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# ABANDONED COFFEE PLANTATIONS: BIODIVERSITY CONSERVATION OR PATH FOR NON-NATIVE SPECIES? CASE STUDY IN A NEOTROPICAL MONTANE FOREST

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## SUMMARY

Abandoned shade coffee plantations are commonplace in Neotropical mountains. Their secondary successional regrowth supports local biodiversity. However, cultivation termination exposes the land to introduced colonizing plants, altering vegetation traits and creating novel communities. We report the vegetation and discuss the possible successional trajectory of a coffee plantation abandoned ~60 years ago on a sloped terrain within a montane forest. Four 400m<sup>2</sup> plots were surveyed and woody individuals >1cm in diameter were tallied, soils were analyzed and microclimate was recorded. The importance value index was calculated for each species, as well as species richness, diversity, equity, stem density, and basal area (BA). Trunk-stem diameter distribution was assessed. Multivariate analyses related vegetation and environment. Seventy-six spe-

cies/morphotypes from 28 families were recorded. Plots contrasted in their dominant canopy trees (*Syzygium jambos* (rose-apple), *Croton megalodendron* (croton) or *Ocotea fendleri* (laurel)), species richness (23-37 species), Shannon diversity (2.65-3.23), stem density (3450-8150 ha<sup>-1</sup>) and BA (19.9-50.7m<sup>2</sup>·ha<sup>-1</sup>). The main discriminating factor was the predominance of rose-apple in one plot aided by active cultivation nearby and by its life history traits. Succession was greatly influenced by the colonization potential and fast growth of rose-apple, establishing a novel forest community type. The answer to the question in the title will depend of the effective protection against non-native invading species. Currently, considering the level of human perturbation in Neotropical montane forests, such protection appears to be hard to achieve.

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 y keeping large native trees, shade coffee plantations resemble the original forest, providing suitable habitats that maintain biodiversity as well as the ecosystem functions and services (Perfecto *et al.*, 1996; Moguel and Toledo, 1999; Philpott *et al.*, 2008). However, as coffee cultivation under full sunlight is more profitable, some shaded plantations have been abandoned. These, if left undisturbed, undergo secondary successions that maintain and gradually upgrade local species richness (Perfecto *et al.*, 1996; Marciano-Vega *et al.*, 2002; Lugo and Helmer, 2004; Bhagwat *et al.*, 2008; López-Gómez *et al.*, 2008; Borkhataria

*et al.*, 2012). The preservation and management of this secondary regrowth is an important share of the 40 to 50% of remaining tropical forested areas (Brown and Lugo, 1990; Chazdon *et al.*, 2009). Cultivation abandonment opens the land for the colonization of either native or non-native plants, which shape secondary successions. The resulting community assemblage is determined by propagule availability and the competitive potential of colonizing species. If non-native colonizing species prevail, the distinctive or typical trajectory of the secondary succession would be altered and a 'novel' community could arise. The current global changes that impact natural

communities increase the importance for the study and appropriate management of these novel systems (Lugo, 2004; Hobbs *et al.*, 2006).

We studied the post-cultivation woody vegetation of an abandoned but protected coffee plantation within a fragment of montane Neotropical forest. The likely effects of local physical, biotic and chronological variables on species composition, diversity and basal area were examined. The dominance of a non-native and rapid colonizing tree was documented and the possible causes and consequences of this colonization on vegetation and its successional trajectory are discussed.

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**KEYWORDS** /Coffee Plantation / Montane Forest / Non-Native Trees / Novel Communities / Secondary Succession / Venezuela /

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## Study site

The abandoned plantation covers 9ha embedded in an ombrophilous sub-montane forest (Huber and Alarcón, 1988) of the Venezuelan Coastal Mountains, on the slopes surrounding the Universidad Simón Bolívar (USB) campus in Caracas (10°24'N; 66°53'W; Figure 1). Shade coffee cultivation began at this site during colonial times and local anecdotic sources mention that it ceased by the 1950's, probably due to low productivity. The abandoned plantation, at 1100-1450masl, is on relatively deep Ultisols with a temperate climate and seasonal rains. Government and private weather stations provided rainfall and air temperature data outside the plantation. During 12 months, air temperature was logged in the center of one of the study plots (HoBo H08-032-08 Logger; Onset, Bourne, MA, USA).

## Soil sampling

Three soil samples, 5 to 20cm deep, were taken around the center of each plot and mixed for uniformity. Texture was determined with the Bouyoucos method, available phosphorus was analyzed with the molybdenic-blue method (Murphy and Riley, 1963) and available potassium and calcium by flame spectrophotometry. Total nitrogen was measured after Kjeldahl digestion. Cation exchange capacity (CEC) and exchangeable aluminum content were determined by extraction with  $\text{NH}_4\text{Cl}$  followed by spectrophotometry (Sparks *et al.*, 1996). Organic matter content (Walkley and Black's method; Jackson, 1982) and pH (1:2.5 in water) were also measured. A synthetic *ad hoc* fertility index (FI) was calculated as the sum of the relative values (with respect to their maximum) of N, P and CEC (maximum FI= 300). In each plot, three samples for soil apparent density were cored with a cylinder (volume= 29.4cm<sup>3</sup>), then dried and weighed. Soil litter was collected with a sampler (area= 78.5cm<sup>2</sup>) from the center of each of the four subplots (see below), dried and weighed.

## Vegetation sampling and data analysis

Vegetation was surveyed in four 20×20m plots separated by 300-800m: two (BN1; BN2) on the upper slopes and two (BN3; BN4) on the lower slopes, (Figure 1). They were selected by their accessibility and permanently marked with metal stakes after assessing slope and exposure. Plots were sub-divided into four 100m<sup>2</sup> subplots to facilitate surveys.

Woody individuals with trunk diameter >1cm at breast height (DBH, at ~1.3m above soil) were tallied and DBH was converted to basal area (BA). Diameter of shorter individuals was taken below the first branching. The presence and abundance of the ground herbaceous vegetation and tree saplings <1cm DBH were visually appraised. Botanical samples were identified at the Venezuelan National Herbarium (VEN) following Hokche *et al.* (2008) and kept in the USB Herbarium. When identification was not possible, samples were named by family or morphotype. In all subplots, hemispheric photography determined canopy cover and leaf area index (LAI). The images were analyzed with the HemiView package (Delta-T Devices Ltd., Houston, TX, USA).

