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Vegetation structure, species diversity, and ecosystem processes as measures of restoration success

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Abstract

Most restoration projects have focused on recovery of vegetation to assess restoration success. Nevertheless if the goal of a restoration project is to create an ecosystem that is self-supporting and resilient to perturbation, we also need information on the recovery of other trophic levels and ecosystem processes. To provide an example on how to assess restoration success, we compared four measures of vegetation structure, four measures of species diversity, and six measures of ecosystem processes among pre-reforested, reforested, and reference sites. In addition, we described how Bray Curtis Ordination could be used to evaluate restoration success. Vegetation structure recovered rapidly due to the increase in vegetation height and the decrease in herbaceous cover. Other measures such as litter cover, number of litter layers, and DBH size class values are recovering at slower rates, but they also have increased vegetation heterogeneity in the reforested site. Species diversity recovered rapidly. The increase in vegetation structure changed the local conditions in the reforested site facilitating the colonization of woody seedlings, ants, reptiles, and amphibians. Ecosystem processes, particularly litter production and turnover, have enhanced the incorporation of nutrients and organic matter in the soil. By including vegetation structure, species diversity, and ecosystem processes measures we have better information to determine the success of a restoration project. Moreover, the Subjective Bray Curtis Ordination is a useful approach for evaluating different restoration techniques or identifying measures that are recovering slowly and would benefit from additional management.

Keywords: Bray Curtis Ordination; Ecosystem restoration; Karst; Limestone

1. Introduction

Most restoration projects have focused on the recovery of vegetation (Young, 2000) to assess restoration success. Nevertheless if the goal of a restoration project is to create an ecosystem that is self-supporting and resilient to perturbation (SER, 2004), we need to measure more than just vegetation. What measures need to be assessed to determine if a restored site is self-supporting? Vegetation structure, species diversity, and ecosystem processes have been identified as essential components for a long-term

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persistence of an ecosystem (Elmqvist et al., 2003; Dorren et al., 2004). Measures of vegetation structure provide information on habitat suitability, ecosystem productivity, and help predict successional pathways (Jones et al., 2004; Silver et al., 2004; Wang et al., 2004). Measures of species diversity provide information on susceptibility to invasions (e.g., proportion of native and exotic species), and trophic structure necessary for ecosystem resilience (Parmenter and MacMahon, 1992; Peterson et al., 1998; Nichols and Nichols, 2003). Measures of ecosystem processes provide information on biogeochemical cycles and nutrient cycling necessary for the long-term stability of the ecosystems (Herrick, 2000). Most restoration projects measure some aspects of vegetation structure or diversity, arthropod diversity or nutrient pools (Ruiz-Jaén and Aide, 2005), but studies rarely assess more than one measure of each component.

Along with assessing many measures in a restored site, it is necessary to compare this information with similar data from pre-restored and reference sites (Hobbs and Norton, 1996). The pre-restored and reference sites should occur in the same life zone, close to the restoration project, and should be exposed to similar natural disturbances (Hobbs and Harris, 2001; SER, 2004). If chosen correctly, these sites can provide endpoints to evaluate the success of a project (Passell, 2000; Purcell et al., 2002). The use of reference points can help to identify whether the response of the restored site is caused by the restoration activity or by unassisted recovery (White and Walker, 1997).

The goal of this study is to provide an example of how to evaluate restoration success in an integrative way using measures of vegetation structure, species diversity, and ecosystems process. We evaluated restoration success by comparing four measures of vegetation structure, four measures of species diversity, and six measures of ecosystem processes among pre-reforested, reforested, and reference sites in Puerto Rico. We addressed the following questions: (1) how does the vegetation structure of the reforested area changed in comparison to both the pre-reforested and reference sites? (2) how does the change in vegetation structure enhance species diversity in the reforested site? and (3) how does the ecosystem processes of the reforested site changed in comparison to both pre-reforested and reference sites?

2. Methods

2.1. Study area

The study was conducted in Sabana Seca, Puerto Rico (18°27′N, 66°12′W). This site is located in the northern limestone region, and is classified as subtropical moist forest (Holdridge, 1967). Mean annual rainfall is 1693 mm with a rainy season between April and December and a dry season between January and May (Eusse and Aide, 1999). The pre-reforested site was a park in a Karst valley where the grass was cut on a regular basis. This site was abandoned (i.e. no longer mowed) in May 2000. The reforested site also was a valley previously maintained as a park, and the grass was frequently mowed. This site was reforested with 22 native species from 18 families including trees and shrubs in January 2000, and was no longer mowed. The species chosen included both pioneer and shade tolerant species common in Karst ecosystems of Puerto Rico (Alvarez-Ruiz et al., 1997; Rivera and Aide, 1998). A total of 516 seedlings were planted (1612.5 seedlings ha^{-1}). Seedling survivorship was high (96% after 15 months and 93% after 27 months). The major goal of the restoration project was to recover native vegetation of a Karst valley to provide habitat for the endangered Puerto Rican boa, *Epicrantes inornatus*. The reference forest is a secondary forest in a Karst valley that was dominated by pastures until abandoned approximately 40 years ago. The most common tree species in this site are *Faramea occidentalis*, *Guarea guidonea*, and *Quararibea turbinata*. Although the reference site is a secondary forest, we selected it because it was the oldest secondary forest in the region with the same environmental conditions as the other two sites (e.g. a valley previously dominated by grasses).

In the past, the most common land use practices in the Karst valleys in Puerto Rico were pastures, shifting agriculture or coffee plantations (Rivera and Aide, 1998). Most of these areas have been abandoned, but previous land use can influence present day species composition (Rivera and Aide, 1998). To control for land use history, we selected sites that were formerly dominated by grasses based on aerial photographs.

The three valleys are surrounded by forested hills, and the area of the sites ranged from 0.75 to 1.0 ha with a minimum distance of 300 m between sites. Each site has a different shape, therefore we used different number of transects in each site, but a total of 200 m of transects were established in all sites. Specifically, the pre-reforested and reforested sites were sampled using two transects of 100 m, and the reference site was sampled with four transects of 50 m. In all sites transects were established systematically at least 5 m away from the edge and 15 m between each transect.

