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Forestry Ecology and Management 99 (1997) 21–42

Forest Ecology and Management

Development of floristic diversity in 10-year-old restoration forests on a bauxite mined site in Amazonia

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Accepted 9 May 1997

Abstract

Patterns of plant and animal diversity were studied in a 10-year-old native species reforestation area at a bauxite-mined site at Porto Trombetas in western Pará State, Brazil. Understorey and overstorey floristic composition and structure, understorey light conditions, forest floor development and soil properties were evaluated in a total of 38 78.5-m^2 plots located in the reforestation area at varying distances up to 640 m from the boundary with the surrounding primary forest. Wildlife surveys focusing primarily on birds and bats were also conducted to assess the role of seed-dispersing animals in regeneration of woody forest species within the plantations and colonization by primary forest species not included in the original reforestation. Regeneration density, species richness and species diversity (Shannon–Wiener index) for woody perennial species, vines, herbs and grasses were strongly correlated with the diversity of planted tree species and structural development parameters, degree of forest floor development and soil pH. The better developed closed-canopy plots (>40% crown closure) were characterized by relatively well-developed litter (O1) and humus (O2) layers, more acidic soils being typical of the surrounding primary forests, and a more diverse herb, vine and woody perennial flora with a greater representation of primary forest species being characteristic of late secondary forests. In closed-canopy plots a total of 125 tree, palm and shrub species were censused (versus 34 in the more open-canopy plots), of which 75 species are known to have been introduced by natural means from the surrounding primary forest (versus 11 species in the open-canopy plots). Among the plantation plots, there was significant colonization by primary forest woody species up to 640 m away from the primary forest edge, although both the abundance and the diversity of colonizing species declined with increasing distance into the plantations. Smaller-seeded primary forest woody species dispersed by mammals and birds represented a higher proportion of the colonizing species compared with the larger-seeded species. These data are consistent with the results of the wildlife surveys, which indicated that most animal seed dispersal is provided by bats, that the most common frugivorous bat and bird species in the plantations feed on small-seeded plant species and that birds and mammals that typically disperse larger-seeded tree species (such as toucans, trogons, tapirs, deer and primates) are still rare in the reforestation area. These results suggest that while the reforestation program has been successful in creating a favorable environment for regeneration of a native primary forest species, further management interventions, such as enrichment plantings, may be required to accelerate regeneration of large-seeded primary forest species. © 1997 Elsevier Science B.V.

Keywords: Brazil; Forest restoration; Plantations; Seed dispersal; Succession; Wildlife

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0378-1127/97/$17.00
PII S0378-1127(97)00192-8

1. Introduction

Natural regeneration of secondary forests on degraded tropical lands is often a slow and uncertain process, impeded by a combination of factors including human and livestock pressures, recurrent fires, persistence of dominant grasses and other non-woody species, unfavorable microclimatic conditions, soil infertility, exhaustion of soil seed banks and rootstocks and low rates of seed inputs from nearby surrounding forests. On surface-mined sites, these obstacles to natural regeneration are generally more acute than on other degraded landscapes due to the removal of topsoil (resulting in the elimination of soil seed bank and rootstocks) and soil profile disturbances (including compaction) that inevitably accompany the mining process. Recent research in a number of tropical countries has shown that tree plantings on such degraded sites can dramatically increase the otherwise slow rate of natural forest succession by ameliorating unfavorable soil and understorey microclimatic conditions and providing a habitat for seed-dispersing wildlife that can lead to a progressive enrichment of floristic diversity (Mathur and Soni, 1983; Bhaskar and Dasappa, 1986; Soni et al., 1989; Soni and Vasistha, 1991; Lugo, 1992; Lugo et al., 1993; Mitra and Sheldon, 1993; Parrotta, 1993, 1995; Brown and Lugo, 1994; Yu et al., 1994; Guariguata et al., 1995; Kuusipalo et al., 1995; Silva Junior et al., 1995; Fimbel and Fimbel, 1996).

In 1979, the Brazilian mining company Mineração Rio do Norte SA established a policy to restore the primary forest cover destroyed during bauxite mining at Trombetas in western Pará State. This policy led to the development of a reforestation program for the rehabilitation of approximately 100 ha of mined land per year (Knowles and Parrotta, 1995). The critical elements of this reforestation program include careful site preparation (overburden leveling, replacement of approximately 15 cm of topsoil and deep-ripping of planting lines) and planting of a diverse mixture of native forest trees (up to 90 species in a given year). This program has been very successful in reestablishing native forest cover on an operational scale at a reasonable cost (approximately \$2500/ha for all reclamation and reforestation activities). However, it is unknown whether this forest is truly self-sustaining and developing into a more species-rich ecosystem that includes the full complement of plant and animal species that comprise the primary forests surrounding the mining concession.

The present study was initiated as part of an international research program supported by the World Bank, the USDA Forest Service, the Center for International Forestry Research (CIFOR) and the Overseas Development Administration (UK) to evaluate the role of planted forests in catalyzing native forest succession on degraded tropical lands. This particular study examines a number of hypotheses regarding the relationship between plant biodiversity development in 10-year-old mixed native species plantation stands and several factors thought to influence this process. These include the proximity of planted stands to potential seed sources (primary forests), their use by potential seed dispersers (birds, bats and other mammals) and the structural features, light environment, forest floor and soil characteristics of these stands.

2. Methods

2.1. Study area

The Trombetas bauxite mine, operated by Mineração Rio do Norte SA, is located in the Saracá-Taquera National Forest on an upland mesa (Saracá plateau) 65 km northwest of the town of Oriximiná and 30 km south of the Trombetas River in western Pará State, Brazil (1°45′S, 56°30′W, Fig. 1). The local climate is characterized as Am (tropical monsoonal) in the Koppen system, with an annual rainfall at Porto Trombetas (1970–1993) of 2185 ± 64 mm (mean ± SE) with distinctly dry (winter) and wet (summer) seasons. The mean maximum and minimum temperatures are 34.6 and 19.9°C, respectively. The regional vegetation is evergreen equatorial moist forest, within which the forests occupying the upland plateau and surrounding slopes are multi-storeyed. Their tree flora is dominated by Leguminosae, Lauraceae, Sapotaceae, Annonaceae, Moraceae, Chrysobalanaceae, Lecythidaceae and Burseraceae (FCAP, 1991), with emergents reaching 45 m in height (Knowles and Parrotta, 1995). Soils are yellow clays with a thin humus layer.

The study area was mined in 1984 and replanted in 1985 with approximately 70 species of native primary

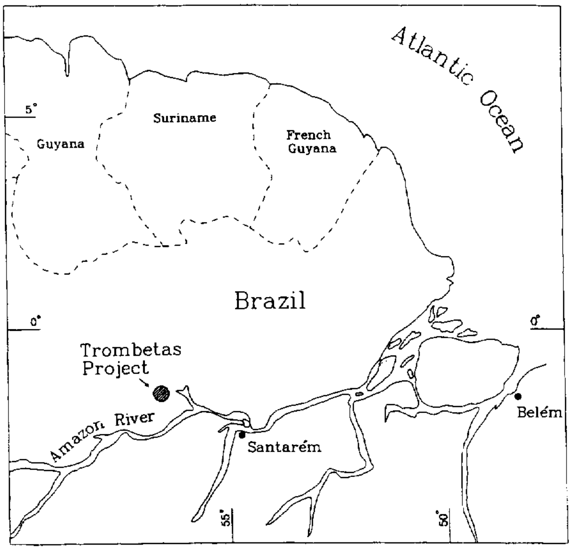

Fig. 1. Location of the study area.

forest tree species following site reclamation measures that included leveling of the clay overburden, replacement of ca. 15 cm of topsoil, deep-ripping of planting lines and planting at 2 × 2 m (2500 plants/ha) using a mixture of large seeds, stumped saplings and potted seedlings. Further details on the mining operations and reforestation methods are provided in Knowles and Parrotta (1995).

2.2. Forest stand structure, floristics and soils

In September 1995, 32 5-m radius circular plots (78.5 m^2) were established along two pairs of parallel transects located in the northern and southeastern sectors of the 1985 reforestation area. These transects began at the boundary with the intact primary forest along the edge of the Saracá plateau and proceeded perpendicular to this boundary into the reforestation area for a distance of 640 m. Plot centers were located at 0, 10, 20, 40, 80, 160, 320 and 640 m along each transect. Thus, a total of four plots at each distance from the primary forest boundary within the reforestation area were included in the study. An additional six plots (three at each site) were established at distances ranging from 20 to 640 m on sites within the reforestation area where there had been very poor survival (<25%) of the original (1985) plantings. These latter plots were used to evaluate the effect of plantation density, or degree of canopy closure, on subsequent patterns of understorey regeneration. To determine the species–area relationship for forest species in the reforestation study areas, all tree, palm and shrub species were censused in 15 78.5-m^2 rectangular plots established along the reforestation area–primary forest boundary at each of the two study locations.

Within each of the 38 study plots, a complete inventory was made of all trees and shrubs, vines, herbs and grasses. For each of these floristic elements, the total number of individuals (or clumps for grasses) of each species was recorded. For trees and shrubs (including palms), height and d.b.h. (stem diameter at breast height (1.3 m) for trees >2 m in height) were also measured. Height and stem diameter data for planted trees occurring in each plot were recorded separately. To distinguish regeneration originating from within the reforestation area from regeneration resulting from seeds transported from the primary forest surrounding the reforestation area, species were classified as either primary forest colonists or internal regeneration. The latter group included all tree and palm species planted (or direct seeded) on the site in 1985 which could have reached reproductive maturity by 1995 plus all species that might have had viable seeds in the topsoil which was applied to the site prior to tree planting in 1985, based on the authors' knowledge of the seed ecology of the local flora (see also Knowles and Parrotta, 1995). Woody species were also classified by their principal mode of seed dispersal, i.e. wind, birds and/or bats and other mammals, and by their expected longevity, or life span (<20, 20–40, 40–80, or >80 years).

In addition to the floristic inventories, several structural, environmental and soil parameters were measured for each plot. Canopy closure was estimated as the mean percentage crown cover measured with a spherical crown densiometer at 1 m from ground level at four points located 3 m from the plot centers (N, S, E, and W compass bearings). Soil organic horizon (O1, O2) depths were measured at 10 randomly located points within each plot, with plot means for each horizon used for subsequent analyses. Mineral soil pH at 0–5 and 10–15 cm was measured for composited ($n = 4$) samples from randomly selected points in each plot using an Oakton soil pH tester. Soil pH was also measured in two nearby primary forest areas and three grass swards (planted with *Bra-*

chiaria decumbens, *B. humidicola* and *Melinus minutiflora*) on the deforested mine site for comparison purposes.