Density of stems (D) and BA of each species were totaled for the plots, whereas percentage frequency (F) was obtained by their presence in each of the subplots. The importance value index (IVI) of each species was calculated as the sum of its relative BA  $\{(RBA_i = (BA_i / \Sigma BA_i) \times 100)\}$ , relative D  $\{(RDi = (D_i / \Sigma D_i) \times 100)\}$  and relative F  $\{(RF_i = (F_i / \Sigma F_i) \times 100)\}$ ; maximum IVI= 300. For each plot, species richness and the Shannon indices of diversity and equity were calculated. Dominance (IVI values) vs rank was drawn for each plot. The completeness of the inventories was calculated with the incidence-based first-order jackknife estimator (Colwell and Coddington, 1994). The vegetation dissimilarity among

plots was evaluated using the species IVI's and the quantitative Sørensen index. Plot species composition was examined with principal components analysis (PCA) following relativization by the maximum of their IVIs. Plot response to selected environmental variables was also examined with PCA. The relationship between plot's environmental variables and vegetation composition was analyzed with the Mantel (1967) test. All multivariate analyses were performed with PC-Ord V.6.0 (McCune and Mefford, 2011). To predict the possible plot succession trajectories, DBHs (as a substitute for age structure of the most important trees) were allocated into size classes and plotted. When appropriate, differences among means were tested with one-way ANOVA (SYSTAT v.10.0, 2002).

## Results

Annual average precipitation was 1143.7mm. May to November was the wettest period. Outside the plantation mean air temperature was 20.2°C. The forest canopy moderated air temperature extremes: maximum temperatures were 1-5°C lower than outside, whereas minimum temperatures were 0.5-3°C higher. Due to the mild air temperature, humidity was relatively high throughout the year. The slope of the predominantly east facing plots ranged from low to moderate (Table I). Due to lack of replication, differences in plot soil properties are qualitative. The soils were acidic



Figure 1. Aerial view of the natural areas of Universidad Simón Bolívar, Caracas, Venezuela. Shown are the location of the four surveyed plots embedded in the native forest, the adjoining pine plantation and part of the university campus buildings. Approx. 1:10,000.

sandy loams and, except in BN4, soil organic carbon content was high (Table I). Overall, soil nutrient content (mainly P) was low although it varied among plots. Sites BN2 and BN3 were the most fertile according to their N and P content, CEC and the FI. Exchangeable Al concentration was higher in BN1 and BN3. Soil bulk density was lowest in BN2 ( $F_{(3,12)} = 5.45$ ;  $p = 0.01$ ) and soil litter was highest in BN3 and lowest in BN2 ( $F_{(3,12)} = 4.07$ ;  $p = 0.03$ ). The plots were clearly separated along the first two axes of PCA considering their slope, soil nutrients, exchangeable aluminum and soil bulk density (Figure 2a).

The abandoned plantation had a continuous canopy 20-25m high. It was dominated by the tallest trees of either *Croton megalodendron* (croton), the introduced *Syzygium jambos* (rose-apple) or *Ocotea fendleri* (laurel). Below, medium sized individuals of *Clusia*, *Inga*, *Miconia*, *Guapira*, *Guatteria*, *Trichilia* and others were established. *Mangifera indica* and *Citrus* spp. are other introduced species probably brought by plantation workers. The enduring coffee shrubs and saplings of the named canopy trees dominated the lower stratum, joining *Anthurium* sp., *Stromanthes* sp. and *Heliconia* sp. herbs. They were supplemented with grasses (mainly

TABLE I  
TOPOGRAPHY, SOIL PROPERTIES, CANOPY COVER, LEAF AREA INDEX (LAI)  
AND VEGETATION TRAITS OF THE SURVEYED PLOTS

|  | BN1           | BN2           | BN3           | BN4           |
|--|---------------|---------------|---------------|---------------|
| <i>Topography and soil</i>                     |               |               |               |               |
| Elevation (masl)                               | 1380          | 1440          | 1270          | 1280          |
| Exposure                                       | NE            | SE            | S             | E             |
| Slope (°)                                      | 20            | 15            | 12            | 27            |
| Sand %   | 49.02         | 46.72         | 51.76         | 48.77         |
| Clay (%)                                       | 17.92         | 25.42         | 21.41         | 19.51         |
| Silt (%)                                       | 33.06         | 27.87         | 26.84         | 31.72         |
| pH 1:2.5 (H <sub>2</sub> O)                    | 4.37          | 4.53          | 5.31          | 5.08          |
| Organic carbon (%)                             | 4.54          | 5.76          | 5.42          | 2.77          |
| Total nitrogen (%)                             | 0.28          | 0.37          | 0.39          | 0.20          |
| CEC (meq/100g)                                 | 17.41         | 27.37         | 26.49         | 15.46         |
| Phosphorus (ppm)                               | 5.67          | 13.50         | 7.00          | 4.50          |
| Calcium (cmol·kg <sup>-1</sup> )               | 1.35          | 4.36          | 2.54          | 1.71          |
| Magnesium (cmol·kg <sup>-1</sup> )             | 0.84          | 1.29          | 2.38          | 0.60          |
| Potassium (cmol·kg <sup>-1</sup> )             | 0.19          | 0.35          | 0.61          | 0.37          |
| Exch. aluminium (cmol·kg <sup>-1</sup> )       | 5.10          | 3.61          | 4.29          | 2.60          |
| Fertility index (FI)                           | 177.40        | 294.87        | 248.63        | 141.10        |
| Bulk density (g·cm <sup>-3</sup> ) (n=3)       | 0.70 (0.17) b | 0.58 (0.07) a | 0.75 (0.08) b | 0.89 (0.10) b |
| Soil litter dry wt. (g·m <sup>-2</sup> ) (n=4) | 603 (315) ab  | 421 (159) b   | 927 (135) a   | 791 (217) ab  |
| <i>Canopy and vegetation traits</i>            |               |               |               |               |
| Canopy cover (%) (n=4)                         | 79.0 (2.0) a  | 81.0 (2.0) a  | 78.0 (2.0) a  | 81.0 (4.0) a  |
| LAI (n=4)                                      | 2.31 (0.37) a | 2.59 (0.33) a | 3.31 (0.57) b | 2.69 (0.25) a |
| Woody vines diam (cm) (n tot= 185)             | 1.75 (0.71) a | 1.68 (0.62) a | 1.89 (0.93) a | 3.03 (1.23) b |
| Species richness                               | 37            | 35            | 23            | 33            |
| Shannon diversity index (H)                    | 2.78          | 3.23          | 2.65          | 2.89          |
| Shannon equity (E)                             | 0.77          | 0.91          | 0.84          | 0.82          |
| Stem density (#/ha)                            | 8150          | 5275          | 3875          | 3450          |
| Basal area (m <sup>2</sup> ·ha <sup>-1</sup> ) | 50.74         | 24.06         | 19.97         | 22.72         |