2.2. Vegetation structure

2.2.1. Ground cover and litter structure

Ground cover and litter structure were estimated in twenty 1 m^2 plots in May 2003. Plots were located every 10 m along each transect. Percent herbaceous, litter, and bare soil cover was determined in each plot. Herbaceous cover included grasses, vines, and herbs. Litter structure was determined by counting the number of leaves perforated with a needle that was pushed down though the leaf litter layer in four points within each plot (Vasconcelos et al., 2000).

2.2.2. Forest structure

Diameter at breast height (DBH) and height of all woody plants $\geq$1 cm DBH were sampled within 800 m^2 along the established transects.

2.3. Species diversity

2.3.1. Woody plant seedlings

Woody seedlings from 5 to 50 cm in height were counted and identified in 20 circular plots (1 m diameter) in February 2003. Plots were located every 10 m along each transect.

2.3.2. Ants

Ants were collected using leaf litter samples and pitfall traps in May 2003. Each sampling technique was applied every 10 m along each transect. Twenty leaf litter samples (1 m^2) were collected. In the field the litter was sifted (100 mm^2-mesh) to eliminate large debris. The sifted samples were placed in Berlese funnels in the laboratory (modified from Agosti and Alonso, 2000). Ants were removed from Berlese traps after 48 h. Twenty pitfall traps (0.005 m^2) were left in the field for 48 h.

2.3.3. Amphibians and reptiles

Composition and abundance of the herpetofauna were determined by diurnal and nocturnal visual and acoustic census. The censuses were conducted monthly in transects of 3 m $\times$ 200 m in each site from January to December of 2002. Diurnal censuses were conducted between 08:30 and 13:30 h, and nocturnal census was conducted between 18:30 and 00:30 h. On average it took 2.5 h to complete a diurnal or nocturnal census.

2.3.4. Birds

Composition and abundance of birds in each site were determined in a 10 m $\times$ 100 m transect in each site in August and September 2004. Six predawn visual and acoustic censuses were conducted (Bibby et al., 2000).

2.4. Ecosystem processes

2.4.1. Litter production and litter turnover

Leaf litter production was estimated by collecting litter from 20 plastic buckets (area 0.071 m^2/bucket) in each site. Buckets were located on the forest floor every 10 m along transects. Leaf litter was collected monthly from April 2003 to March 2004 and ground litter was collected in June 2003, October 2003, and March 2004 from 20 plots of 0.25 m^2. Litter samples were separated into leaves and miscellaneous (wood, fruits, flowers) before drying at 70 °C for 72 h. The Olson (1963) formula $k = L_f/L_s$ was used to determine the decomposition constant (k), where L_f is the annual leaf litter fall (g m^{-2} yr^{-1}) and L_s is the standing leaf litter biomass (g m^{-2}).

2.4.2. Nutrient content

In each site, soil was sampled in three randomly located plots separated by at least 30 m. In each plot, three soil cores of 31.4 cm^3 each were collected at a depth of 0–10 cm and three at 10–20 cm. Samples from the same depth and plot were combined for analyses. Soil pH, bulk density, total P, N, organic C, Ca, K, Mg, and exchangeable cations of Ca, K, and Mg were determined for each soil sample. Soil pH was measured in water in a ratio of 1:5. Bulk density was measured with a soil core of 31.4 cm^3, samples were oven-dry at 110 °C and weighted. Exchangeable cations were extracted with ammonium acetate 1 M

(Thomas, 1982), and by atomic absorption spectrometer. Total organic carbon was determined by the colorimetric method with digestions of sulphuric acid and potassium dichromate at 5% (Anderson and Ingram, 1993). Nitrogen was analysed using Kjeldahl procedure involving digestion with sulphuric acid (Jackson, 1968). Phosphorus, calcium, potassium, and magnesium were determined by atomic absorption spectrometer with sulphuric and perchloric acid digestions (Murphy and Riley, 1962; Olsen and Sommers, 1982). Total nutrient content of P, N, Ca, K, and Mg were measured in the monthly litter fall samples from the three sites. Litter nutrient analysis was based on the same procedures described for the soil analysis. Nutrient content of monthly litter fall was used to determine potential nutrient inputs to each site. Potential nutrient inputs were determined by multiplying monthly values of litter fall with its corresponding nutrient concentration.

2.4.3. Earthworms

Earthworms were collected in 12 plots of 25 cm × 25 cm × 20 cm every 15 m along transects in July 2003 (Zou and Gonzalez, 1997). Each soil sample was separated in two profiles: 0–10 and 10–20 cm. Each soil section was placed on a cloth sheet and earthworms were hand sorted and stored in plastic bags in a cooler with ice. The same day, fresh weight was determined in the laboratory after the worms have been rinsed with water and dried with paper towels. Soil moisture was measured in each soil sample because the earthworm distribution is strongly dependent on water content. Soil moisture was calculated for each site by oven-drying 15 g of fresh soil sample at 105 °C for 48 h.

2.4.4. Carbon isotope ratios

Soil samples (0–10 and 10–20 cm) used for analysis of nutrient content were also used to measure the carbon stable isotope ratio (δ^{13}C). Samples from these depths best reflect changes between C_3 and C_4 vegetation (Jobbágy and Jackson, 2000). Leaf samples consisted on 10 green leaves of the most abundant species within each soil-sampling plot. Soil organic matter (SOM) composition was assessed using the stable isotope proportion of carbon 13 and 12 (δ^{13}C). Carbonates were extracted from each soil sample with 0.5N HCl because our sites were located in the limestone region of Puerto Rico. Both soil and plant samples were oven dried at 70 °C for 48 h and grounded to powder before isotopic proportion determination. Carbon isotope analyses for both soil and leaf samples followed procedures explained elsewhere (see Martin et al., 1990; Eshetu, 2002). The δ^{13}C values of soil organic matter are mainly dependent on plant composition input material. Most tropical grasses (C_4) exhibit values of −9 to −19‰ and shrubs and trees (C_3) show values −23 to 40‰ (Smith and Epstein, 1971). Contribution of C_3 and C_4 plants to soil organic matter composition was determined by using the formula in Trouve et al. (1994). $C_t = C_4 + C_3$, and $C_t \times \delta_t = (C_4 \times \delta_4) + (C_3 \times \delta_3)$, where δ_t is the measure of δ^{13}C value of soils, and δ_3 and δ_4 are δ^{13}C value of C_3 and C_4 plants, respectively. The relative abundance was calculated as C_3/C_t (%) = $[(\delta_t - \delta_4)/(\delta_3 - \delta_4)] \times 100$ and C_4/C_t (%) = $[(\delta_t - \delta_3)/(\delta_4 - \delta_3)] \times 100$.