Vesicular-arbuscular (VAM) spore density and morphotype composition were evaluated for each plot, as well as in nearby primary forest and planted grass swards at 0–5 and 10–15 cm depths using composited ($n = 4$) 5-cm diameter core samples taken 3 m from plot centers on N, S, E and W compass bearings. A wet sieving procedure was used to separate spores from organic debris and mineral soil components and to segregate spores by size class using 500, 180 and 45 μm mesh sizes. The separated and dried spore samples were analyzed for morphotype composition and abundance at the Department of Plant Sciences, University of Oxford, UK.

Relative frequencies (proportion of plots containing each species) and relative densities (proportion of total understorey regeneration comprised of each species) were calculated for all plant taxa surveyed. Species richness for each floristic category in each plot was expressed simply as the number of species. Diversity for each floristic category was estimated by the Shannon–Wiener index (H'):

$$H' = -\sum_{i=1}^{n} p_i \log_{10} p_i$$

where p_i is the proportion of individuals in species i, and n is the number of species surveyed.

Reforestation plot structural, environmental and soil characteristics, regeneration density, species richness and species diversity for woody species, vines, herbs and grasses were compared among open- and closed-canopy treatments using unpaired two-group t-tests and one-way analyses of variance (ANOVA). Relationships between understorey floristics and plot biophysical characteristics were explored through correlation and regression analyses. Analysis of tree seed size involved the use of the non-parametric Mann–Whitney U-test, because distribution of seed size did not meet assumptions of normal distribution.

2.3. Wildlife surveys

Preliminary censuses of birds and mammals in each of the two vegetation plot transects areas were conducted from 21–28 March 1996. Animals were detected by walking slowly through the transects during the daylight hours, recording all observations and signs. The fixed-radius point count method of Hutto et al. (1986) was used to obtain a quantitative measure of avian abundance. A single observer recorded all birds seen and heard during a 10-min period at each point. Counts were initiated at 0615–0640 h and completed by 0900 h. A total of 32 points were completed, with each point 150 m from each other, and all points were located at least 50 m from the primary forest edge. All birds detected at a point were noted, but analysis was restricted to individuals within a 25-m radius of the observer. For many bird detections it was not possible to identify the individual to a species.

Mist nets were used to sample bird and bat populations in the understorey of the reforestation plots. A total of 13 nets with four shelves were set to a height of 2.5 m at each site, which included a 6-m net (30 mm mesh) and 12 nets of 12-m length (half 30 mm mesh, half 36 mm mesh). Nets were usually run in a continuous line at four different sites located at both ends ('edge' and 'distant') of the 640-m long transects in each of the reforestation study areas. Edge nets were set up from the reforestation–primary forest border and run 150 m into the reforestation area, and distant nets were run for 150 m from 490 to 640 m from the reforestation–primary forest border. Bats were sampled only in the edge and distant sites in the southeastern study area where nets were open from sunset (1800 h) to 2020 h on 1 night each. Nets were open for birds for a full day (0615–0640 to 1700–1800 h) followed by a half day (0615–0630 to 1130–1230 h) at all sites, except the edge site in the northern study area, which was open for only 1 day (0615–1600 h). Birds were identified to species and bats to genus and all captured individuals were released after marking by clipping the end of a primary feather for birds, or a toe claw for bats. Capture rates are reported in captures per 100 net h in which one net h is equivalent to one 12-m net open for 1 h.

3. Results

3.1. Understorey floristics as influenced by planted overstorey development

Within the study area, there were important differences between the closed-canopy and open-canopy

Table 1

Characteristics of 10-year-old reforestation plots at the Trombetas bauxite-mined site (mean ± SE; n = 32 for closed-canopy treatment, n = 6 for open-canopy treatment)[a]

	Closed-canopy treatment	Open-canopy treatment
Total plot area (m^2)	2512	471
Planted trees		
Density (stems/ha)	1700 ± 90^1	510 ± 100^2
Species richness (no. species/plot)[b]	8.8 ± 0.4^1	3.2 ± 0.5^2
Height (m)	7.7 ± 0.3^1	4.5 ± 0.6^2
d.b.h. (cm)	8.0 ± 0.3^1	4.6 ± 4.7^2
Basal area (m^2/ha)	11.3 ± 0.8^1	1.5 ± 0.6^2
Crown cover (%)	56.0 ± 1.0^1	28.7 ± 4.8^2
Litter (O1) depth (mm)	32.4 ± 1.4^1	14.0 ± 4.2^2
Humus (O2) depth (mm)	8.3 ± 1.0^1	1.1 ± 0.1^2
Litter + humus depth (mm)	40.8 ± 2.2^1	15.0 ± 4.4^2
Soil pH, 0–5 cm depth	4.09 ± 0.02^1	4.57 ± 0.10^2
Soil pH, 10–15 cm depth	4.14 ± 0.02^1	4.93 ± 0.15^2

The total number of planted tree species surviving in all plots surveyed was 56 in closed-canopy treatment and 14 in open-canopy treatment.

Closed-canopy crown cover >40%; open-canopy crown cover <40%.

[a]Similar superscript numbers within a row indicate that means were not significantly different between treatments ($P < 0.05$, ANOVA).

[b]The plot area was 78.5 m^2.

plots with respect to diversity and structural development of the originally planted trees, forest floor development and soil pH. Closed-canopy plots had significantly greater numbers of planted tree species, higher stem density, basal area and crown cover, greater mean tree heights and stem diameters, deeper litter (O1) and humus (O2) horizons and lower soil pH values than open-canopy plots (Table 1). Soil pH values in the closed-canopy plots were somewhat lower than those recorded in the primary forest, which averaged 4.3 and 4.6 at 0–5 and 10–15 cm depths, respectively, while the much higher soil pH values in the open-canopy plots were similar to those of the planted grass swards elsewhere on the mined plateau, which averaged 4.9 (0–5 cm) and 5.2 (10–15 cm).

VAM spore and sporocarp densities and distribution of taxa in soils at 0–5 and 10–15 cm depth were very similar between open- and closed-canopy treatments, and no consistent differences were noted between reforestation plots and either primary forest or planted grass swards. These similarities are most likely due to the fact that primary forest topsoil recovered during the mining operation was reapplied on the site prior to reforestation in 1985. Based on preliminary analyses, VAM spore populations at this site were dominated by several species of *Glomus*, with much lower densities of *Endogyne* spp., *Gigaspora* spp. and *Sclerocystis* spp.

Understorey floristic composition was markedly different between closed- and open-canopy plots, or treatments (Table 2). With respect to regeneration density, there was no significant difference between treatments for all woody species (i.e. those arising from both internal regeneration and colonization from external primary forest sources), which averaged 2.80–2.88 individuals/m^2 across treatments. Consid-

Table 2

Understorey species abundance and diversity in 10-year-old reforestation plots at the Trombetas bauxite-mined site (mean ± SE; n = 32 for closed-canopy treatment, n = 6 for open-canopy treatment[a]

	Closed-canopy treatment	Open-canopy treatment
Regeneration density (individuals/m^2)		
All woody species	2.88 ± 0.55^1	2.80 ± 0.87^1
Woody primary forest colonists	0.30 ± 0.07^1	0.045 ± 0.020^1
Vines	0.40 ± 0.06^1	0.24 ± 0.08^1
Grasses	0.40 ± 0.08^1	2.74 ± 0.51^2
Herbs	0.022 ± 0.006^1	0^2
Species richness (no. species/plot)		
All woody species	23.5 ± 1.3^1 (125)	11.8 ± 2.4^2 (34)
Woody primary forest colonists	9.2 ± 1.0^1 (75)	2.2 ± 0.9^2 (11)
Vines	5.3 ± 0.04^1 (24)	2.8 ± 0.7^2 (8)
Grasses	2.6 ± 0.2^1 (9)	2.2 ± 0.5^1 (6)
Herbs	0.7 ± 0.1^1 (7)	0^2 (0)
Species diversity (Shannon–Wiener index (H'))		
All woody species	0.85 ± 0.06^1	0.65 ± 0.08^1
Woody primary forest colonists	0.27 ± 0.04^1	0.04 ± 0. 02^2
Vines	0.52 ± 0.04^1	0.24 ± 0.08^2
Grasses	0.26 ± 0.03^1	0.08 ± 0.06^2
Herbs	0.04 ± 0.02^1	0^1

The total area was 2512 and 471 m^2 in closed- and open-canopy treatments, respectively. Closed-canopy crown cover >40%; open-canopy crown cover <40%.

Numbers in parentheses indicate the total number of species in treatment, all plots combined. [a]Similar superscript numbers within a row indicate that means were not significantly different between treatments ($P < 0.05$, ANOVA).

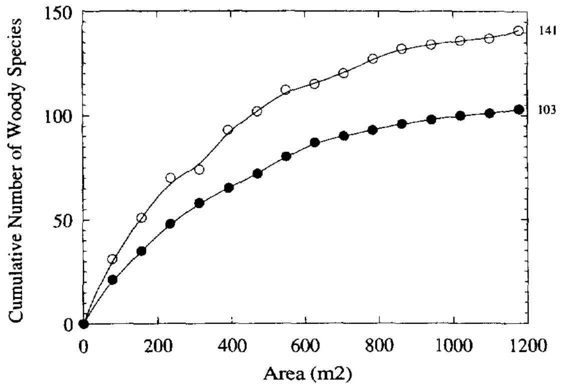

Fig. 2. Species–area relationship for tree and shrub species in 10-year-old reforestation plots at the Trombetas bauxite-mined site, based on transect surveys conducted in August 1995 along the reforestation–primary forest boundary. Closed and open circles indicate data collected in the northern and southeastern sector study areas, respectively.

ering only the woody primary forest colonists, however, regeneration density was significantly greater in the closed-canopy (0.30 ± 0.07 individuals/ m^2) than in open-canopy plots (0.05 ± 0.02 individuals/m^2). The density of grasses was nearly seven times greater in the open-canopy treatment, which is clearly a reflection of the favorable light conditions for grass growth in these plots.

With the exception of grasses, species richness (number of species/78.5-m^2 plot) for all floristic categories was significantly greater in the closed- than the open-canopy treatment. In the former (total area surveyed, 2512 m^2), a total of 125 woody species were found (25.3 ± 1.3 species/plot), of which 75 species (60%) were determined to have colonized the reforestation area from the primary forest after plantation establishment. In contrast, open-canopy plots (total area surveyed, 471 m^2) contained only 34 woody species (11.8 ± 2.4 species/plot), of which only 11 species (32%) were colonists from the primary forest. The greater collective woody species richness in the closed-canopy plots is only partly due to the greater area surveyed. As indicated in the species accumulation curve for the reforestation area–primary forest boundary (Fig. 2), approximately 70% of the total number of woody species present would be expected in a sample area of 471 m^2, while open-canopy plots contained only 27% of the total number of woody species and 15% of the colonizing primary forest species found in the closed-canopy plots.