Standard deviation in parentheses. Different letters indicate statistically significant differences ( $p < 0.05$ ).

*Lasiasis* sp.) and ferns (*Blechnum* sp., *Polypodium* sp., *Nephrolepis* sp. and *Pteris* sp.) sparsely covering the forest floor. Overall, 182 herbarium samples

were collected from 1249 individuals of the 76 species/morphotypes tallied (Table II). The first-order jackknife method estimated 109 species due to the high

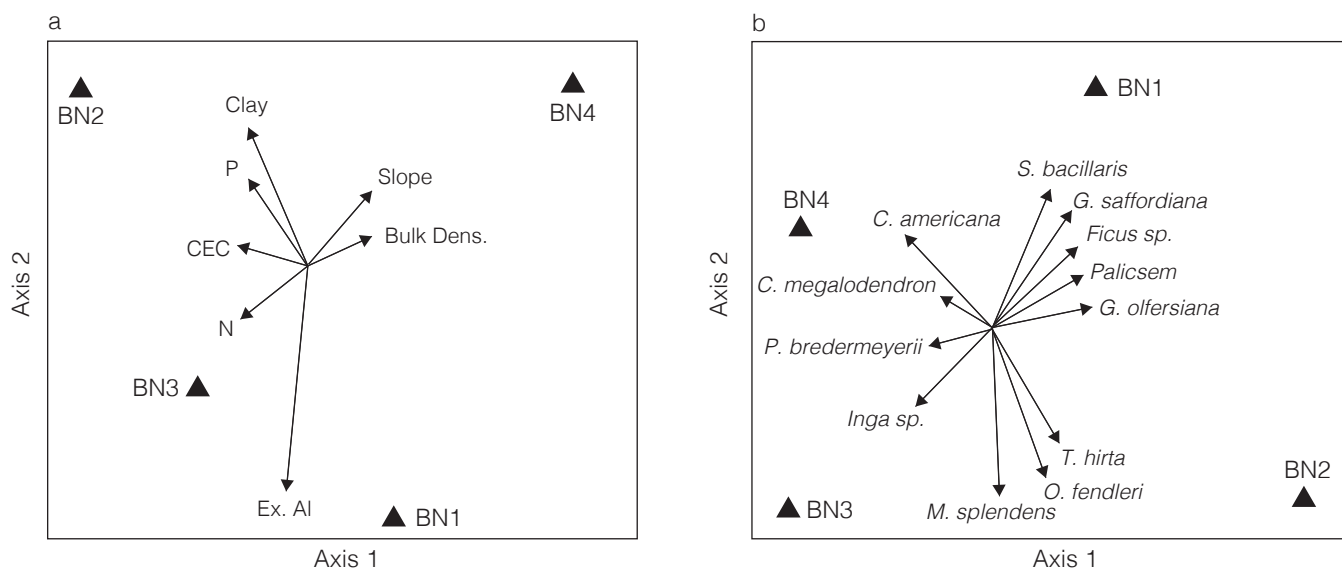


Figure 2. a: PCA of the relationships among plots based on selected environmental variables; the variance explained by the first two axes is 91.5%. b: PCA of the relationship among plots considering the effect of 12 important species; the variance explained by the first two axes is 83.6%. The out-layers *Syzygium jambos* (rose-apple), *Clusia alata* and *Miconia dodecandra* were excluded from the analysis.

number of species (68.1%) with only one occurrence. The families with most genera/species were Melastomataceae and Rubiaceae. Woody lianas were present in all plots but were difficult to collect and to quantify confidently, and were excluded from the multivariate analysis; plots BN2 and BN4 had the most occurrences but lianas from the later were significantly thicker ( $F_{(3,181)} = 39.80$ ;  $p < 0.001$ ; Table I). Most coffee shrubs were slender, ~1m tall and ~1cm DBH. They appeared to be saplings of the few remaining reproductive individuals and represented between 8.9 and 35.6% of the total stem density in BN1 in BN4, respectively. However, due to their slenderness, they comprised a minute proportion of the plot's BA (0.23 and 3.03%, respectively). As they would probably disappear, they were excluded from further numerical analysis. Despite differences in species composition, forest canopy cover was ~80% in all plots ( $F_{(3,12)} = 1.16$ ;  $p = 0.36$ ), but LAI was highest in BN3 and lowest in BN1 ( $F_{(3,12)} = 4.52$ ;  $p = 0.02$ ) (Table I).

Rose-apple was by far the most important tree in BN1 and with croton structured the canopy at this site; below, medium sized trees *Gutteria saffordiana*, *Trichilia hirta*, *Guapira olfersiana* and *Senna bacillaris* were the most prominent (Table II and Figure 3). The residual small coffee individuals and numerous rose-apple saplings dominated the lower stratum, joining the herbs, ferns and grasses mentioned above. This plot was the densest in stems (Table I), but ~30% of them were <2.5cm DBH, mostly rose-apple and croton saplings (Figure 4). Although it had the most species, BN1 had the lowest equity (Table I and Figure 3).