2.5. Data analyses

Given that treatments (i.e. pre-reforested, reforested, and reference) were not replicated, statistical analyses are not included. Rank-density graphs were used to assess difference in community dominance (e.g. seedlings, ants, herpetofauna, and birds) among sites (Feinsinger, 2001). These graphs ranked species in each site from the highest to the lowest density. Moreover, rank-density graphs provide information on species richness in each site.

Restoration success was estimated with a Subjective Bray Curtis Ordination (McCune and Mefford, 1999; Pcord4 Software). The Subjective Bray Curtis Ordination places points in relationship to selected reference sites (i.e. endpoints). Specifically, the data from the reforested site was arrayed relative to the endpoints (i.e., pre-reforested and reference sites) along a horizontal axis by using the Sorensen coefficient of similarity as the distance measure (Bray and Curtis, 1957; McCune and Grace, 2002). The position of the reforested site along this axis indicates the percent of restoration success relative to the endpoints. In contrast to other commonly used ordination methods (e.g. NMS, PCA, DCA, and CCA), the Subjective Bray Curtis Ordination is specific for evaluating data with conceptual references points (McCune and Grace, 2002).

For the Subjective Bray Curtis analysis we used five measures of vegetation structure, three measures of species diversity, and five measures of ecosystem processes. For the analyses of vegetation structure, the values (e.g., herbaceous cover, litter cover, litter layers, DBH size classes, and plant height) were categorized into ranges to reflect the variability in these measures. For the analyses of woody seedlings and herpetofauna, we used species abundance. For ant species, presence and absence data were used to avoid the spatial clumping of their distribution due to nesting behaviour (Longino, 2000). For litter production we used monthly average of each site. For litter turnover rates we used the decomposition constant of each site. Nutrients inputs were compared using monthly values (litterfall × nutrient concentration). For soil nutrient content, we used the mean value of P, N, Ca, K, and Mg for each site. Bulk density was compared using mean values from two soil profiles (0–10 and 10–20 cm).

Birds and earthworms were not included in the Subjective Bray Curtis Ordination. Birds were not included because only one species was found in the pre-reforested site, and any increase in species diversity would result in a higher recovery rate. Earthworm fresh weight was also excluded because values in the reforested site were outside the range of the endpoints (e.g., pre-reforested and reference sites).

3. Results

3.1. Vegetation structure

Three years after planting, the growth of woody stems in the reforested site created a diverse vegetation structure (Fig. 1). The number of stems in the 1 to <5 cm DBH size classes was higher in the reforested site (171 stems) than in the pre-reforested site, which had only one stem in this category. The reforested site had fewer stems in the 5–10 cm DBH classes ($n = 8$) in comparison with the reference site ($n = 156$; Fig. 1a). Nevertheless the reforested site has stems >10 cm DBH ($n = 3$). Vegetation height in the reforested site ranged from 1.4 to 12 m with a mean height of approximately 3.0 m (Fig. 1b). Although there is some vertical stratification in the reforested site, the reference site had a greater range of tree heights (e.g., 1.4–17 m). The tallest trees in the reforested site were the pioneer species, *Cecropia schreberiana*, *Senna siammea*, and *Thespesia grandiflora*.

Herbaceous cover and litter cover also varied among sites. Herbaceous cover was highest in the pre-reforested site (94%), lower in the reforested site (40%), and lowest in the reference site (Fig. 1c). In contrast, litter cover was lowest in the pre-reforested site (6%), higher in the reforested site (47%), and highest in the reference site (88%). Similarly, the number of litter layers was lowest in the pre-reforested site (1.5), higher in the reforested site (2.1), and the highest in the reference site (3.0; Fig. 1d). The litter layers in the reforested site were dominated by the pioneer species, *Cecropia schreberiana*, *Hura crepitans*, *Senna siammea*, and *Thespesia grandiflora*. The litter in the pre-restored site was dominated by herbaceous vegetation, while the reference site was dominated by woody species (e.g. *Chrysophyllum argenteum*, *Faramea occidentalis*, *Guarea guidonea*, and *Quararibea campalunata*).

3.2. Species diversity

The development of a complex vegetation structure in the reforested site has changed the microhabitat and facilitated the colonization of other organisms (Appendix A and Fig. 2). For example, the low herbaceous cover in the reforested site was associated with the colonization of 22 woody plant seedlings, while there was low colonization of woody plants in the pre-reforested with high herbaceous cover (Fig. 1c and 2a). The dominant species in the reforested site was the wind-dispersed vine, *Hippocratea volubilis* (Appendix A and Fig. 2a). Other species in the reforested site included some common Karst species (e.g., *Casearia sylvestris*, *Guarea guidonea*, and *Tabebuia heterophylla*), but there were still species common to disturbed sites (e.g., *Urena sinuata* and *U. lobata*). Moreover, animal dispersed seeds species (e.g., *Andira inermis*, *Casearia sylvestris*, *Cupania americana*, and *Thespesia grandiflora*) were only present in the reforested and reference sites (Appendix A).