Species diversity, as measured by the Shannon–Wiener index (H'), was consistently and significantly greater in the closed-canopy plots for woody primary forest colonists, vines, grasses and herbs. A complete listing of plant species found in the closed- and open-canopy plots, with regeneration densities, frequencies, importance values, regeneration sources, seed dispersal agents and estimated life spans (of trees) are presented in Appendices A and B.

There were several important qualitative differences in the composition and dominance of the regenerating woody flora (trees, shrubs, palms) between the closed- and open-canopy plots. In the closed-canopy treatment, 28 species (of a total of 125 species) comprised 75% of the total importance value (IV, for each species calculated as the sum of relative abundance and relative frequency), of which nine species were known to have colonized the site from the primary forest after plantation establishment (Appendix A). In contrast, only 11 woody species (of a total of 34 species) comprised 75% of the total IV, none of which were classified as colonists from the primary forest (Appendix B). Of these (dominant) species in the open-canopy plots, 82% were short-lived (<20 years) pioneer species such as *Vismia* spp., *Miconia* sp., *Belucia dichotoma* and *Rollinia* sp. In the closed-canopy plots, however, there was a much more even mixture of pioneer, late secondary and primary forest species among the dominant woody flora, of which only 59% were short-lived pioneers, and 19% which typically live >40 years in the native primary forest.

Comparing the total number of woody species found in study plots with those comprising the native primary forests surrounding the reforestation area (total number of species, 248), species richness in the 10-year-old reforestation area (125 species) is approximately 50% of the theoretical maximum represented by the primary forest. As shown in Fig. 3, there is a clear under-representation of longer-lived woody species in the open-canopy plots, while in the closed-canopy plots there is a more even distribution of species among tree life-span classes more typical of the native primary forest tree flora, though longer-lived species are somewhat under-represented.

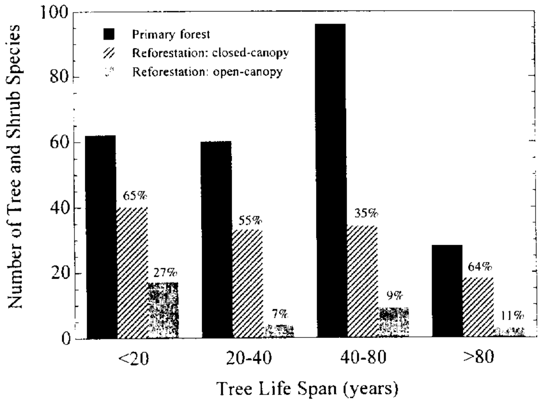

Fig. 3. Distribution of average expected life spans for tree species found in primary forest and in 10-year-old reforestation plots at the Trombetas bauxite-mined site. Figures above bars represent percentages of tree species in each life span class in closed- or open-canopy plots relative to primary forest.

3.2. *Understorey floristics in relation to plot location and biophysical characteristics*

Understorey regeneration density, species richness and diversity among all plots surveyed were significantly correlated with stand structural features, forest floor and soil characteristics and proximity to the undisturbed primary forest surrounding the mine site. Understorey regeneration density of woody species colonizing the site from the primary forest was positively correlated with planted tree basal area, humus depth and overstorey crown cover, and negatively correlated with plot distance from the primary forest edge. Density of vines was positively correlated with planted tree stem density and basal area. Grass density, in contrast, was negatively correlated with overstorey crown cover, planted tree stem density and basal area, litter and humus depth, and positively correlated with soil pH.

Understorey species richness for all woody species and woody primary forest colonists was negatively correlated with plot distance from the primary forest edge, grass density and soil pH at 10–15 cm depth, and positively correlated with overstorey crown cover, planted tree stem density and basal area and litter and humus depths. Species richness of vines was positively correlated with crown cover, planted tree stem density and basal area, litter and humus depths, and negatively correlated with plot distance from the primary forest, grass density and soil pH at 10–15 cm depth. Understorey species diversity (Shannon–Wiener index, H') followed very similar correlation patterns with stand structural and soil parameters as those for species richness for both woody primary forest colonists and vines. No significant relationships were found between either species richness or diversity for herbs and grasses and plot location, stand structural characteristics or soil properties.

These results indicate very strong positive relationships between understorey regeneration density, species richness and species diversity for woody species and vines, structural development of the planted overstorey trees and forest floor development (O1 and O2 horizon depth), and negative relationships between these floristic development indices and both grass density and plot distance from the primary forest boundary. For woody primary forest colonists, regeneration density, species richness and species diversity were most strongly correlated with plot distance from the primary forest boundary, planted tree basal area and humus (O2 horizon) depth (Figs. 4–6).

Although there was significant colonization by woody primary forest species up to 640 m away from the primary forest edge, both the abundance and diversity of colonizing species declined with increasing distance into the reforestation area, which suggests that seed dispersal may be limiting the process of tree flora enrichment within the reforestation area. A comparison of seed sizes between tree species regenerating in the reforestation area and those found in the primary forest (Fig. 7) indicates that while the smaller-seeded tree flora are already well-represented in the reforestation area, larger-seeded species are less well represented. The maximum seed length for zoochoric (bird- and mammal-dispersed) woody primary forest colonists in the reforestation plots (median 13 mm) was significantly less (Mann–Whitney U = 2375, P = 0.001) than that for zoochoric primary forest species not found in the reforestation area (median 17 mm).

It appears that while increased grass density, characteristic of the open-canopy plots, did not have any significant effect on overall woody perennial regeneration density, it does favor a more limited number of early pioneer species. The overwhelming majority of these species were already present on the site at the time of plantation establishment either in the planted overstorey or in the soil seed bank. Increased over-

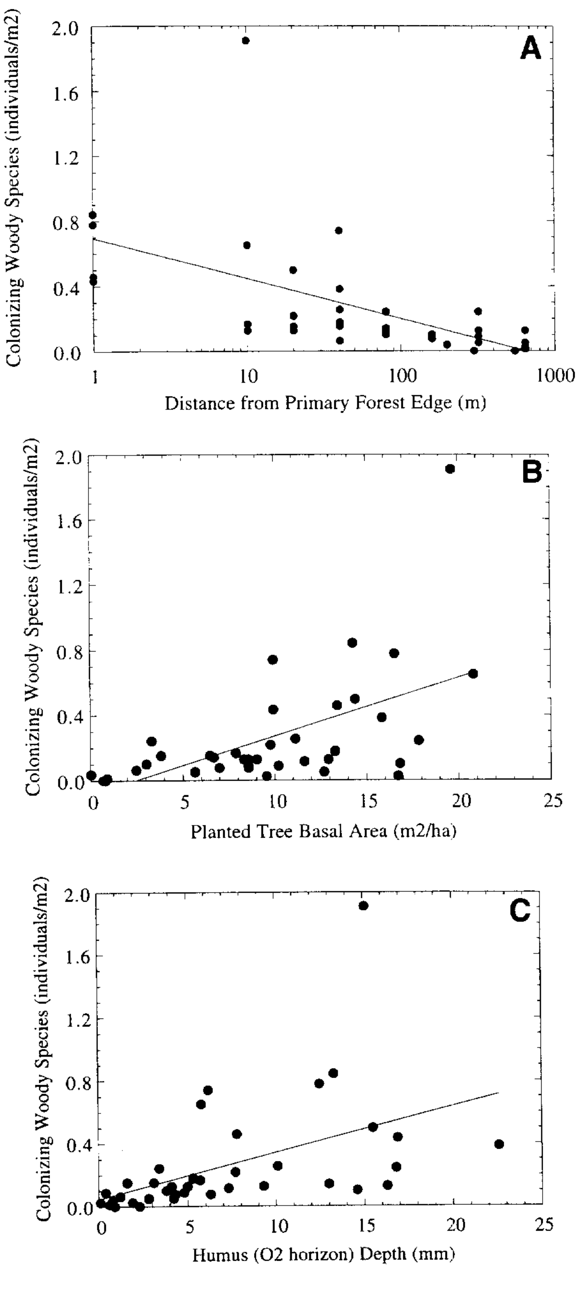

Fig. 4. Relation between understorey regeneration density of woody primary forest colonists and selected plot biophysical characteristics in 10-year-old reforestation plots at the Trombetas bauxite-mined site. (A) Plot distance from primary forest: $y = 0.69 - 0.24 \log_{10}x$ ($r^2 = 0.33$, $F = 17.6$, $P < 0.001$); (B) planted tree basal area: $y = -0.089 + 0.036x$ ($r^2 = 0.31$, $F = 16.3$, $P < 0.001$); (C) humus (O2) depth: $y = 0.048 + 0.029x$ ($r^2 = 0.23$, $F = 10.9$, $P < 0.01$).

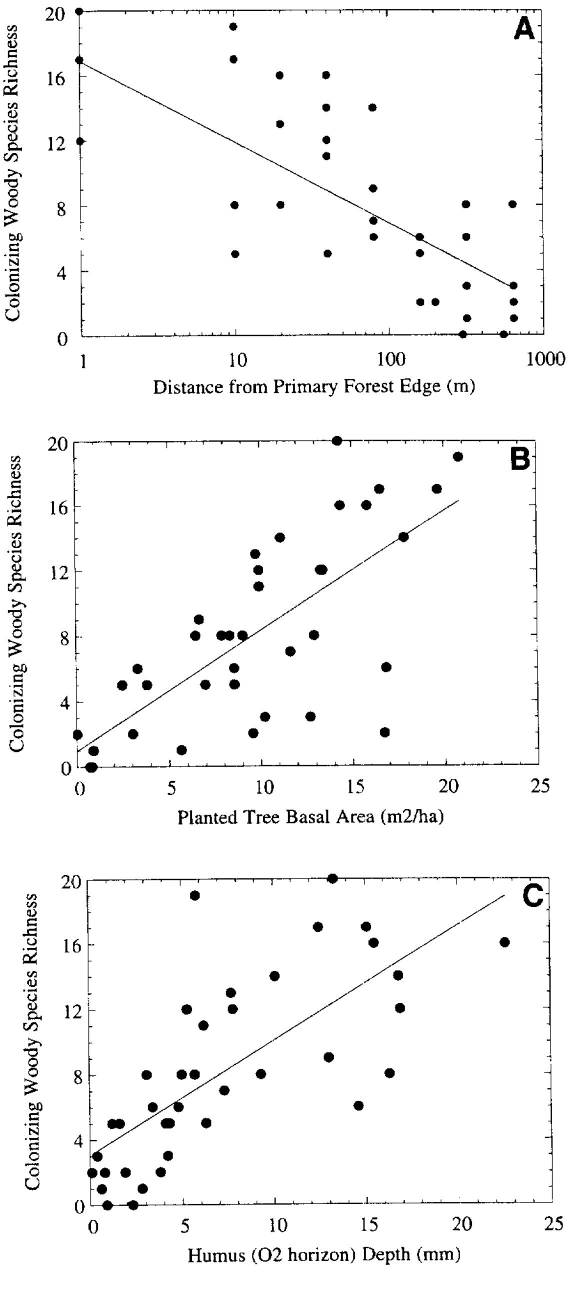

Fig. 5. Relation between species richness (number of species per 78.5-m^2 plot) of woody primary forest colonists and selected plot biophysical characteristics in 10-year-old reforestation plots at the Trombetas bauxite-mined site. (A) Plot distance from primary forest: $y = 18.8 - 4.96 \log_{10}x$ ($r^2 = 0.54$, $F = 41.6$, $P < 0.001$); (B) planted tree basal area: $y = 0.97 + 0.73x$ ($r^2 = 0.51$, $F = 37.6$, $P < 0.001$); (C) humus (O2) depth: $y = 3.1 + 0.70x$ ($r^2 = 0.52$, $F = 39.3$, $P < 0.001$).