Plot BN2 was second in species richness and stem density, but with the highest diversity and equity (Table I and Figure 3). Here, laurel and croton shared the canopy whereas the medium height trees *Cordia toqueve*, *T. hirta*, *G. saffordiana*, *G. olfersiana*, *Citrus* sp., *Cupania americana* and *Prunus occidentalis* were dispersed below (Table II). The leftover coffee shrubs and the usual herbs, ferns and grasses were present in the lower stratum. Although not tallied, this plot had the most vascular epiphytes.

Plot BN3 was the poorest in species and the least diverse (Table I). Here, the canopy was

TABLE II  
IMPORTANCE VALUE INDEX (IVI) OF THE WOODY SPECIES IN  
THE SURVEYED PLOTS (NON-NATIVE SPECIES MARKED WITH ASTERISKS)

|   | BN1   | BN2   | BN3   | BN4   |
|---|-------|-------|-------|-------|
| Anacardiaceae sp.   | 0.00  | 3.14  | 0.00  | 0.00  |
| Boraginaceae sp.  | 0.00  | 0.00  | 0.00  | 3.00  |
| <i>Bunchosia argentea</i> (Jacq.) DC. (Malpighiaceae)                     | 0.00  | 1.86  | 0.00  | 2.76  |
| <i>Byrsonima spicata</i> (Cav.) DC. (Malpighiaceae)                       | 0.00  | 0.00  | 0.00  | 3.54  |
| <i>Casearia sylvestris</i> Sw. (Flacourtiaceae)                           | 0.00  | 0.00  | 0.00  | 2.74  |
| <i>Cecropia peltata</i> L. (Cecropiaceae)                                 | 0.00  | 0.00  | 5.74  | 0.00  |
| <i>Chomelia venezuelensis</i> Steyerl. (Rubiaceae)                        | 1.85  | 0.00  | 0.00  | 2.76  |
| <i>Cinnamomum triplinerve</i> (Ruiz & Pav.) Kosterm. (Lauraceae)          | 2.06  | 9.84  | 0.00  | 0.00  |
| <i>Citrus</i> sp. (Rutaceae) ***  | 0.00  | 21.03 | 0.00  | 3.17  |
| <i>Clethra lanata</i> M. Martens & Galeotti (Clethraceae)                 | 0.00  | 0.00  | 9.12  | 0.00  |
| <i>Clidemia</i> sp. (Melastomataceae)                                     | 4.32  | 0.00  | 3.54  | 0.00  |
| <i>Clusia alata</i> Planch. & Triana (Clusiaceae)                         | 0.00  | 0.00  | 50.17 | 0.00  |
| <i>Clusia</i> sp. (Clusiaceae)  | 2.24  | 8.45  | 0.00  | 0.00  |
| <i>Cordia</i> cf. <i>toqueve</i> Aubl. (Boraginaceae)                     | 0.00  | 14.49 | 0.00  | 0.00  |
| <i>Croton megalodendron</i> Müll. Arg. (Euphorbiaceae)                    | 43.93 | 18.76 | 51.50 | 87.82 |
| <i>Cupania americana</i> L. (Sapindaceae)                                 | 2.59  | 0.00  | 2.88  | 3.52  |
| <i>Cybianthus fendleri</i> Mez (Myrsinaceae)                              | 0.00  | 0.00  | 0.00  | 5.97  |
| <i>Dendropanax arboreum</i> (L.) Decne. & Planch (Araliaceae)             | 1.87  | 0.00  | 0.00  | 2.80  |
| <i>Erythroxylum amazonicum</i> Peyr. (Erythroxylaceae)                    | 0.00  | 1.88  | 0.00  | 0.00  |
| Fabaceae sp.  | 6.21  | 0.00  | 12.19 | 0.00  |
| <i>Faramea spathacea</i> Müll. Arg. ex Standl. (Rubiaceae)                | 0.00  | 0.00  | 0.00  | 27.05 |
| <i>Ficus guianensis</i> Desv. ex Ham. (Moraceae)                          | 2.66  | 0.00  | 0.00  | 0.00  |
| <i>Ficus</i> sp. (Moraceae)   | 4.54  | 5.33  | 0.00  | 2.99  |
| <i>Ficus tonduzii</i> Standl. (Moraceae)                                  | 0.00  | 0.00  | 0.00  | 10.78 |
| <i>Guapira olfersiana</i> (Link, Klotzsch & Otto) Lundell (Nyctaginaceae) | 11.92 | 16.17 | 2.89  | 5.49  |
| <i>Gutteria saffordiana</i> Pittier (Annonaceae)                          | 20.90 | 11.64 | 5.85  | 0.00  |
| <i>Inga edulis</i> Mart. (Mimosaceae)                                     | 0.00  | 11.79 | 0.00  | 0.00  |
| <i>Inga fastuosa</i> (Jacq.) Willd. (Mimosaceae)                          | 2.30  | 4.20  | 0.00  | 0.00  |
| <i>Inga fendleriana</i> Benth. (Mimosaceae)                               | 3.01  | 0.00  | 0.00  | 0.00  |
| <i>Inga</i> sp. (Mimosaceae)  | 4.50  | 0.00  | 21.25 | 6.26  |
| <i>Mangifera indica</i> L. (Anacardiaceae) ***                            | 0.00  | 8.30  | 2.89  | 0.00  |
| <i>Matayba longipes</i> Radlk. (Sapindaceae)                              | 0.00  | 1.89  | 0.00  | 0.00  |
| Meliaceae sp. 1   | 0.00  | 4.45  | 0.00  | 0.00  |
| Meliaceae sp. 2   | 0.00  | 0.00  | 0.00  | 8.27  |
| <i>Miconia dodecandra</i> Cogn. (Melastomataceae)                         | 0.00  | 0.00  | 45.75 | 0.00  |
| <i>Miconia ibaguensis</i> (Bonpl.) Triana (Melastomataceae)               | 0.00  | 2.34  | 0.00  | 0.00  |
| <i>Miconia prasina</i> (Sw.) DC. (Melastomataceae)                        | 0.00  | 0.00  | 0.00  | 15.58 |
| <i>Miconia serrulata</i> (DC.) Naudin (Melastomataceae)                   | 0.00  | 5.43  | 0.00  | 0.00  |
| <i>Miconia</i> sp. 1 (Melastomataceae)                                    | 4.83  | 0.00  | 0.00  | 2.73  |
| <i>Myrcia fallax</i> (Rich.) DC. (Myrtaceae)                              | 3.72  | 1.91  | 0.00  | 0.00  |
| <i>Myrcia splendens</i> (Sw.) DC. (Myrtaceae)                             | 2.21  | 5.79  | 8.41  | 0.00  |
| <i>Myrcia tomentosa</i> (Aubl.) DC. (Myrtaceae)                           | 3.63  | 0.00  | 0.00  | 0.00  |
| Myrtaceae sp. 1   | 0.00  | 6.98  | 6.46  | 0.00  |
| Myrtaceae sp. 2   | 2.03  | 0.00  | 0.00  | 0.00  |
| <i>Neea anisophylla</i> Ernst (Nyctaginaceae)                             | 0.00  | 7.56  | 0.00  | 0.00  |
| <i>Ocotea fendleri</i> (Meisn.) Rohwer (Lauraceae)                        | 4.03  | 35.33 | 14.97 | 13.85 |
| <i>Palicourea semirasa</i> Standl. (Rubiaceae)                            | 4.64  | 6.36  | 0.00  | 2.93  |
| <i>Piper bredemeyeri</i> Jacq. (Piperaceae)                               | 1.85  | 1.86  | 5.76  | 8.74  |
| <i>Piptocoma</i> sp. (Asteraceae)   | 4.31  | 0.00  | 0.00  | 0.00  |
| <i>Prunus occidentalis</i> Sw. (Rosaceae)                                 | 0.00  | 17.01 | 0.00  | 0.00  |
| <i>Psychotria fendleri</i> Standl. (Rubiaceae)                            | 0.00  | 14.43 | 0.00  | 0.00  |
| <i>Psychotria nervosa</i> Sw. (Rubiaceae)                                 | 0.00  | 0.00  | 12.20 | 6.44  |
| <i>Psychotria</i> sp. (Rubiaceae)   | 5.56  | 0.00  | 0.00  | 0.00  |
| Rubiaceae sp.   | 1.87  | 0.00  | 0.00  | 0.00  |
| <i>Rutgea hostmanniana</i> Benth (Rubiaceae)                              | 2.80  | 2.64  | 0.00  | 0.00  |
| <i>Schefflera glabrata</i> (Kunth) Frodin (Araliaceae)                    | 1.87  | 0.00  | 2.98  | 4.10  |
| <i>Senna bacillaris</i> (L.f.) H.S. Irwin & Barneby (Caesalpinaceae)      | 7.47  | 4.23  | 2.88  | 2.74  |
| Shrub 1   | 0.00  | 0.00  | 0.00  | 10.16 |
| Shrub 2   | 0.00  | 0.00  | 0.00  | 8.40  |
| Shrub 3   | 0.00  | 0.00  | 0.00  | 8.74  |
| <i>Solanum</i> sp. (Solanaceae)   | 0.00  | 2.64  | 0.00  | 0.00  |
| <i>Sorocea</i> sp. (Moraceae)   | 2.31  | 0.00  | 0.00  | 0.00  |
| <i>Syzygium jambos</i> (L.) Alston (Myrtaceae) ***                        | 91.76 | 2.34  | 0.00  | 2.73  |
| <i>Terminalia amazonica</i> (J.F. Gmel.) Exell (Combretaceae)             | 0.00  | 0.00  | 0.00  | 2.87  |