Ant richness and density also varied among sites. Ant species richness was lowest in the pre-reforested site (15 species), higher in the reforested site (21 species), and highest in the reference site (30 species; Appendix A and Fig. 2b). Ten species were present in all sites and seven species only occurred in the reforested and reference sites (Appendix A). Ant densities also differed among sites. *Solenopsis geminata*, an exotic

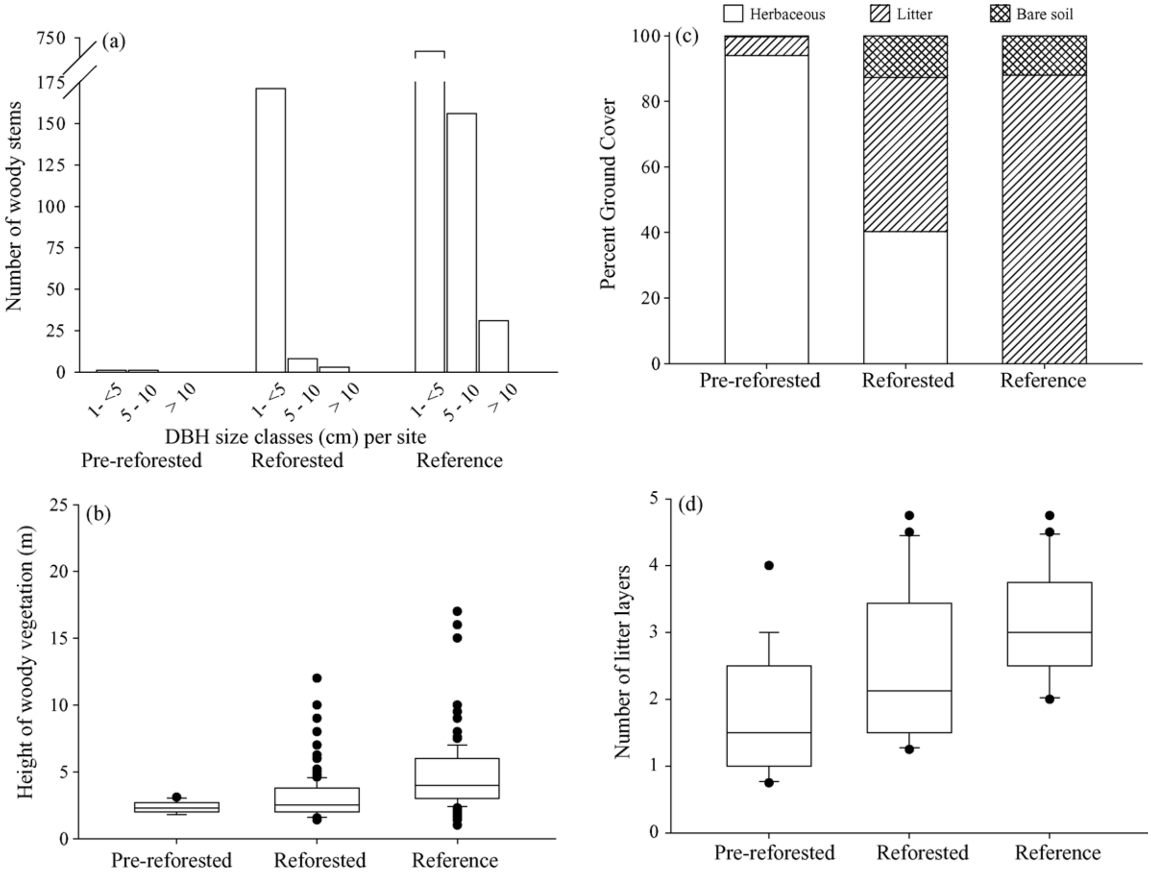

Fig. 1. Recovery of vegetation structure in the reforested site in comparison to pre-reforested, and reference sites: (a) number of woody stems in different DBH size classes, (b) vegetation height of woody stems in meters, (c) percent of ground cover (herbaceous, litter, and bare soil), and (d) number of litter layers. Boxes (Fig. 1b and d) represent 25–75 percentiles, lines within boxes represent the median value, and bars indicate the 90th and 10th percentiles, and points are outliers.

invasive, had the highest density in the pre-reforested site (6000 individuals m^{-2}), a lower density in the reforested site (363 individuals m^{-2}), and the lowest density in the reference site (50 individuals m^{-2}; Fig. 2b). In contrast, *Odontomachus ruginodis*, a native predator, has the lowest densities in the pre-reforested site (20 individuals m^{-2}), the highest in the reforested site (140 individuals m^{-2}), and 90 individuals m^{-2} in the reference site.

The composition and density of the herpetofauna varied among sites. Two exotic species were observed in the pre-reforested site, nine species in the reforested site, and eight species in the reference site (Appendix A). Four of the nine species in the reforested site are arboreal (*Anolis cristatellus*, *Eleutherodactylus cochranae*, *E. coqui*, and *Anolis cuvieri*), but the three most abundant species (*Anolis pulchellus*, *A. krugi*, and *Eleutherodactylus antillensis*) are associated with herbs and grasses (Fig. 2c). *Epicrates inornatus*, the Puerto Rican boa, the target species of this restoration project, colonized the reforested site, once prey species increased (Rios-Lopez and Aide, unpublished data). The overall herpetofauna density increased from 17 individuals ha^{-1} in the pre-reforested site to 1339 individuals ha^{-1} in the reforested and 1361 individuals ha^{-1} in the reference site (Fig. 2c).