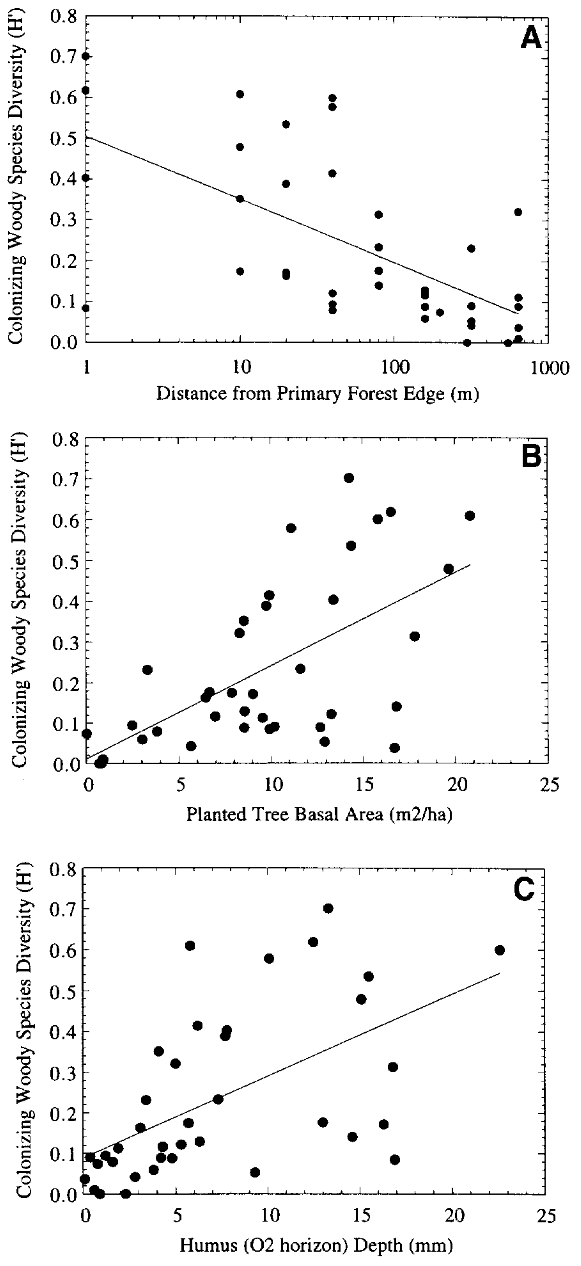

Fig. 6. Relation between species diversity (Shannon–Wiener index, H') of woody primary forest colonists and selected plot biophysical characteristics in 10-year-old reforestation plots at the Trombetas bauxite-mined site. (A) Plot distance from primary forest: $y = 0.50 - 0.15 \log_{10}x$ ($r^2 = 0.39$, $F = 22.7$, $P < 0.001$); (B) planted tree basal area: $y = 0.011 + 0.023x$ ($r^2 = 0.39$, $F = 22.2$, $P < 0.001$); (C) humus (O2) depth: $y = 0.088 + 0.020x$ ($r^2 = 0.33$, $F = 17.7$, $P < 0.001$).

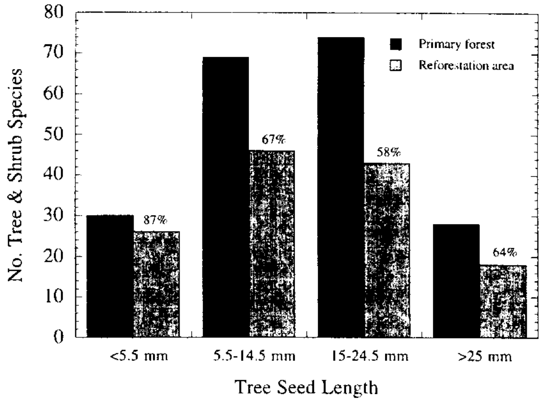

Fig. 7. Distribution of average seed lengths for tree species found in primary forest and in 10-year-old reforestation plots at the Trombetas bauxite-mined site. Figures above bars represent percentages of tree species in each seed size class in reforestation area relative to primary forest.

storey (planted tree) stem density, basal area, species richness and crown closure, characteristic of the closed-canopy plots, favors understorey regeneration by suppressing competing grasses in the understorey, accelerating forest floor (litter) and humus development, increasing soil fauna activity and lowering soil pH. All of these processes may play some important role in improving germination, survival and growth of regenerating or colonizing woody perennials, vines and herbs, although a more conclusive evaluation of the importance of these processes, singly and in combination with others, would require further experimentation.

3.3. Wildlife surveys

Mist nets were operated during the daylight hours for a total of 760 net h which included 348 net h in the two edge sites and 412 h in the two distant (from primary forest) sites. A total of 32 individuals of 12 bird species were captured and the species accumulation curve reached an asymptote at 11–12 species, indicating that most common understorey species had been captured. The overall capture rate was low at 4.2 captures/100 net h, with similar capture rates in edge (4.0 captures/100 net h; range 3.4–6.5 captures/100 net h) and distant nets (4.4 captures/100 net h; range 2.4–6.5 captures/100 net h).

Analysis of the net captures by diet indicates that potential seed dispersers were rare among the captures as frugivores/seed-eaters were represented by only three species of one individual each (Guianan toucanet, ruddy quail-dove and golden-headed manakin, see Appendix C for scientific names). These frugivores/seed-eaters accounted for 25% of the species and 9% of the individuals captured in the plots. Among species, insectivores accounted for the largest percentage of captured species (58%) and nectarivores accounted for the least (17%). In contrast, nectarivores accounted for 59% of the captured individuals while insectivores accounted for 31%. Fixed radius point counts conducted at 32 points in the reforestation plot were consistent with the netting results in indicating a very low density of birds in the plots. An average of 2.2 ± 1.8 SD individuals were detected per point (no detections recorded in five points) and an average of 1.8 ± 1.4 SD species were detected per point.

A total of 45 bird species were identified during 8 days in the reforestation plots of which 51% are known to consume fruit. Similarly, Pedreira Gonzaga (1991) found 56 species in the southeastern study area, of which 50% are known to feed on fruit. However, not all of these fruit-eating birds are likely to be important seed dispersers as some are seed predators (parrots and parakeets) or seed predators which are suspected to disperse some seeds (pigeons and doves, Olson and Blum, 1968). Therefore, if major seed predators are excluded a total of 44% of the species found in this study and 38% of those observed by Pedreira Gonzaga (1991) are potential seed dispersers. Most of these species are omnivores in which fruit may make up a sizable portion of the diet (29% of the species in this study, 34% of the species observed by Pedreira Gonzaga (1991)).

In contrast to the low net capture rate of birds, the capture rate of bats was very high at 147 captures/100 net h. Captures were higher in the edge nets (215 captures/100 net h, in 20 net h) than in the distant nets (63 captures/100 net h, in 16 net h). All captured bats were in the Phyllostomidae family with most in the subfamily Carolliinae, genus *Carollia* (40 in edge nets, seven in distant nets) and fewer in the Stenodermatinae, genus *Artibeus* (three in edge nets, three in distant nets).

Other mammals found in the reforestation plot included common opossum (*Didelphis marsupialis*, two), tayra (*Eira barbara*, one), red brocket deer (*Mazama americana*, four), red-rumped agouti (*Dasyprocta agouti*, five), and nine-banded long-nosed armadillo (*Dasypus novemcinctus*, one). Scats of Brazilian tapir (*Tapirus terrestris*) were also found at two sites in the plots. Although two troops (six to eight individuals) of red howler monkeys (*Alouatta seniculus*) were observed in the primary forest along the border of the reforestation plots, none were detected in the plots.

4. Discussion

The results of this study strongly suggest that the mixed-native species reforestation approach developed for the rehabilitation of bauxite-mined areas in the Brazilian Amazon region has been largely successful in establishing a dynamic and sustainable successional environment. Careful site preparation, the application of topsoil recovered during the mining process and the inclusion of a broad array of native primary and secondary forest species in the initial planting scheme has accelerated at least the initial stages of forest succession on a site which would otherwise require decades, perhaps centuries, to regenerate in the absence of management. Our surveys indicate that of the 125 tree species and 24 species of vines found regenerating within the 10-year-old reforestation area, up to 40% of the tree species and 75% of the vines were present in the soil seed bank at the time of plantation or were regenerated from seeds produced by planted trees. This internal regeneration represents a significant 'head start' for forest restoration or successional processes.

The long-term viability and further development of these 'induced' secondary forests depends ultimately on their progressive colonization by additional forest trees, vines, other floristic elements, soil biota and wildlife that are essential for the resilient functioning of natural forest ecosystems in this region. During the 10 years since their establishment, these forests have been enriched by colonization of at least 50 primary forest tree species and several species of lianas and herbs. In comparison with the primary forests surrounding the reforestation area, the abundance and diversity of birds and mammals either residing in or otherwise utilizing this site is still fairly low, with a predominance of birds and mammals characteristic of fairly young secondary forests. Similar findings were reported by Majer (1996), whose study of ant recolonization along a chronosequence of reforestation areas at this site found that relative to the native forest, the rehabilitation area was characterized by proportionately more generalist species and fewer specialists.

While the overall results appear favorable, there was considerable variability among plots within the reforestation area with respect to the abundance and diversity of the regenerating flora. Although this variability may be comparable to that found in natural succession, a better understanding of the factors influencing these patterns of floristic composition is worth pursuing, particularly if this knowledge can be translated into improved plantation design and management prescriptions to yield more rapid and uniform acceleration of natural succession.

4.1. Overstorey influences on plantation understorey floristic development

The results of this study clearly show a number of significant relationships between the structural development of the planted overstorey trees and patterns of colonization by primary forest trees, vines and herbs. While the abundance (density) of total woody species regeneration within the 10-year-old reforestation area was insensitive to overstorey composition, basal area density and degree of crown closure, this regeneration was dominated by a relatively limited number of short-lived, early successional tree and shrub species that were either present at the time of plantation establishment in the soil seed bank, or were the result of internal regeneration by reproductively mature species included in the original planting mixture.