|  | BN1   | BN2   | BN3   | BN4   |
|--|-------|-------|-------|-------|
| <i>Toxicodendron striatum</i> (Ruiz & Pav.) Kuntze (Anacardiaceae) | 2.49  | 0.00  | 4.24  | 0.00  |
| Tree 1   | 7.50  | 0.00  | 0.00  | 0.00  |
| Tree 2   | 8.32  | 0.00  | 0.00  | 0.00  |
| Tree 3   | 6.62  | 0.00  | 0.00  | 0.00  |
| Tree 4   | 0.00  | 5.03  | 0.00  | 0.00  |
| Tree 5   | 0.00  | 0.00  | 0.00  | 5.78  |
| Tree 6   | 0.00  | 0.00  | 0.00  | 6.38  |
| Tree 7   | 0.00  | 0.00  | 0.00  | 5.68  |
| <i>Trichilia hirta</i> L. (Meliaceae)                              | 13.34 | 23.59 | 16.26 | 13.21 |
| <i>Turpinia occidentalis</i> (Sw.) G. Don (Staphyleaceae)          | 1.91  | 2.00  | 0.00  | 0.00  |
| <i>Vismia baccifera</i> (L.) Triana & Planch. (Clusiaceae)         | 0.00  | 0.00  | 7.23  | 0.00  |
| <i>Zanthoxylum rhoifolium</i> Lam. (Rutaceae)                      | 0.00  | 9.32  | 4.84  | 0.00  |

trunk-stem diameter distribution differed among dominant trees and sites. Overall, rose-apple had the largest number (>50%) of young individuals <2.5cm DBH in BN1 (Figure 4). Croton DBHs were more uniformly spread in BN1 than in BN4, where young individuals <10cm DBH were absent (Figure 4). Laurel had contrasting stem diameter distributions, from relatively uniform size classes in BN2 (not shown) to only very young individuals in BN4 (Figure 4).

dominated by croton, *Clusia alata* and *Miconia dodecandra*. The latter two are medium-sized trees restricted to this plot. Below, *Erithroxylon amazonicum*, *Inga* sp., laurel and *T. hirta* were tallied but coffee shrubs and the usual herbs and ferns were scarce (Table II).

In BN4 croton was the absolute dominant canopy tree (Table II and Figure 3) under which some laurel, *Faramea spathacea* and *T. hirta* were dispersed. This site had medium species richness and diversity but the highest density of remaining coffee shrubs as well as the thickest individual woody lianas (Table I). The usual herbs, ferns, and grasses dominated the lowest stratum.