In a rapid assessment of the bird community, only one species was observed in the pre-reforested site, three species in the reforested site, and nine species in the reference site (Appendix A and Fig. 2d). Six of the

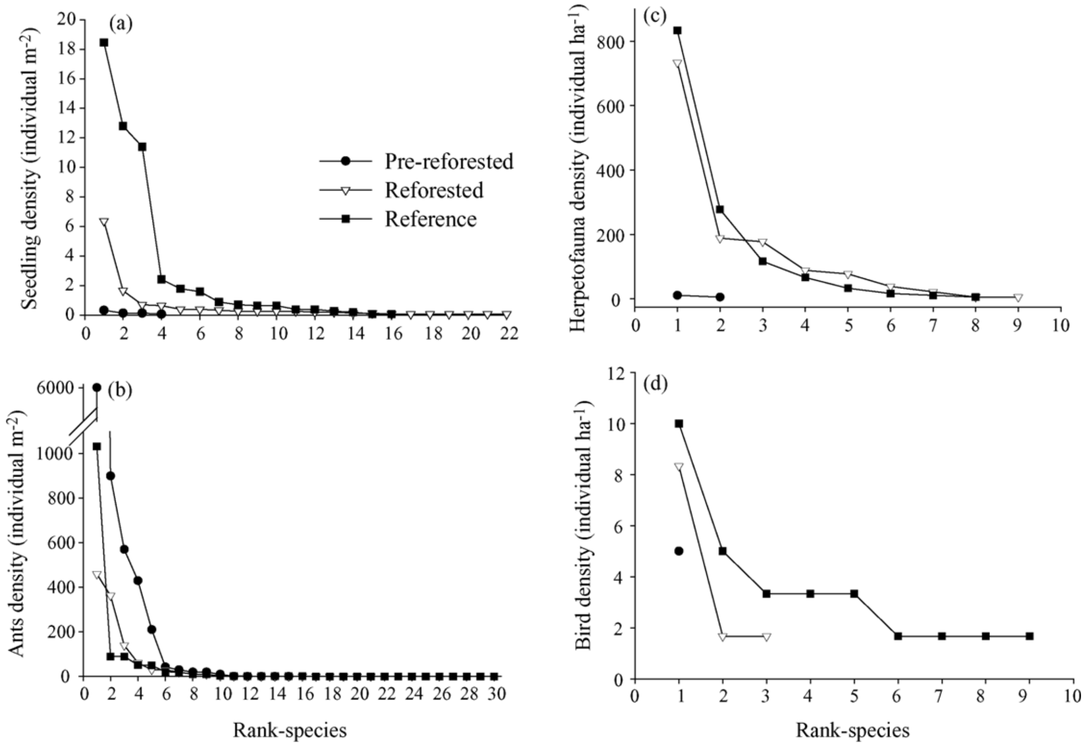

Fig. 2. Species rank-density curves: (a) woody plant seedlings (20 plots each 0.78 m^2), (b) ants (20 plots each 1 m^2), (c) herpetofauna (n = 12 census during Feb. 2001 through Feb. 2002 in 600 m^2), and (d) birds (n = 6 census in August and September 2004 in 1000 m^2). Species are plotted in rank order based on density. Data for each species are means of plots or census. Note in Fig. 2b *Solenopsis geminata* reached densities of 6000 individuals m^{-2} in the pre-reforested site, and in Fig. 1d, the pre-reforested site had only one bird species.

nine species in the reference site are endemic (*Dendroica adelaidae*, *Melanerpes portoricensis*, *Saurothera vieilloti*, *Spindalis portoricensis*, *Todus mexicanus*), and one species is a top predator (*Otus nudipes*). This rapid assessment approach provides a good estimate of the bird diversity in the pre-reforested and reforested sites, but failed to encounter all species that are present in the reference site (circa 20, Acevedo, unpublished data).

3.3. Ecosystem processes

Ecosystem processes varied among sites. Litterfall production, an indirect measure of productivity, was higher in sites with developed vertical stratification (i.e. reforested and reference sites; Table 1 and Fig. 1a and b). For example, total litter fall was lowest in the pre-reforested site (101 g m^{-2} yr^{-1}), higher in the reforested site (467 g m^{-2} yr^{-1}), and highest in the reference site (838 g m^{-2} yr^{-1}; Table 1). Litter turnover of the in the reforested site had values similar to the reference site (Table 1). Leaf litter residence time in both the reforested (230 d) and reference sites (139 d) are less than 8 months, while in the pre-reforested site is it was more than 2 years (763 d).

Litterfall nutrient inputs varied among the sites (Table 1). Phosphorus, nitrogen and calcium inputs were lower in the pre-reforested site, higher in the in the reforested site, and highest in the reference site (Table 1). Potassium and magnesium inputs were much lower in the reforested than the reference site (Table 1).

Soil nutrient content in the soil also varied among sites, as did the other ecosystem processes. Total phosphorus content in the soil was lower in the pre-reforested site (3.2 g m^{-2}) and higher in reforested (6.16 g m^{-2}) and reference (6.82 g m^{-2}) sites (Table 2). Similarly, nitrogen content in the soil was lower in the pre-reforested site (20.5 g m^{-2}), and higher in refor-

Table 1
Litter production, mean forest floor mass, litter turnover coefficient, residence time, an nutrient inputs for leaf litter in the pre-reforested, reforested, and reference sites

Measures	Sites		
	Pre-reforested	Reforested	Reference
Litterfall production (g m^{-2} yr^{-1})	101.3 (78)	466.8 (279)	838.4 (322)
Mean forest floor mass (g m^{-2})	121.6 (38)	212.4 (44)	296.7 (63)
Litter turnover coefficient (k) (yr^{-1})[a]	0.8 (0.5)	2.0 (0.9)	2.8 (0.5)
Residence time (1/k)	2.1 (1.7)	0.6 (0.4)	0.4 (0.1)
Phosphorus inputs (kg ha yr^{-1})	0.6 (0.1)	3.2 (0.2)	10.9 (0.4)
Nitrogen inputs (kg ha yr^{-1})	14.9 (1.1)	74.2 (4.4)	227.4 (8.4)
Calcium inputs (kg ha yr^{-1})	16.9 (1.3)	75.2 (4.5)	242.8 (9.0)
Potassium inputs (kg ha yr^{-1})	2.2 (0.2)	9.4 (0.6)	38.0 (1.4)
Magnesium inputs (kg ha yr^{-1})	5.5 (0.4)	17.6 (1.0)	83.2 (3.1)

[a] Total annual litterfall divided by the mean forest floor litter mass.

ested (24.5 g m^{-2}) and reference (26.5 g m^{-2}) sites. Magnesium content and bulk density were similar in the pre-reforested and reforested sites, but different from the reference site (Table 2). Soil pH, total calcium and exchangeable cations (Ca, K, and Mg) did not vary among the three sites. N, C, K, and Mg content and bulk density varied with soil depth (Table 2). N and C were higher and bulk density, K, and Mg were lower in the 0–10 cm soil profile in comparison with the 10–20 cm profile.