Although woody species colonizing the site from the surrounding primary forest subsequent to plantation establishment comprised 10% or less of the total woody regeneration density, these species comprised 60% of the total woody species richness in the reforestation area. Regeneration density, species richness and diversity of primary forest colonists tended to be extremely low in study plots in which the planted tree survival and growth rates were poor and increased with planted tree basal area, crown cover and humus depth. Very similar patterns were found with respect to vines, which are critical components of floristic diversity and structure in native primary and secondary forests in this region.

The degree of dominance of grasses appears to be an extremely important factor affecting the recruitment of woody primary forest species into the reforestation area. Study plots with more open canopies (and higher understorey light levels) tended to be dominated by a very limited number of short-lived early secondary forest species that can, apparently, compete well with grasses. These pioneer tree species may eventually shade out understorey grasses and thus facilitate seed germination, survival and growth of mid- and late-successional tree species. There is a danger, however, that this process may be arrested by the mortality of these short-lived overstorey trees and re-opening of the overstorey canopy which increases the risk of fire. In those plots with better overstorey development, arrested succession is a far less likely possibility, as grasses have been largely suppressed, litter and humus layers have developed steadily and regeneration of a large number of primary forest species of varying successional stages has occurred.

The negative influence of grasses and the facilitating role of naturally occurring shrubs and trees has been discussed by several authors in recent studies of forest succession in abandoned pastures in the Brazilian Amazon region (Uhl et al., 1988; Nepstad et al., 1991; Vieira et al., 1994) and elsewhere in the neotropics (Guevara et al., 1986; Guevara et al., 1992; Aide et al., 1995). In studies of young plantations of *Albizia lebbek* in Puerto Rico, the abundance of trees and shrubs colonizing the plantation understorey was inversely correlated with understorey light intensity, which in turn was directly correlated with dominance of grasses (Parrotta, 1992; Parrotta, 1993). Similar results and conclusions were reported for rehabilitation plantings on phosphate-mined sites in India (Soni et al., 1989), *Acacia mangium* and *Paraserianthes falcataria* plantations established on *Imperata cylindrica*-dominated grasslands in South Kalimantan, Indonesia (Kuusipalo et al., 1995) and in native species plantations in Costa Rica (Guariguata et al., 1995; Haggar et al., 1997; Powers et al., 1997).

These findings have important implications for the design of restoration plantings on severely degraded sites such as mined lands. The selection of tree species that are capable of rapid early growth under stressful site conditions is essential for rapid occupancy of the reforestation site and suppression of grasses that can very often be a severe barrier to regeneration of all but a very limited number of pioneer tree and shrub species. A mixture of both fast-growing pioneer species and slower-growing (and longer-lived) native species is recommended to provide greater canopy habitat diversity within the reforestation area, increase structural and biochemical diversity of redeveloping forest floor and soil humus layers, and to act as 'insurance' against the early mortality of short-lived species, opening of the forest canopy and reestablishment of dominant grasses. Finally, the planting density of nursery-grown seedlings, stumped saplings and/or large seeds should be adequate to minimize the early mortality resulting from competition with grasses and thus facilitate rapid site capture; the planting density of 2500 trees/ha used at Trombetas appears to be an acceptable minimum.

4.2. The effect of proximity to native forest seed sources

The regeneration density for woody primary forest colonists and species richness and diversity for regenerating trees and vines in the reforestation area study plots were very clearly influenced by proximity to the primary forests surrounding the mine site. The abundance and diversity of regeneration declined from the primary forest boundary to about 100–200 m into the reforestation area, with a much more gradual decline up to 640 m from the primary forest. This general pattern supports the hypothesis that proximity to potential seed sources significantly affects the abundance and diversity of plantation understorey colonization by species not present in the initial (1985) reforestation, and suggests that seed dispersal is increasingly a limiting factor at greater distances from the primary forest, at least during the early years of forest development. These results are consistent with those of a number of previous recolonization studies of woody species on mined lands (e.g. McClanahan, 1986; McClanahan and Wolfe, 1987; Hardt and Forman, 1989) and secondary forests (e.g. Peterken and Game, 1984; van Ruremonde and Kalkhoven, 1991; Dzwonko, 1993) in various parts of the world. Similar results were reported for 7-year-old plantations of *Albizia lebbek* in Puerto Rico with reference to the plantation distance from secondary forest seed sources (Parrotta, 1993), and more recent studies of isolated, 5- to 7-year-old restoration plantings in Queensland, Australia located at varying distances from native rain forest remnants (Tucker and Murphy, 1997).

It appears that the development of floristic diversity within the reforestation area is proceeding at a fairly rapid pace near the primary forest boundary but significantly slower at increasing distances away from the native forest. The overwhelming importance of wildlife for seed dispersal of primary forest species in this region (discussed below) suggests that the future colonization of the reforestation area by additional primary forest species will depend on the continued development of the planted trees and regenerating understorey and its increased habitat value for seed-dispersing wildlife. While this process is expected to be slower at greater distances from the primary forest (seed sources), it is encouraging that both the planted overstorey and regenerating understorey of all study plots up to 640 m from the primary forest are comprised of both short- and long-lived pioneer and late successional species. This should ensure that the system will continue to provide favorable understorey conditions for germination and growth of tree, shrub, palm and vine species brought into the site by wildlife in the years ahead.

4.3. Wildlife and seed dispersal

The overall mist net capture rate of 4.2 birds/100 net h in the reforestation plot was very low relative to other lowland tropical sites. Elsewhere in primary forest in the Brazilian Amazon, for example, values ranged from 19 to 26 captures/100 net h north of Manaus (Bierregaard and Lovejoy, 1989) and a small sample south of Santarém yielded 27 captures/100 net h (Wunderle and Willig, unpublished data). Earlier stages of succession are usually expected to have higher capture rates partially because nets in the younger stages sample a greater proportion of vegetation in shorter (younger) habitats and, therefore, are more likely to capture birds using the foliage–air interface (Blake et al., 1990). Therefore, the absence of a shrubby understorey in the reforestation plots may have contributed to the low capture rate of birds. In addition, plant families such as Melastomataceae, Rubiaceae and Solanaceae, which produce fruits known to attract birds, were mostly absent from the understorey. Although a few fruiting melastomes and *Heliconia* sp. (Musaceae) were found, fruit was mostly absent from the understorey. Given the paucity of fruit in the understorey there was reason to expect low captures of frugivores as previous studies have demonstrated that frugivores are especially responsive to spatial and temporal changes in fruit abundance at a variety of different scales (e.g. Leighton and Leighton, 1983; Terborgh, 1983; Wheelwright, 1983; Fleming, 1988; Blake and Loiselle, 1991; Loiselle and Blake, 1991). Thus, it is not surprising that the capture rate of frugivores was low and that they were poorly represented in the net sample (15% of all species and 9% of all individuals).

Point counts and general observations of birds were consistent with the mist netting results and indicate that overall avian abundance was low in the reforestation plots. However, the proportion of birds which are known to consume fruits and act as potential seed dispersers was reasonably high. Although it is likely that some entered the plots to feed on fruiting trees, such as *Cecropia* sp., most probably foraged on other resources such as insects or spiders. This was the case in the trogons, woodpeckers, flycatchers and oropendulas which were observed foraging in the plots. Omnivorous species which feed primarily on insects, but consume fruit opportunistically, made up the predominance of species known to consume fruit. Thus, it is likely that most omnivorous birds were primarily attracted by the vegetation cover of the reforestation plots to forage on invertebrates and only consumed fruit as it was encountered in the plots. Some of these omnivorous visitors, however, may have been responsible for transporting seeds of primary forest species into the reforestation area.

Proximity to the primary forest did not appear to affect bird population densities as mist net capture rates were similar in edge and distant locations, although larger samples might indicate species differences between the two locations. The absence of a primary forest edge effect suggests that the overall vegetation structure (e.g. tree height, foliage height profile, etc.) was adequate to attract secondary forest bird species throughout the reforestation plots. However, most secondary forest bird species are likely to disperse seeds from within the reforestation plots rather than carrying seeds from the surrounding primary forest into the reforestation plots. This is a result of habitat specialization in which primary forest birds, particularly in the understorey, are mostly restricted to primary forest, and secondary forest dwellers are mostly restricted to secondary forests or treefall gaps in primary forest (e.g. Pearson, 1971). Some canopy species, however, may be less discriminating than understorey dwellers and readily move between canopies of primary and secondary forests (Pearson, 1971). For example, toucans, toucanets and aracaris were observed moving between the canopy of primary forest to the canopy of the reforestation plots. Some of these movements undoubtedly involved seed dispersal as toucans dropped seeds from calling perches in the tops of the tallest trees in the reforestation plots. Therefore, it appears likely that while secondary forest bird species may have facilitated seed dispersal within the reforestation area, the enrichment of the tree flora in the reforestation area was facilitated by canopy-dwelling birds species that transported seeds from the primary forest.

In contrast to birds, the densities of bats were relatively high. The two captured bat genera, *Carollia* and *Artibeus* are common in disturbed and second growth areas throughout the neotropics where they are important seed dispersers (e.g. Emmons and Feer, 1990). For example, bats in the genus *Carollia* consume fruits of a large number of tree and shrub species from a variety of families (e.g. Fleming, 1988 for *C. perspicillata*). Unlike the smaller *Carollia*, which feeds heavily on understorey fruits, *Artibeus* only rarely takes subcanopy fruits (Morrison, 1983). In Central America, *Artibeus jamaicensis* plucks fruits from a large variety of tree species (Bonaccorso, 1975) and is capable of carrying relatively heavy fruits (e.g. 16 g *Andira inermis*) to feeding roosts from 25 to over 200 m away (Janzen et al., 1976; Morrison, 1978).

The variety and relative abundance of fruit-eating birds and mammals detected on the 10-year-old reforestation plots at Trombetas suggest that the patterns of seed dispersal there are mostly consistent with those found in early successional sites in the lowland tropics elsewhere. Previous studies have indicated that bird- and bat-disseminated seeds predominate in seed banks of early successional sites elsewhere in Amazonia (Uhl et al., 1981; Uhl and Clark, 1983; Uhl and Jordan, 1984). In French Guyana, bats (primarily *Carollia* sp., *Sturnira* sp. and *Artibeus* spp.) were responsible for dispersing the seeds of eight early successional species (one *Cecropia*, three *Vismia* and four *Solanum* species) and birds (16 species) dispersed another 15 species, especially those in the Rubiaceae and Melastomataceae families (de Foresta et al., 1984; Charles-Dominique, 1986). Although birds and bats may sometimes consume the same fruits, diet overlap between the two taxa is small suggesting that they are dispersing different seeds of different species (Gorchov et al., 1995). Given the abundance of bats relative to birds in the reforestation plots it is likely that bats play the dominant role in seed dispersal at this stage of regeneration.