The PCA of species IVIs clearly differentiated among plots (Figure 2b). BN1 was characterized by

the presence and importance of the five sub-canopy trees mentioned above (Figure 2b); BN2 and BN3 were defined by laurel and three other species, whereas BN4 was plainly defined by the dominance of croton and two sub-canopy trees (Figure 2b). The vegetation composition of the plots was very heterogeneous as shown by their high dissimilarity indices (range: 63.8-76.9%).

Basal area was >100% higher in BN1 than in the other plots (Table I) mostly due to rose-apple dominance with 35% of total BA. Stem density was also highest in BN1 with rose-apple seizing 45% of the total (Table I). There was no significant correspondence ( $p=0.24$ ) between vegetation traits (BA, D and LAI) and environmental variables as evaluated by the Mantel test. The

## Discussion

The surveyed plots differed markedly in vegetation composition, structure and BA. Time lapsed after cultivation abandonment as well as differences in topography, soils or qualities of some dominant trees could have influenced vegetation traits but the colonization and dominance of rose-apple was the key discriminating factor.

Time after cultivation termination is the main factor affecting vegetation and trajectory of secondary successions (Aide *et al.*, 1996; Pascarella *et al.*, 2000; Marceno-Vega *et al.*, 2002, Howarth and Pendry, 2006; Chazdon *et al.*, 2009). In the present study, other than the anecdotic reference that cultivation ceased ~60 years ago, documented

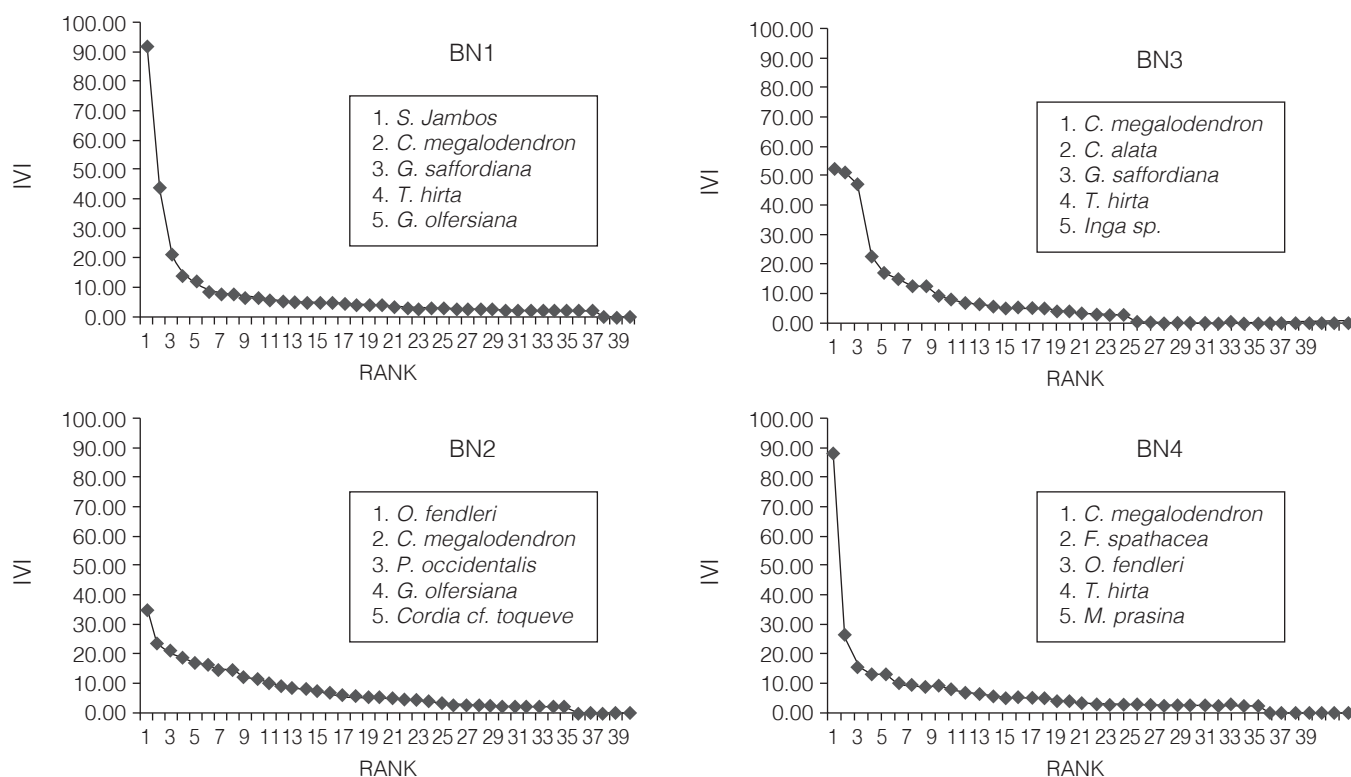


Figure 3. Dominance (as expressed by the IVI) vs rank curves of the four plots studied. The first five most important species are listed.

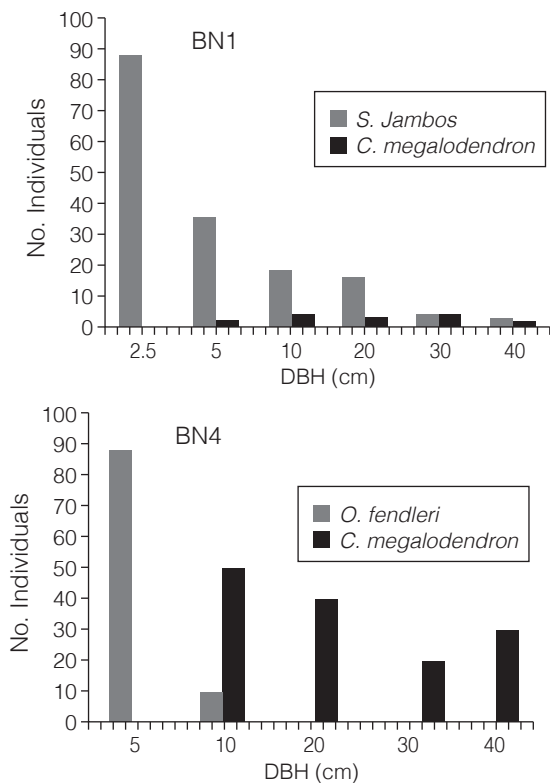


Figure 4. Comparative trunk diameter (DBH) distributions of *Croton megalodendron* (croton) with *Syzygium jambos* (rose-apple) in BN1 and with *Ocotea fendleri* (laurel) in BN4. Note the different scales of the Y axis in the diagrams.

