.	Mistletoe
D. albescens Urb. & Ekman	Mistletoe
Phoradendron sp.	Mistletoe
Vitaceae	
Cissus verticillata (L.) Nicolson & Jarvis	Vine
Zingiberaceae	
Renealmia jamaisensis var. *puberula* (Gagn.) Mass	Epiphyte
Ferns	
Asplenium auriculatum Sw.	Ground fern
A. cristatum La.	Ground fern
A. praemorsum Sw.	Ground fern
A. cf. *radicans* L.	Ground fern
A. serra Langsd. & Fisch	Ground fern
Blechnum gragile (Liebm.) Morton & Lell	Vine
B. occidentale L.	Ground fern
B. underwoodianum (Broadh) C. Chr.	Ground fern
Botrychium virginanum (L.) Sw.	Ground fern
Danaea urbanii	Ground fern

APPENDICE *Continued*

Family and species	Growth form
Diplazium altissimum (Jenm) C. Chr.	
D. centripetale (Baker) Maxon	Ground fern
D. cf. *fuertesii* Brause	Ground fern
D. unilobum (Poret) Hieron	Ground fern
Dryopteris wallichiana (Spreng). Hy.	Ground fern
Elaphoglossum ihaequalifolium (Jenm.)	Ground fern
C. Chr.	Ground fern
Lastreopsis effuse (Sw.) Tindale	
Lophosoria quadripinnata (Gmel.) C.	Ground fern
Chr	Ground fern
Marattia kaulfussii J. Smith	Ground fern
Nephrolepsis pectinata (Willd) Schott	Ground fern
N. quadripinnata (Gmel.) C. Chr.	Ground fern
Odontosoria uncinella (Kunze) Fee	Ground fern
Ophioglossum reticulatum L.	Ground fern
Peltapteris peltata (Sw.) Morton	Ground fern
Phlebodium aureum (L.) J. Sm.	Ground fern
Plagiogyra semicordata (Presl.) Christ	Ground fern
Polypodium loriceum L.	Ground fern
P. cr. *squamatum* L.	Ground fern
P. thysanolepis A. Braun	Ground fern
Pteris podophylla Sw.	Ground fern
P. stridens A. Garda	
Thelypteris piedrensis (C. Chr.) C. V.	Ground fern
Morton	Ground fern
T. reptans (J. F. Gmel.) Morton	Ground fern