The relative contributions of birds and bats to the dispersal of small-seeded species on early successional sites is expected to differ given their behavioral differences. For example, bats contribute most of the seed rain in open areas (de Foresta et al., 1984; Gorchov et al., 1993), whereas birds deposit seeds around fruiting trees and in the forest understorey (de Foresta et al., 1984). This occurs primarily because of differences in fruit processing behavior, i.e. bats defecate seeds under their night roosts and in flight, whereas birds are more likely to defecate (or regurgitate) seeds while perched (McDonnell and Stiles, 1983; Charles-Dominique, 1986; Stiles and White, 1986).

Large seeds (>10 mm long) are more likely to be dispersed shorter distances than small seeds based on distribution patterns of juveniles of large-seeded plants (e.g. Hubbell, 1979) and the seed handling behavior of dispersers (e.g. de Foresta et al., 1984). For example, monkeys and birds dropped about 89% of the large seeds (14 mm long) of *Tetragastris panamensis* under the parent crown (Howe, 1980). Similarly, the large seeds of *Virola surinamensis* (2 cm long) were dispersed at least 40 m from the parent tree by only three of seven bird species (one guan and two toucan species) which consumed the fruits (Howe and Vande Kerckhove, 1981). Our data, which show a pronounced primary forest edge effect with respect to colonizing tree species richness and diversity, are consistent with these findings. Thus, it is reasonable to expect that dispersal of most large seeds deep into the reforestation plots is a relatively rare event, particularly given the apparent absence of primates which are important dispersers of large seeds (Terborgh, 1983).

Based on observations in the reforestation plots and findings of previous studies it is likely that the reforestation plots are still in the early stages of succession in terms of seed dispersal. Most of the seed rain is probably now provided by bats which move small-seeded species throughout the plots. Although most avian seed dispersers are currently rare, the larger species (e.g. curassows, toucans, toucanets and aracaris) appear to play a valuable role by bringing large-seeded species onto the plots. Terrestrial mammals (deer, agouti, tapir and opossum) undoubtedly move some seeds onto the plots, but the absence of primates suggests that many large-seeded species will be absent. It is likely that it will be many years before the plots have the stature to attract primates which would be expected to move large seeds, albeit slowly due to the relatively low dispersal rate of large seeds. To accelerate the restoration process, managers should plant large-seeded species which are normally established in shaded conditions and dispersed by arboreal mammals (Terborgh, 1983; Foster and Janson, 1985), most of which are currently rare or absent from the plots.

Acknowledgements

This work was conducted in cooperation with the University of Puerto Rico and supported in part by a grant from the World Bank to the International Institute of Tropical Forestry, USDA Forest Service (Research Support Budget Grant RPO #680-05: 'The catalytic effect of tree plantings on the rehabilitation of native forest biodiversity on degraded tropical lands'). The authors thank Mineração Rio do Norte for permitting access to the reforestation area for research purposes and offer special thanks to Sr Pedro Ferreira for his special expertise in identifying trees and seedlings in the field. The assistance of M. Ivory of the University of Oxford (UK) in VAM spore and sporocarp identifications is gratefully acknowledged. Critical reviews of an earlier version of this manuscript were provided by J.K. Francis, A.E. Lugo, F.H. Wadsworth and P.L.Weaver.

Appendix A Plant species in 10-year-old reforestation plots at a bauxite-mined site, Porto Trombetas, Pará, Brazil (closed-canopy plots)

Scientific name	Family	Common name	Density		IV[a]	Source[b]	Dispersal agents[c]	Longevity[d]
			No./ha	Frequency				
Trees and shrubs								
Tatapira guianensis	Anacardiaceae	Tatapiririca	13180.7	0.813	49.15	i	B	2
Vismia guianensis	Guttiferae	Lacre marrom	3121.0	0.875	14.55	i	B	1
Vismia sp.	Guttiferae	Lacre vermelho	2277.1	0.875	11.63	i	B	1
Guateria sp.	Anonaceae	Envira preta	1273.9	0.813	7.88	i	B	2
Belucia dichotoma	Melastomataceae	Muuba	1126.6	0.844	7.50	i	B, M	1
Rollinia sp.	Anonaceae	Envira conde	370.2	0.813	4.75	i	B	1
Protium sp.	Burseraceae	Breu branco	597.1	0.625	4.74	e	B	2
Oenocarpus bacaba	Palmae	Palmeira bacaba	473.7	0.688	4.58	i	B	2
Palcourea sp.	Rubiaceae	Erva de rato amarela	644.9	0.531	4.50	i	B	1
Conceveiba sp.	Euphorbiaceae	Pau de indio	684.7	0.406	4.11	i	B	1
Croton sp.	Euphorbiaceae	Pau gaviota	286.6	0.625	3.66	i	B	1
Byrsonima sp.	Malpighiaceae	Murici da mata	358.3	0.563	3.64	i	B	3
Stryphnodendron pulcherimum	Leg.-Mimos.	Faveira camuze	163.2	0.625	3.23	i	B, M	2
Laetia procera	Flacourtiaceae	Pau jacare	139.3	0.469	2.48	i	B	3
Vismia sp.	Guttiferae	Lacre branco	171.2	0.406	2.33	i	B	1
Unidentified	Euphorbiaceae	Caxixa	218.9	0.344	2.23	i	B	1
Inga sp.	Leg.-Mimos.	Inga veluda	314.5	0.219	2.02	e	B, M	1
Miconia sp.	Melastomataceae	Maramara preta	159.2	0.344	2.02	i	B	1
Ocotea myriantha	Lauraceae	Louro abacate	99.5	0.375	1.94	e	B	3
Unidentified	Unidentified		218.9	0.250	1.83	e	?	
Brosimum lactescens	Moraceae	Janita	111.5	0.313	1.72	e	B	1
Duguetia riparia	Anonaceae	Envira branca	71.7	0.313	1.58	i	B	1
Sclerolobium racemosa	Leg.-Caes.	Tachi dos campos	55.7	0.313	1.53	i	W	1
Hymenolobium excelsum	Leg.-Papil.	Angelim da mata	79.6	0.281	1.48	e	W	4
Inga sp.	Leg.-Mimos.	Inga branca	71.7	0.281	1.45	e	B, M	1
Pouteria sp.	Sapotaceae	Abiurana	67.7	0.281	1.43	e	B, M	3
Cassia sp.	Leg.-Caes.	Cassia piolho	218.9	0.156	1.43	i	W	1
Inga sp.	Leg.-Mimos.	Inga xixica	95.5	0.250	1.40	e	B, M	2
Unidentified	Rubiaceae		123.4	0.219	1.36	e	W	2
Hymenaea sp.	Leg.-Caes.	Jutai	43.8	0.281	1.35	i	B, M	4
Pourouma sp.	Moraceae	Imbaubarana	71.7	0.250	1.32	e	B	1
Astronium lecointei	Anacardiaceae	Muiracatiara	103.5	0.219	1.29	e	W	4
Miconia sp.	Melastomataceae	Maramara branca	63.7	0.250	1.29	i	B	1
Miconia sp.	Melastomataceae	Miconia arbusto	171.2	0.156	1.26	i	B	1
Parkia gigantocarpa	Leg.-Mimos.	Faveira arara tucupi	47.8	0.250	1.23	i	M	3
Clusia sp.	Clusiaceae	Clusia	59.7	0.219	1.14	e	B	2
Goupia glabra	Celestraceae	Cupiuba	55.7	0.219	1.13	i	B	4
Myrciaria sp.	Myrtaceae	Murta	43.8	0.219	1.09	e	B, M	2
Protium sp.	Burseraceae	Breu preto	39.8	0.219	1.07	e	B	3
Eschweilera sp.	Lecythidaceae	Matamata	35.8	0.219	1.06	e	B	3
Trattinickia burserifolia	Burseraceae	Breu sucuruba	31.8	0.219	1.04	i	B	4
Bowdichia cf. *nitida*	Leg.-Papil.	Sucupira amarela	99.5	0.156	1.01	i	W	3
Cordia sp.	Boraginaceae	Uruazeiro	51.8	0.188	0.98	i	B	2
Tabebuia serratifolia	Bignoniaceae	Pau d'arco amarelo	47.8	0.188	0.97	e	W	4
Ocotea guianensis	Lauraceae	Louro prata	23.9	0.188	0.88	e	B	2
Enterolobium schomburgkii	Leg.-Mimos.	Faveira de rosca	23.9	0.188	0.88	i	B, M	3
Bowdichia sp.	Leg.-Papil.	Sucupira preta	23.9	0.188	0.88	e	W	3
Cecropia sp.	Moraceae	Imbauba	23.9	0.188	0.88	i	B	2
Virola sp.	Myristicaceae	Ucuuba vermelha	23.9	0.188	0.88	e	B, M	3

Appendix A (*continued*)