information is lacking. Nevertheless, thickness of woody vines has been employed as surrogate for successional age (DeWalt *et al.*, 2000; Howorth and Pendry, 2006). Vines were significantly thicker in BN4, possibly pointing to an earlier abandonment and older successional stage. However, this assumption was unsupported, neither by increased diversity nor BA buildup. Consequently, the effect of age on secondary succession in the USB plots remains undefined.

Overall, soil fertility was low when compared to other montane forests in Venezuela (Cuenca and Herrera, 1987; Monedero and Gonzalez, 1994; Howorth and Pendry, 2006) and the absence of the usual shade trees, as the N fixing *Erythrina* or *Inga* species, probably was a contributing cause. However, plots differed qualitatively in soil nutrient concentration. The fertility index was 41.4% lower in the steeply sloped BN1 and BN4, where increased rainfall run-off possibly increased nutrient leaching. The differences in fertility and slope among plots could have caused differences in vegetation traits but this relationship is complex and could not be identified. Nevertheless, the toxic level of exchangeable aluminum in

the soils of BN1 and BN3 (Cuenca *et al.*, 1990) was associated with the dominance of *M. dodecandra*, a known tolerant species (Cuenca and Herrera, 1987) in BN3. The tentative aluminum tolerance of rose-apple, dominant in BN1, is worth of future studies.

Microclimate filters vegetation composition and succession through initial propagule colonization and establishment. Reduced irradiance at soil level probably favored colonization by shade tolerant species but delayed their seedling growth. The prominence of some wide leafed trees as *M. dodecandra* and *Clusia alata* in BN3, which increased canopy LAI by ~20%, further reduced irradiance. This factor could be held 4 accountable for the low species richness and diversity in this plot. All the biophysical differences discussed have the potential to influence plot vegetation composition and structure. However, we didn't find significant correlations between causes and effects due to the complex and indirect nature of these relationships and to the limited number of surveyed plots.

The predominance of rose-apple ('pomarrosa' in Venezuela) in BN1 was the most notorious finding of this study. Although it is known to colonize secondary successions in the tropics (Di Stefano *et al.*, 1998; Lugo, 2004; Martin *et al.*, 2004; Mascaro *et al.*, 2008) as well as abandoned shade coffee plantations in Puerto Rico (Marcano-Vega *et al.*, 2002), the absolute dominance of adult individuals was unreported except in a few Puerto Rican riparian sites (Brown *et al.*, 2006). This very aggressive medium-sized tree from Southeast Asia was widely planted in the USB gardens during the early 1970's owing to its fast growth, showy flowers and edible fruits. Rose-apple's life history traits support its colonization of the nearby abandoned coffee plantation. The fruits are edible and readily dispersed by frugivorous bats (Brown *et al.*, 2006; Muñoz-Romo and Herrera, 2010; Garcia-Estrada *et al.*, 2012) and by large birds such as the locally very common chachalaca (*Ortalis* sp.; 'guacharaca' in Venezuela). Rose-apple's big seeds (2.0-2.5cm in diameter) generate large shade tolerant seedlings that dominate the 'juvenile bank' of the forest (Horvitz *et al.*, 1998), persisting until a gap is opened in

the canopy, when active growth is resumed (Brown *et al.*, 2006). Although rose-apple showed an incipient presence in BN2 and BN4, its supremacy only in BN1 is challenging to explain. It is possible that this east-facing and high elevation plot was preferentially selected for roosting and perching by bats and birds since it lies in a straight flight path from the USB gardens. The associated seed dispersion promoted rose-apple colonization. Direct observation and seed trapping could assess this framework.

The effect of fast colonizing trees is contingent to their life history traits, environmental settings and successional stages, but their specific role in secondary successions is not entirely understood. In Puerto Rico, the light demanding and wind dispersed African tulip (*Spathodea campanulata*) promotes the recovery of native species richness and successional convergence towards the native forests (Marcano-Vega *et al.*, 2002; Lugo, 2004; Lugo and Helmer, 2004). The outcome of rose-apple colonization is different. In Hawaii it initially increased native species richness but with a minute share of community biomass (Mascaro *et al.*, 2008), while in Puerto Rico rose-apple strongly decreased species diversity (Brown *et al.*, 2006). However, in both of the above instances productivity, as measured by BA accumulation, increased after rose-apple colonization. The present results resemble those from Hawaii (Mascaro *et al.*, 2012) but the paucity of our data advices for a restrained interpretation.

Currently, the plots in the abandoned USB plantation appear to follow diverging successional speeds and trajectories. The succession in BN1 is fast due to rose-apple's rapid growth and its trajectory and persistence is reliant on its high levels of recruitment, age structure, shade tolerance and longevity (Marcano-Vega *et al.*, 2002; Brown *et al.*, 2006). We predict that it will remain dominant in BN1 and may even colonize new areas in the USB forest. This dominance has already triggered a successional path towards new species groupings resulting in a novel forest community (Lugo, 2004; Lugo and Helmer, 2004; Hobbs *et al.*, 2006). Thanks to the rose-apple predominance and fast growth, in only 30 to 40 years plot BN1 has reached the upper limit of BA buildup close to relatively intact montane forests in Venezuela (Monedero and Gonzalez, 1994; Howorth and Pendry, 2006). Experimental removals and long term observation are needed to reveal the future role of this fast colonizing tree in the USB forest.