There was no difference in earthworm fresh weights among the three sites (Table 2). Earthworm fresh weight in the 0–10 cm soil profile was highly variable within sites, the pre-reforested site had 43.84 ± 41.2 g m^{-2}, the reforested site had 48.22 ± 33.3 g m^{-2}, and the reference site had 34.78 ± 30.2 g m^{-2}. In the 10–20 cm profile, there were no earthworms in the reforested site, but the pre-reforested site had 0.8 ± 1.3 g m^{-2} and the reference site had 5.2 ± 7.8 g m^{-2}.

After planting C_3 species (−31.7‰) in an area dominated by grasses (C_4; −13.4‰), there has been a change in ^{13}C of SOM (Table 2). $\delta^{13}C$ of SOM was higher in the 0–10 cm profile than in the 10–20 cm profile. $\delta^{13}C$ values of SOM at 0–10 cm profile were highest in the pre-reforested site, lower in the

Table 2
Soil pH, water content, bulk density, nutrient content, $\delta^{13}C$ values, and proportion of C_3 and C_4 in organic carbon at 0–10 and 10–20 cm soil profile in the pre-reforested, reforested, and reference sites

Measures/soil depth	Pre-reforested		Reforested		Reference	
	0–10 cm	10–20 cm	0–10 cm	10–20 cm	0–10 cm	10–20 cm
pH	5.8 (0.1)	5.8 (0.1)	5.5 (0.1)	5.7 (0.1)	5.8 (0.3)	5.5 (0.3)
Water content (%)	20.2 (1.5)	18.5 (1.9)	26.4 (1.4)	23.8 (1.8)	26.6 (4.3)	26.6 (8.8)
Bulk density (g cm^{-3})	1.0 (0.0)	1.2 (0.0)	0.9 (0.1)	1.1 (0.0)	0.9 (0.0)	1.0 (0.1)
P (g m^{-2})	3.2 (0.3)	3.2 (0.4)	6.6 (0.8)	7.0 (0.7)	6.3 (0.6)	6.1 (0.6)
N (g m^{-2})	22.6 (2.6)	18.5 (2.2)	26.4 (2.2)	26.6 (2.4)	26.8 (2.8)	22.2 (2.1)
Organic C (%)	4.1 (0.6)	3.5 (0.1)	4.4 (0.5)	3.9 (0.6)	4.3 (0.3)	2.1 (0.4)
Ca (g m^{-2})	9.0 (1.1)	8.1 (0.8)	10.8 (0.8)	11.2 (1.8)	12.4 (5.6)	6.5 (2.0)
K (g m^{-2})	11.3 (1.5)	12.2 (1.8)	12.8 (1.1)	17.6 (2.5)	9.5 (1.5)	11.3 (3.0)
Mg (g m^{-2})	0.3 (0.1)	0.5 (0.4)	0.4 (0.3)	1.1 (0.1)	1.0 (0.2)	1.6 (0.7)
Ca cations (meq Ca/100 g)	2.3 (0.9)	1.9 (0.9)	2.7 (0.6)	2.0 (0.6)	3.3 (1.7)	1.7 (0.8)
K cations (meq K/100 g)	0.1 (0.0)	0.1 (0.0)	0.1 (0.0)	0.1 (0.0)	0.1 (0.1)	0.1 (0.0)
Mg cations (meq Mg/100 g)	0.9 (0.4)	0.7 (0.2)	0.8 (0.1)	0.6 (0.2)	0.8 (0.3)	0.5 (0.2)
$\delta^{13}C$ values (‰)	−18.4 (1.1)	−21.4 (1.2)	−22.7 (2.1)	−21.7 (1.4)	−26.9 (1.0)	−25.9 (0.9)
Proportion of C_3 in organic carbon (%)	27.1 (5.8)	43.5 (6.7)	51.0 (11.4)	45.5 (7.9)	73.8 (5.7)	68.5 (5.0)
Proportion of C_4 in organic carbon (%)	72.9 (5.9)	56.5 (6.8)	49.0 (11.4)	54.5 (7.9)	26.2 (5.7)	31.5 (5.0)

Values are mean and standard deviation in parenthesis (n = 3).

reforested site, and highest in the reference site (Table 2). In contrast, $\delta^{13}C$ values of SOM at 10–20 cm profile were similar in the pre-reforested and reforested sites, and the reference site had the lowest $\delta^{13}C$ values (Table 2). Moreover, the proportion of total organic carbon of C_4 origin in the 0–10 cm soil profile was higher in the pre-reforested site, lower in the reforested site, and the lowest in the reference site (Table 2).

3.4. Restoration success—Bray Curtis Ordination

Vegetation structure, species diversity, and ecosystem processes have responded rapidly to planting. The Bray Curtis analyses showed that most measures of vegetation structure and species diversity have recovered >50% compared with the reference site (Table 3). For vegetation structure, litter cover had the slowest rate of recovery, while height of woody stems had the fastest. For species diversity, ants had the fastest recovery, followed by the herpetofauna, and woody seedlings had the slowest recovery. In general, ecosystem processes were slower to recover in comparison with vegetation structure and species diversity. Litter production had the fastest recovery, while litter turnover rates, litter nutrients, soil nutrients in 0–10 cm soil profile, and bulk density will take longer to recover.

Table 3
Percent of restoration success for measures of vegetation structure species diversity, and ecosystem processes using Bray Curtis Ordinations

Measures	Recovery (%)
Vegetation structure	
Woody vegetation height	74
DBH size classes	66
Herbaceous cover	65
Number of litter layers	56
Litter cover	46
Average	61
Species diversity	
Ants	76
Herpetofauna	68
Woody seedlings	54
Average	66
Ecosystem processes	
Litter production	70
Litter turnover rates	60
Nutrient inputs	57
Soil nutrient content (0–10 cm profile)	49
Bulk density	44
Average	56

The values indicate the position of the reforested site in comparison with the pre-forested and reference sites, as endpoints.