Scientific name	Family	Common name	Density		IV[a]	Source[b]	Dispersal agents[c]	Longevity[d]
			No./ha	Frequency				
Acacia mangium	Leg.-Mimos.	Acacia mangium	47.8	0.156	0.83	e	B	1
Guateria sp.	Anonaceae	Envira pindauba preta	39.8	0.156	0.80	e	B	2
Bocageopsis sp.	Anonaceae	Envira turi preta	31.8	0.156	0.78	e	B	1
Sacoglottis sp.	Humiriaceae	Achua	19.9	0.156	0.74	i	B	3
Virola sp.	Myristicaceae	Ucuuba preta	47.8	0.125	0.70	e	B, M	3
Unidentified	Unidentified	Tapioca	39.8	0.125	0.67	e	B	1
Mezilaurus itauba	Lauraceae	Itauba amarela	31.8	0.125	0.64	e	B	3
Anona ambotay	Anonaceae	Envira taia	27.9	0.125	0.63	e	B	1
Unidentified	Unidentified	Pau de rego	23.9	0.125	0.62	e	B	1
Vantanea paraensis	Humiriaceae	Uchi morcego	23.9	0.125	0.62	i	B	3
Piptadenia communis	Leg.-Mimos.	Faveira timborana	19.9	0.125	0.60	e	B, M, W	4
Dipteryx magnifica	Leg.-Papil.	Cumaru rosa	19.9	0.125	0.60	i	B, M	4
Miconia longifolia	Melastomataceae	Sapateiro	15.9	0.125	0.59	e	B	1
Helicostylus sp.	Moraceae	Muiratinga preta	15.9	0.125	0.59	e	B	3
Buchenavia sp.	Combretaceae	Cuiarana	47.8	0.094	0.57	i	B	4
Andira retusa	Leg.-Papil.	Andira-uchi	23.9	0.094	0.48	i	B	4
Unidentified	Unidentified	Acariquarana	19.9	0.094	0.47	e	B	2
Mouriria brachyanthera	Melastomataceae	Muirauba	19.9	0.094	0.47	e	B	3
Duroia sp.	Rubiaceae	Purui	19.9	0.094	0.47	e	B	2
Micropholis sp.	Sapotaceae	Abiurana rosadinha	19.9	0.094	0.47	e	B, M	3
Unidentified	Leg.-Mimos.	Faveira mapuchiqui	15.9	0.094	0.46	e	B, M	3
Inga sp.	Leg.-Mimos.	Inga cipo	15.9	0.094	0.46	e	B, M	1
Peltogyne paradoxa	Leg.-Papil.	Coataquicaua	15.9	0.094	0.46	e	W	3
Apeiba sp.	Tiliaceae	Acoita cavalo	15.9	0.094	0.46	e	W	3
Unidentified	Unidentified	Canela brava	11.9	0.094	0.44	e	B	1
Schlefflera morototoni	Araliaceae	Morototo	11.9	0.094	0.44	e	B	2
Cassia leiandra	Leg.-Caes.	Faveira marimari grande T.F.	11.9	0.094	0.44	e	B, M	2
Dalbergia spruceana	Leg.-Papil.	Jacaranda do Para	11.9	0.094	0.44	i	W	2
Brosimum potabile	Moraceae	Amapa doce	11.9	0.094	0.44	e	B	4
Rinorea sp.	Violaceae	Jacamin preto	11.9	0.094	0.44	e	B	1
Siparuna amazonica	Monimiaceae	Capitiu	19.9	0.063	0.34	e	B	1
Endopleura uchi	Humiriaceae	Uchi pucu	15.9	0.063	0.32	i	B	3
Unidentified	Leg.-Mimos.	Faveira mucuna	11.9	0.063	0.31	i	B, M	2
Vatairea sericea	Leg.-Papil.	Faveira amargosa	11.9	0.063	0.31	e	W	3
Rinorea sp.	Violaceae	Jacamin branco	11.9	0.063	0.31	e	B	1
Unidentified	Unidentified	Pau tucandeira	8.0	0.063	0.29	e	B	1
Aspidospermum oblongum	Apocynaceae	Araracanga	8.0	0.063	0.29	e	W	4
Jacaranda copaia	Bignoniaceae	Parapara	8.0	0.063	0.29	i	W	2
Sacoglottis sp.	Humiriaceae	Uchi coroa	8.0	0.063	0.29	i	B, M	3
Octea fragrantissima	Lauraceae	Louro canela	8.0	0.063	0.29	e	B	3
Swartzia corrugata	Leg.-Caes.	Coracao de negro	8.0	0.063	0.29	e	B	2
Dinizia excelsa	Leg.-Mimos.	Angelim pedra	8.0	0.063	0.29	i	W	4
Hymenolobium sp.	Leg.-Papil.	Angelim aroeira	8.0	0.063	0.29	e	W	4
Ormosia sp.	Leg.-Papil.	Tento	8.0	0.063	0.29	i	B	3
Simaruba amara	Simarubaceae	Marupa	8.0	0.063	0.29	e	B	3
Theobroma sp.	Sterculiaceae	Cacaurana	8.0	0.063	0.29	e	M	1
Apeiba echinata	Tiliaceae	Pente de macaco	8.0	0.063	0.29	e	B	2
Clusia sp.	Clusiaceae	Apui	8.0	0.031	0.16	e	B	2
Diospyros sp.	Ebenaceae	Caqui	8.0	0.031	0.16	e	B, M	4

Appendix A (*continued*)

Scientific name	Family	Common name	Density		IV[a]	Source[b]	Dispersal agents[c]	Longevity[d]
			No./ha	Frequency				
Parkia pendula	Leg.-Mimos.	Faveira bolota	8.0	0.031	0.16	i	B, M	3
Psidium guianensis	Myrtaceae	Araca	8.0	0.031	0.16	e	B, M	1
Unidentified	Unidentified	Acariquara branca	4.0	0.031	0.15	e	B	2
Bocageopsis sp.	Anonaceae	Envira turi vermelho	4.0	0.031	0.15	e	B	1
Aspidospermum oblongum	Apocynaceae	Carapanauba	4.0	0.031	0.15	e	W	3
Tabebuia impetignosa	Bignoniaceae	Pau d'arco roxo	4.0	0.031	0.15	e	W	4
Protium sp.	Burseraceae	Breu vermelho	4.0	0.031	0.15	e	B	3
Couepia bracteosa	Chrysobalanaceae	Pajura	4.0	0.031	0.15	i	?	3
Licania cf. *micrantha*	Chrysobalanaceae	Caraiperana	4.0	0.031	0.15	i	M	3
Hevea guianensis	Euphorbiaceae	Seringa itauba	4.0	0.031	0.15	i	B, M	2
Joanesia princips	Euphorbiaceae	Boleira	4.0	0.031	0.15	i	M	2
Casearia sp.	Flacourtiaceae	flacourtiaceae	4.0	0.031	0.15	e	B	1
Aniba parviflora	Lauraceae	Louro pucherin	4.0	0.031	0.15	e	B	2
Ocotea sp.	Lauraceae	Louro branco	4.0	0.031	0.15	e	B	2
Pithecelobium sp.	Leg.-Mimos.	Faveira dentinha	4.0	0.031	0.15	e	B, M	2
Sclerolobium melanocarpum	Leg.-Caes.	Tachi vermelho	4.0	0.031	0.15	e	W	2
Tachigalia myrmecophylla	Leg.-Caes.	Tachi pitomba	4.0	0.031	0.15	e	W	2
Acacia auriculiformis	Leg.-Mimos.	Acacia auriculiformis	4.0	0.031	0.15	e	B	1
Inga sp.	Leg.-Mimos.	Inga guariba	4.0	0.031	0.15	e	B, M	1
Parkia sp.	Leg.-Mimos.	Faveira japacanim	4.0	0.031	0.15	i	B, M	3
Dipteryx odorata	Leg.-Papil.	Cumaru	4.0	0.031	0.15	i	B, M	4
Carapa guianensis	Meliaceae	Andiroba	4.0	0.031	0.15	i	M	3
Brosimum rubescens	Moraceae	Muirapiranga	4.0	0.031	0.15	e	B	4
Minquartia guianensis	Olacaceae	Acariquara	4.0	0.031	0.15	e	B	2
Astrocaryum murumuru	Palmae	Palmeira murumuru	4.0	0.031	0.15	i	M	2
Desmoncus polycanthos	Palmae	Palmeira jacitara	4.0	0.031	0.15	e	B	1
Euterpe oleracea	Palmae	Palmeira acai	4.0	0.031	0.15	e	B	1
Total			28853.5		200.00			
Vines								
Mikania sp.	Asteraceae	Mikania	1425.2	0.938	53.34	i	W	
Davilla sp.	Dillenaceae	Cipo de fogo	859.9	0.844	37.45	i	B, M	
Mimosa myriadena	Leg.-Mimos.	Rabo de cameleão	629.0	0.375	22.81	i	W	
Piper sp.	Piperaceae	Piperaceae	179.1	0.375	11.57	i	B	
Pasiflora serrato-digitata	Passifloraceae	Maracuja urubu	115.4	0.375	9.98	i	B, M	
Machaerium sp.	Leg.-Papil.	Fabaceae	238.9	0.188	9.51	i	W	
Abuta sp.	Menispermaceae	Cipo X	99.5	0.250	7.22	e	B	
Banisteriopsis sp.	Malpighiaceae	Malpighiaceae	91.6	0.250	7.02	e	W	
Securidaca sp.	Polygalaceae	Securidaca	87.6	0.250	6.92	i	W	
Arrabidaea sp.	Bignoniaceae	Bignoniaceae	51.8	0.281	6.62	i	W	
Odonadenia sp.	Apocynaceae	Apocynaceae	27.9	0.219	4.84	i	W	
Senna latifolia	Leg.-Caes.	Senna	47.8	0.188	4.74	i	B, M, W	
Smilax sp.	Smilacaceae	Smilax	31.8	0.188	4.35	i	B	
Unidentified	Unidentified	Unknown	19.9	0.125	2.86		?	
Passiflora coccinea	Passifloraceae	Maracuja da mata	23.9	0.094	2.37	i	B, M	
Passiflora sp.	Passifloraceae	Maracuja alada	27.9	0.063	1.88	i	B, M	
Paulinia sp.	Sapindaceae	Sapindaceae	11.9	0.063	1.48	e	W	
Bauhinia splendens	Leg.-Caes.	Bauhinia	11.9	0.031	0.89	i	W	
Aristoloquia sp.	Aristoloquiaceae	Aristoloquia	4.0	0.031	0.69	i	W	
Gurania cissoides	Cucurbitaceae	Gurania	4.0	0.031	0.69	e	B	
Hippocratea aspera	Hippocrataceae	Hippocrataceae	4.0	0.031	0.69	i	W	

Appendix A (*continued*)

Scientific name	Family	Common name	Density		IV[a]	Source[b]	Dispersal agents[c]	Longevity[d]
			No./ha	Frequency				
Dalbergia monetaria	Leg.-Papil.	Dalbergia	4.0	0.031	0.69	i	W	
Phaseolis pilosus	Leg.-Papil.	Phaseolis	4.0	0.031	0.69	e	B	
Lygodium sp.	Polypodiaceae	Cipo samambaia	4.0	0.031	0.69	i	W	
Total			4000.8		200.00			
Grasses								
Andropogon bicomis	Gramineae	Rabo de cavalo	1393.3	0.563	56.85	i	W	
Unidentified	Cyperaceae	Navalho	1102.7	0.656	53.23	i	B	
Unidentified	Gramineae	Capim mole	732.5	0.719	46.39	i	B	
Olyra micrantha	Gramineae	Taboquinha	549.4	0.219	22.30	i	B	
Scleria pratensis	Cyperaceae	Tiririca	127.4	0.219	11.73	i	B	
Brachiaria decumbens	Gramineae	Capim braquiaria	71.7	0.063	4.23	i	B	
Cyperus sp.	Cyperaceae	Capim bolota	8.0	0.063	2.64	i	B	
Cyperus ligularis	Cyperaceae	Flexa de urubu	4.0	0.031	1.32	i	B	
Unidentified	Gramineae	Tarapucu	4.0	0.031	1.32	i	B	
Total			3984.9		200.00			
Herbs								
Heloconia sp.	Musaceae	Heliconia	167.2	0.406	131.53	i	B	
Unidentified	Polypodiaceae	Samabaia	23.9	0.094	23.76	i	W	
Unidentified	Rubiaceae	Rubiaceae	11.9	0.063	14.05	i	B	
Cyrtopodium sp.	Orchidaceae	Orquidea	8.0	0.063	12.27	i	W	
Ischnosiphon gracilis	Amarantaceae	Aruma	4.0	0.031	6.13	i	B	
Unidentified	Solanaceae	Solanum	4.0	0.031	6.13	i	B	
Unidentified	Unidentified	Chicoria brava	4.0	0.031	6.13	i	B	
Total			218.9		200.00			

[a]Importance value (IV) for each species was calculated as the sum of relative density and relative frequency.

[b]e, propagules were known to have been introduced into plantations by natural means from surrounding forest areas; i, species may have been present in the soil seed bank or were the result of natural regeneration of planted trees.