The non-invaded plots follow a typical but slower secondary succession. Basal area was 50-60% lower than in secondary forests of comparable age in Puerto Rico (Aide *et al.*, 1996; Pascarella *et al.*, 2000; Marcano-Vega *et al.*, 2002). This slower biomass buildup could have been caused by poorer growth rates due to lower air temperature and rainfall, less fertile soils and possibly aluminum toxicity, as discussed above. According to their trunk diameter distribution, laurel is regenerating effectively in BN2 and BN4 and could become the dominant tree in later successional stages. If protected from rose-apple arrival and other disturbances, succession might converge towards montane forests resembling those surveyed previously in the region (Aristeguieta and Matos, 1959; Cuenca and Herrera, 1987; Monedero and González, 1994) since dominant families and tree species richness are comparable. Long term studies are needed to establish the fate of the abandoned plantation: succession towards a native montane forest or complete dominance by apple-rose and the establishment of a large scale novel community.

The spontaneous or assisted reclamation of abandoned coffee plantations embedded in the montane forests contributes to keep the high species and genetic diversity and endemism distinctive of this biome (Steyermark, 1979), which provides important ecological services to the downslope populations. Currently, montane forests in Latin-America are threatened due to fragmentation by urbanization and by future land use and climate changes (Huber, 1997; Armenteras *et al.*, 2003). Those in the Venezuelan Coastal Mountains have already lost a large part of their former area (Portillo-Quintero *et al.*, 2011). Besides the colonization by rose-apple, the studied forested fragment is vulnerable to fire hazards and human encroachment. Fencing and launching it as a national natural area may provide limited protection (Edgard Yerena, personal communication). The desired goal is to establish a step-stone ecological corridor, assembled with montane forest fragments, around the southern edge of Caracas city.

We infer that the answer to the question posed in the title is contingent to the effectiveness of protection from colonization by perennial non-native species or their prompt eradication if already established. At present, under the levels of human encroachment in Neotropical montane forests, this goal seems difficult to achieve.

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## PLANTACIONES DE CAFÉ ABANDONADAS: CONSERVACIÓN DE LA BIODIVERSIDAD U OPORTUNIDAD PARA ESPECIES INTRODUCIDAS? EL CASO DE UN BOSQUE MONTANO NEOTROPICAL

Zdravko Baruch y Shingo Nozawa

### RESUMEN

Los cafetales abandonados son comunes en las montañas neotropicales. Los bosques secundarios desarrollados posteriormente mantienen y aumentan la biodiversidad y otros servicios ambientales, pero el abandono del cultivo expone el área a especies invasoras que cambian las características de la vegetación creando nuevas comunidades. Reportamos la vegetación actual de una plantación de café abandonada hace ~60 años. La precipitación y temperatura promedios fueron 1143mm y 20,2°C. Se censaron los individuos leñosos >1cm de diámetro en cuatro parcelas de 400m<sup>2</sup>. Se calculó el índice del valor de importancia de cada especie, riqueza de especies, diversidad, equidad, densidad de troncos y área basal (BA). Con análisis multivariados se relacionó la vegetación y el ambiente. Se muestrearon 76 especies o morfotipos de 28 familias. Las parcelas contrastaron en cuan-

to a especies dominantes (*Syzygium jambos* (pomarrosa), *Croton megalodendron* (croton) u *Ocotea fendleri* (laurel)), riqueza de especies (23-37), densidad de individuos (3450-8150ha<sup>-1</sup>) y BA (19,9-50,7m<sup>2</sup>ha<sup>-1</sup>). El factor discriminante más resaltante fue la invasión y dominancia del árbol exótico *S. jambos* en una parcela, atribuible a la historia de vida de esa especie y su cultivo en jardines cercanos. Los resultados sugieren que la trayectoria sucesional de la plantación dependerá de la colonización y expansión de este árbol invasor que ha establecido una nueva comunidad boscosa en la zona. La respuesta a la pregunta del título dependerá de la efectiva protección contra la colonización de especies invasoras no nativas. Actualmente, con los niveles de perturbación humana en los bosques montanos neotropicales, tal protección parece difícil de alcanzar.

## PLANTAÇÕES DE CAFÉ ABANDONADAS: CONSERVAÇÃO DA BIODIVERSIDADE OU OPORTUNIDADE PARA ESPÉCIES INTRODUZIDAS? O CASO DE UMA FLORESTA NEOTROPICAL DE ENCOSTA

Zdravko Baruch e Shingo Nozawa

### RESUMO

Os cafezais abandonados são comuns nas montanhas neotropicais. Os bosques secundários desenvolvidos posteriormente mantêm e aumentam a biodiversidade e outros serviços ambientais, mas o abandono do cultivo expõe a área a espécies invasoras que mudam as características da vegetação criando novas comunidades. Relatamos a vegetação atual de uma plantação de café abandonada há ~60 anos. A precipitação e temperatura médias foram 1.143 mm e 20,2 °C. Foram censados os indivíduos lenhosos >1cm de diâmetro em quatro lotes de 400m<sup>2</sup>. Foi calculado o índice do valor de importância de cada espécie, riqueza de espécies, diversidade, equidade, densidade de troncos e área basal (AB). Com análises multivariadas se relacionou a vegetação e o ambiente. Realizou-se a amostragem de 76 espécies ou morfotipos de 28 famílias. As parcelas con-

trastaram em quanto a espécies dominantes (*Syzygium jambos* (jambo-rosa), *Croton megalodendron* (cróton) ou *Ocotea fendleri* (louro)), riqueza de espécies (23-37), densidade de indivíduos (3450-8150ha<sup>-1</sup>) e AB (19,9-50,7m<sup>2</sup>ha<sup>-1</sup>). O fator discriminante mais ressaltante foi a invasão e dominância da árvore exótica *S. jambos* em um lote, atribuível à história de vida dessa espécie e seu cultivo em jardins próximos. Os resultados sugerem que a trajetória sucessional da plantação dependerá da colonização e expansão desta árvore invasora que tem estabelecido uma nova comunidade florestal na zona. A resposta à pergunta do título dependerá da efetiva proteção contra a colonização de espécies invasoras (não nativas). Atualmente, com os níveis de perturbação humana nas florestas neotropicais de encostas, tal proteção parece difícil de alcançar.