4. Discussion

4.1. Vegetation structure

Woody vegetation height and herbaceous cover were the measures of vegetation structure that changed most rapidly due to the planting and early establishment of pioneer species in the reforested site. These pioneer species (e.g., *Cecropia shreberiana*, *Roystonea borinquena*, and *Thespesia grandiflora*, planted; *Delonix regia* and *Senna siammea*, colonizers) quickly accumulate biomass (Guariguata and Ostertag, 2002), and provide a diverse vertical structure and canopy cover necessary for arboreal faunal species to colonized the restored site (McClanahan and Wolfe, 1993; Passell, 2000; George and Zack, 2001; DeWalt et al., 2003). Moreover the increase in canopy cover decreased herbaceous cover, and the presence of pioneer species with short-lived leaves contributed to the increase in litter cover and the increase in the number of litter layers in the reforested site. The recovery of these vegetation structure measures have changed conditions in reforested site and have facilitated the colonization of plants and animals (species diversity) and improved nutrient cycling (ecosystem processes).

4.2. Species diversity

The increase in woody seedlings and ant diversity and abundance was associated with changes in ground cover and number of litter layers. Woody seedling recruitment was probably influenced by the decrease in herbaceous cover in the reforested site, due to a decrease in belowground root competition and above ground physical barriers (Horvitz and Schemske, 1994; Otsamo, 2000; Hooper et al., 2002). Moreover, both the pre-reforested and reforested sites were very close to intact forest (i.e. less than 15 m), thus seed dispersal limitation should not be a limiting factor (Cubiña and Aide, 2001; Holl, 1999). Similarly, ants responded to the increase in litter cover and number of litter layers in the reforested site. Ant composition has been positively correlated with litter cover (Andersen, 1993), litter depth (Carvalho and Vasconcelos, 1999), and litter biomass (Barberena-Arias and Aide, 2003), which can explain the similar species composition in the reforested and reference sites.

The herpetofauna responded positively to the establishment of woody vegetation in the reforested site with the colonization of arboreal species (e.g., *Anolis cristatellus*, *Eleutherodactylus coqui*, and *E. cochranae*). This increase in species richness as well as species abundance (Fig. 2c) have been reported elsewhere (Pearman, 1997; Fogarty and Vilella, 2003; Jellinek et al., 2004). Moreover, an increase in abundance of both amphibians and reptiles in the reforested site to levels similar to the reference site, explains the colonization of two predators, *Anolis cuvieri* and *Epicrates inornatus*, which depended on a high abundance of prey.

In contrast to the herpetofauna, birds have not responded as rapidly to the changes in vegetation structure in the reforested site. This suggests that the reforested site does not provide the appropriate structural characteristics found in the surrounding matrix. The three species found in the reforested site are common species, which are present in many habitats in Puerto Rico and included two insectivores (*Coereba flaveola* and *Dendroica adelaide*) and a predator (*Coccyzus minor*) (Raffaele et al., 1998; Oberle, 2003). The presence of these species suggests that there was enough prey for insectivores and predator species that are not habitat restricted, but there were not enough resources for frugivorous birds (Fig. 2b and c).

In addition to the planting effect, the short distance to the forested limestone hills has also contributed to the rapid recovery of species diversity. An increase in vegetation structure enhanced the recovery of ants, reptiles, amphibians, and woody seedlings by providing the appropriate habitat (e.g., microclimate). Nevertheless, the rapid colonization of these groups would not have occurred without the presence of propagules and fauna in the surrounding limestone hills that served as a source for the reforested site (Hanski, 2002). Although the proximity to the forested hills has assisted the recovery process, the poor colonization in the pre-reforested site demonstrates the importance of restoration (i.e. planted woody species).

4.3. Ecosystem processes

Planting, growth, and colonization of woody plants have enhanced aboveground ecosystem processes in the reforested site. This is mainly due to the high litter production of pioneer species that allocate their energy to the leaf production and have short-lived leaves (Brown and Lugo, 1990; Guariguata and Ostertag, 2001). Moreover, litter turnover (k) in the reforested site was two times faster in comparison with the pre-reforested site. The litter turnover rates in the reforested and reference sites are comparable with other tropical ecosystems (Olson, 1963; Wieder and Wright, 1995). In addition, the increase in litterfall explained most of the difference in nutrient inputs among sites (Burghouts et al., 1998; Herbohn and Congdon, 1998).

Changes in aboveground ecosystem processes contributed to the changes in belowground processes in the reforested site. There was an increase in phosphorus and nitrogen soil content, but there was no change in calcium content. The increase in phosphorus and nitrogen content in the soil is not surprising, because these nutrients are mainly influenced by plant inputs (Vitousek, 1984). Soil calcium content was not influenced by plant inputs as suggested by Vitousek (1984). In our sites, the geology (i.e., Karst) has a much stronger influence, resulting in no difference among sites. The change in plant composition from C_4 to C_3 contributed to changes in the composition of SOM in the 0–10 cm profile, while no difference was detected in 10–20 cm profile in the reforested site. The rapid incorporation of SOM in the topsoil can be explained by the rapid increase in litter production and decomposition in the reforested site. This rapid change in $\delta^{13}C$ values (−18.4‰ in the pre-reforested to −22.7‰ in the reforested site) suggests that incorporation of soil organic matter can be more rapid than previously reported. $\delta^{13}C$ values in studies of natural regeneration from pastures (C_4) to forest (C_3) have taken more than 15 years to reach levels similar to those in the 3-year-old reforested site (Rhoades et al., 1998; Guillet et al., 2001; Eshetu, 2002; Biedenbender et al., 2004). In contrast to the topsoil, C composition in the 10–20 cm profile is still dominated by C_4 in the reforested site (Table 2). This can be partially explained by the high bulk density (i.e., high soil compaction) and the absence of earthworms in the 10–

20 cm soil profile (Table 2 and Knoepp et al., 2000). High bulk densities reduced earthworm activity that can be critical for the movement of organic matter in the soil (Herrick, 2000; Tian et al., 1997).