[c]Seeds typically dispersed by bats and/or birds (B), mammals other than bats (M) and wind (W).

[d]Tree longevity indicates average life span: 1, <20 years; 2, 20–40 years; 3, 40–80 years; 4, >80 years.

Appendix B Plant species in 10-year-old reforestation plots at a bauxite mined site, Porto Trombetas, Pará, Brazil (open-canopy plots)

Scientific name	Family	Common name	Density		IV[a]	Source[b]	Dispersal agents[c]	Tree longevity[d]
			No./ha	Frequency				
Trees and shrubs								
Vismia sp.	Guttiferae	Lacre vermelho	7983.0	1.000	36.9	i	B	1
Vismia guianensis	Guttiferae	Lacre marrom	5668.8	1.000	28.7	i	B	1
Vismia sp.	Guttiferae	Lacre branco	4331.2	0.500	19.7	i	B	1
Miconia sp.	Melastomataceae	Miconia arbusto	4097.7	0.333	17.4	i	B	1
Belucia dichotoma	Melastomataceae	Muuba	1741.0	0.833	13.2	i	B, M	1
Rollinia sp.	Anonaceae	Envira conde	445.9	1.000	10.0	i	B	1
Byrsonima sp.	Malpighiaceae	Murici da mata	467.1	0.500	5.9	i	B	3
Duguetia riparia	Anonaceae	Envira branca	339.7	0.500	5.4	i	B	1
Tatapira guianensis	Anacardiaceae	Tatapiririca	615.7	0.333	5.0	i	B	2

Appendix B (*continued*)

Scientific name	Family	Common name	Density		IV[a]	Source[b]	Dispersal agents[c]	Tree longevity[d]
			No./ha	Frequency				
Croton sp.	Euphorbiaceae	Pau gaviota	169.9	0.500	4.8	i	B	1
Cassia sp.	Leg.-Caes.	Cassia piolho	509.6	0.333	4.6	i	W	1
Palcourea sp.	Rubiaceae	Erva de rato amarela	148.6	0.333	3.3	i	B	1
Vantanea paraensis	Humiriaceae	Uchi morcego	84.9	0.333	3.1	i	B	3
Guateria sp.	Anonaceae	Envira preta	42.5	0.333	3.0	i	B	2
Buchenavia sp.	Combretaceae	Cuiarana	42.5	0.333	3.0	i	B	4
Acacia mangium	Leg.-Mimos.	Acacia mangium	63.7	0.333	3.0	e	B	1
Cecropia sp.	Moraceae	Imbauba	63.7	0.333	3.0	i	B	2
Unidentified	Unidentified		63.7	0.333	3.0	e	?	
Sclerolobium racemosa	Leg.-Caes.	Tachi dos campos	339.7	0.167	2.6	i	W	1
Bowdichia cf. *nitida*	Leg.-Papil.	Sucupira amarela	191.1	0.167	2.1	i	W	3
Conceveiba sp.	Euphorbiaceae	Pau de indio	169.9	0.167	2.0	i	B	1
Inga sp.	Leg.-Mimos.	Inga preta	106.2	0.167	1.8	e	B, M	1
Couepia bracteosa	Chrysobalanaceae	Pajura	42.5	0.167	1.6	i	?	3
Sacoglottis sp.	Humiriaceae	Achua	63.7	0.167	1.6	i	B	3
Pouteria sp.	Sapotaceae	Abiurana	63.7	0.167	1.6	e	B, M	3
Astronium lecointei	Anacardiaceae	Muiracatiara	21.2	0.167	1.5	e	W	4
Tabebuia serratifolia	Bignoniaceae	Pau d'arco amarelo	21.2	0.167	1.5	e	W	4
Clusia sp.	Clusiaceae	Clusia	21.2	0.167	1.5	e	B	2
Laetia procera	Flacourtiaceae	Pau jacare	21.2	0.167	1.5	i	B	3
Endopleura uchi	Humiriaceae	Uchi pucu	21.2	0.167	1.5	i	B	3
Peltogyne paradoxa	Leg.-Papil.	Coataquicaua	21.2	0.167	1.5	e	W	3
Miconia longifolia	Melastomataceae	Sapateiro	21.2	0.167	1.5	e	B	1
Unidentified	Unidentified	Pau de rego	21.2	0.167	1.5	e	B	1
Unidentified	Unidentified	Fel de veado	21.2	0.167	1.5	e	?	1
Total			28046.7		200.0			
Vines								
Mikania sp.	Asteraceae	Mikania	1719.7	1.000	107.0	i	W	
Davilla sp.	Dillenaceae	Cipo de fogo	360.9	0.500	32.7	i	B, M	
Odonadenia sp.	Apocynaceae	Apocynaceae	84.9	0.500	21.2	i	W	
Banisteriopsis sp.	Malpighiaceae	Malpighiaceae	84.9	0.167	9.4	e	W	
Senna latifolia	Leg.-Caes.	Senna	63.7	0.167	8.5	i	B, M, W	
Passiflora coccinea	Passifloraceae	Maracuja da mata	42.5	0.167	7.7	i	B, M	
Gurania cissoides	Cucurbitaceae	Gurania	21.2	0.167	6.8	e	B	
Mimosa myriadena	Leg.-Mimos.	Rabo de cameleão	21.2	0.167	6.8	i	W	
Total			2399.2		200.0			
Grasses								
Andropogon bicomis	Gramineae	Rabo de cavalo	14437.4	0.833	91.2	i	W	
Brachiaria decumbens	Gramineae	Capim braquiaria	8492.6	0.333	46.4	i	B	
Melinus minutiflora	Gramineae	Capim gordura	4246.3	0.167	23.2	i	B	
Unidentified	Cyperaceae	Navalho	84.9	0.333	15.7	i	B	
Unidentified	Gramineae	Capim mole	42.5	0.333	15.5	i	B	
Olyra micrantha	Gramineae	Taboquinha	63.7	0.167	7.9	i	B	
Total			27367.3		200.0			

[a]Importance value (IV) for each species was calculated as the sum of relative density and relative frequency.

[b]e, propagules were known to have been introduced into plantations by natural means from surrounding forest areas; i, species may have been present in the soil seed bank or were the result of natural regeneration of planted trees.

[c]Seeds typically dispersed by bats and/or birds (B), mammals other than bats (M) and wind (W).

[d]Tree longevity indicates average life span: 1, <20 years; 2, 20–40 years; 3, 40–80 years; 4, >80 years.

Appendix C Fruit-eating birds observed in reforestation plots on a bauxite-mined site in Trombetas, Pará, Brazil

Common name	Scientific name	Observer[a]	Potential fruit diet[b]
Variegated tinamou	*Crypturellus variegatus*	P	
Little chachalaca	*Ortalis motmot*	P and W	
Black curassow	*Crax alector*	W	Myrtaceae, Meliaceae, Palmae[c]
Ruddy pigeon	*Columba plumbea*	P	Thymelaeaceae, Euphorbiaceae, Solanaceae, Verbenaceae[d]
Common ground dove	*Columbina passerina*	P and W	
White-tipped dove	*Leptotila verreauxi*	W	Solanaceae[d]
Ruddy quail-dove	*Geotrygon montana*	W	
Black-tailed trogon	*Trogon melanurus*	P	Rubiaceae, Lauraceae, Ulmaceae, Moraceae, Flacourtiaceae, Ericaceae, Symplocaceae, Melastomataceae, Solanaceae[e]
White-tailed trogon	*Trogon viridis*	P and W	
Violaceous trogon	*Trogon violaceus*	P and W	
Channel-billed toucan	*Ramphastos vitellinus*	P and W	Lauraceae, Moraceae, Urticaceae, Symplocaceae, Myrsinaceae, Rosaceae[f]
Red-billed toucan	*Ramphastos tucanus*	P and W	
Guianan toucanet	*Selenidera culik*	P and W	Annonaceae, Lauraceae, Moraceae, Urticaceae, Nyctaginaceae, Theaceae, Marcgraviaceae, Clusiaceae, Malvaceae, Flacourtiaceae, Cucurbitaceae, Symplocaceae, Myrsinaceae, Thymelaeaceae, Myrtaceae, Melastomataceae, Olacaceae, Celastraceae, Euphorbiaceae, Rhamnaceae, Erythroxylaceae, Malpighiaceae, Sapindaceae, Simaroubaceae, Meliaceae, Rutaceae, Araliaceae, Solanaceae, Boraginaceae, Verbenaceae, Rubiaceae, Caprifoliaceae, Asteraceae, Smilacaceae[g]
Green aracaris	*Pteroglossus viridis*	P and W	
Ringed woodpecker	*Celeus torquatus*	P	
Scale-br. Woodpecker	*Celeus grammicus*	W	
Lineated woodpecker	*Dryocopus lineatus*	P	
Screaming piha	*Lipagus vociferans*	P	
Golden-headed manakin	*Pipra erythrocephala*	W	Araliaceae, Euphorbiaceae, Melastomatacea[h]
Variegated flycatcher	*Empidonomus varius*	P	
Tropical kingbird	*Tyrannus melancholicus*	P and W	Lauraceae, Rhamnaceae, Solanaceae[d]
Boat-billed flycatcher	*Megarhynchus pitangua*	W	Lauraceae, Ulmaceae, Flacourtiaceae, Rosacea, Euphorbiaceae, Sapindaceae, Solanaceae, Verbenaceae, Caprifoliaceae[d]
Red-eyed vireo	*Vireo olivaceus*	P	Melastomataceae, Sapindaceae, Papaveraceae, Solanaceae, Verbenaceae, Malvaceae[i]
Green oropendula	*Psarocolius viridis*	P and W	
Olive oropendula	*Gymnostinops guracares*	W	
Yellow-rumped cacique	*Cacicus cela*	W	
Blue-gray tanager	*Thraupis episcopus*	P and W	Araliaceae, Melastomataceae, Moraceae[j]
Palm tanager	*Thraupis palmarum*	P and W	Araliaceae, Melastomataceae, Moraceae[j]
Silver-beaked tanager	*Ramphocelus carbo*	P	Araliaceae, Melastomataceae, Moraceae[j]
Yellow-backed tanager	*Hemithraupis flavicollis*	P	
Yellow-browed sparrow	*Ammodramus aurifrons*	P	

[a]W, observations of Wunderle in this study; P, previous observations of Pedreira Gonzaga (1991).
[b]Families of fruiting plants in which the corresponding bird species or genus may disperse seeds.
[c]Érard et al. (1991).
[d]Wheelwright et al. (1984).
[e]Wheelwright et al. (1984) for *T. aurantiiventris*.
[f]Wheelwright et al. (1984) for *R. sulfuratus*.
[g]Wheelwright et al. (1984) for *Aulacorhynchus prasinus*.
[h]Snow (1962).
[i]Wheelwright et al. (1984) for *V. solitarius*, *V. flavoviridis*, *V. eucophrys*.
[j]Snow and Snow (1971).

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