4.4. Bray Curtis Ordination

The Subjective Bray Curtis Ordination is a useful approach for assessing restoration success (Table 3). Practitioners can predefined minimum percent of success (e.g., 70%) for the project as a whole or for specific measures. This technique can be useful for comparing large number of measurements and identifying measures that are recovering slowly and would benefit from additional management. Although this approach is promising as a simple way to present restoration success, it has limitations: (1) when values in the pre-reforested site are zero, only a slight recovery will be classified as a high recovery, and (2) when values of the reforested site are lower than the pre-reforested site or higher than the reference site, the analysis will give negative or >100% recovery.

5. Conclusion

This restoration project has initiated rapid changes in vegetation structure, species diversity, and ecosystem processes, but has restoration been successful? The rapid increase of vertical stratification, low herbaceous cover, rapid colonization of species from different trophic levels, high litter production, and rapid C_3 incorporation in SOM suggest that the reforested site could be left without further management assistance. These results indicate that the restoration project has been successful. Other measures such as litter cover, bird diversity, litter turnover, nutrient inputs, and bulk density will take longer to recover. To accelerate the recovery rate of these measures management efforts could focus on planting higher densities of pioneer species in the first years of restoration to assure an increase in litter cover and for providing resources for birds. The recovery of the bird community could be enhanced by planting pioneer species (e.g., *Cecropia schreberiana*, *Cordia sulcata*, *Miconia serrulata*, and *Schefflera morototoni*) that will offer both vertical vegetation structure and food resource in the short-term (Carlo et al., 2003).

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Appendix A

Presence/abscence of woody seedlings, ants, amphibians, reptiles, and bird species in the pre-reforested, reforested, and reference sites

Group/scientific name	Pre-reforested	Reforested	Reference
Woody seedlings			
Asteraceae spl	X		
Urena lobata L.	X	X	
Urena sinuata L.	X	X	
Spathodea campalunata Beauv.	X	X	X
Andira inermis (Wright) DC.		X	
Ardisia obovata Desv. ex Hamilt.		X	
Asteraceae sp2		X	
Bignoniaceae spl		X	

Appendix A (*Continued*)

Group/scientific name	Pre-reforested	Reforested	Reference
Casearia arborea (L.C. Rich.) Urban		X	
Casearia sylvestris Sw.		X	
Eugenia monticola (Sw.) DC.		X	
Senna siamea (Lam.) Irwin and Barnaby		X	
Tabebuia heterophylla (DC) Britton[a]		X	
Terminalia catappa L.		X	
Thespesia grandiflora (DC.) Urban[a]		X	
Casearia guianensis (Aublet) Urban		X	X
Chrysophyllum argenteum Jacq.		X	X
Dendropanax arboreus (L.) Decne. and Planch.		X	X
Guarea guidonea L.		X	X
Hippocratea volubilis L.		X	X
Miconia laevigata (L.) DC.		X	X
Quararibea turbinata (Sw.) Poir		X	X
Woody seedlings			
Thouinia striata Radlk.		X	X
Bambusa vulgar is Schrad ex Wendl.			X
Eugenia biflora (L.) DC			X
Faramea Occident alis (L.) A. Rich.			X
Ocotea leucoxylum (Sw.) Mez.			X
Phyllanthus juglandifolius Wild.			X
Syzygium jambos (L.) Alst.			X
Trichilia pallida Sw.			X
Ants			
Cardiocondyla emergi Forel	X		
Pheidole fallax Mayr	X		
Pheidole sp6	X		
Brachymyrmex spl	X	X	X
Hypoponera opaciceps Mayr	X	X	X
Monomorium ebeninum Forel	X	X	X
Odontomachus ruginodis Smith	X	X	X
Pheidole morens Wheeler	X	X	X
Pheidole sp2	X	X	X
Solenopsis corticalis Forel	X	X	X
Solenopsis geminata Fabricius	X	X	X
Strumygenys rogeri Emery	X	X	X
Wasmannia auropuctata Roger	X	X	X
Solenopsis wagneri Santschi.	X		X
Wasmannia spl	X		X
Ants			
Camponotus sexguttatus Frabricius		X	
Odontomachus spl		X	
Pheidole sp5		X	
Strumygenys emmae Emery		X	
Anochetus mayri Emery		X	X
Mycocepurus smithi Forel		X	X
Odontomachus bauri Emery		X	X
Paratrechina longicornis Latreille		X	X
Pheidole spl		X	X
Pheidole sp4		X	X
Pyr arnica mar gar it ae Forel		X	X
Cyphonomyrmex minutus Mayr			X

Appendix A (*Continued*)

Group/scientific name	Pre-reforested	Reforested	Reference
Dolichoderinae			X
Hypoponera puntatissima Roger			X
Linepithema melleum Wheeler			X
Monomorium floricola Jerdon			X
Paratrechina steinheili Forel			X
Pheidole exigua Mayr			X
Plachycondyla spl			X
Rogeria foreli Emery			X
Solenopsis spl			X
Strumygenys spl			X
Amphibians			
Bufo marinus L.	X		
Leptodactylus albilabris Gunther	X	X	X
Eleutherodactylus coqui Thomas		X	X
Eleutherodactylus cochranae Grant		X	X
Eleutherodactylus antillensis Reinhardt and Lutken		X	
Reptiles			
Anolis pulchellus Dumeril and Bribon		X	
Anolis krugii Peters		X	X
Anolis cristatellus Dumeril and Bribon		X	X
Anolis cuvieri Merrem		X	X
Epicrates inornatus Reinhardt		X	X
Anolis stratulus Cope			X
Birds			
Estrilda melpoda Vieillot	X		
Coccyzus minor G.K. Gmelin		X	
Coereba flaveola L.		X	X
Dendroica adelaidae Baird		X	X
Melanerpes portoricensis Daudin			X
Otus nudipes Daudin			X
Saurothera vieilloti Bonaparte			X
Spindalis puertoricensis Bryant			X
Todus mexicanus Lesson			X
Turdus plumbeus L.			X
Zenaida aurita Temminck			X

[a] Species planted and producing fruits.

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