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Vegetation Dynamics of a Permanent Pasture Plot in Puerto Rico[1]

ABSTRACT

I set up a 250 m^2 plot and found after five years that (1) grass dominated by ferns and woody species was gradually increasing over time; (2) woody genera (*Syzygium*, *Calophyllum*, and *Clidemia*) common here have not been found elsewhere on the island and "successional" trees, such as *Cecropia* sp. and *Shefflera* sp., were completely absent; (3) smaller, earlier trees were also found away from the forest; and (4) the plot had multiple strata and was recovering forest structural characteristics such as productivity and richness.

Key words: *invasibility; land use; LTER; Luquillo Experimental Forest; old fields; succession.*

Approximately 1.9 billion ha of the earth's tropical forests have been cut (Grainger 1988), with the vast majority converted to agriculture and pasture (Skole & Tucker 1993). The recovery of these areas after they are abandoned affects important social and scientific issues such as tropical deforestation and succession, land reclamation and restoration, sustainability, maintenance of biodiversity, and global climate change (Padoch & Vayda 1983). Consequently, the study of tropical old-field succession is a key ecological concern (Purata 1986, Borhidi 1988). Old-field succession studies in the temperate zones of the United States and Europe have greatly benefited from using permanent plots (Buell *et al.* 1971, Pickett 1982, Myster 1993), but similar studies are rare in the Neotropics (Uhl *et al.* 1988). This is unfortunate because such studies can show the actual successional species replacement sequences and changes in species abundances and composition through time, instead of relying on chronosequences that attempt to "cut and paste" succession sequences using different fields sampled at different times.

I set up permanent plots in an abandoned pasture in Puerto Rico and sampled them annually for five years to record the process of temporal change in structural parameters of the plant community (species composition, species abundance, species richness, density, height, basal area, stratification, productivity, and spatial invasion pattern) and compare them to recovery patterns after the abandonment of a coffee plantation.

The study was conducted at Luquillo Experimental Forest (LEF) within the Caribbean National Forest, Puerto Rico, U.S.A. The LEF is the tropical long-term ecological research (LTER) site of the National Science Foundation. It has a rough topography with deeply dissected drainages and steep slopes, ranges in elevation between 250 and 1100 m, an annual rainfall between 2 and 5 m, and a mean annual temperature of 17°C. The region is underlain by very thick-bedded volcanic sandstone, on which the most common soil types are upland Ultisols, well-drained clays, and silty clay loams. The study region is classified as subtropical wet forest (Ewel & Whitmore 1973), dominated by tabonuco (*Dacryodes excelsa*) at the low elevation of this study. I selected a pasture bordering the northwest corner of the LEF close to the town of Sabana (18°18′N, 65°50′W), which has been studied by several other LTER researchers (Aide *et al.* 1995, Thomlinson *et al.* 1996, Liu & Zou 2002). This pasture was *ca* 4 ha in size and had been converted to pasture from tabonuco forest before 1936. It has been pasture ever since. It has an elevation of 420 m, a mean monthly temperature of between 22 and 26°C, and an annual precipitation of *ca* 3500 mm. Its soil is an Oxisol belonging to the Zarzal series with high clay content (Liu & Zou 2002).

Within that pasture, I set up a 25 × 10 m plot, with the 25 m side on the forest border, in order to investigate edge effects such as greater tree density and tree species turnover, which are common in other old-field succession studies (Myster 1993). I then subdivided this plot into 25 contiguous 5 × 2 m subplots for sampling in February 1996, when the pasture was abandoned following exclusion of cattle. Every February or March in years 1997 through 2001, percent cover (an indicator of a species' ability to capture light) of all plant species was estimated visually as the percent of a plot's area covered by each species (all of a plant's aboveground biomass; Myster & Pickett 1994) in each subplot. All tree

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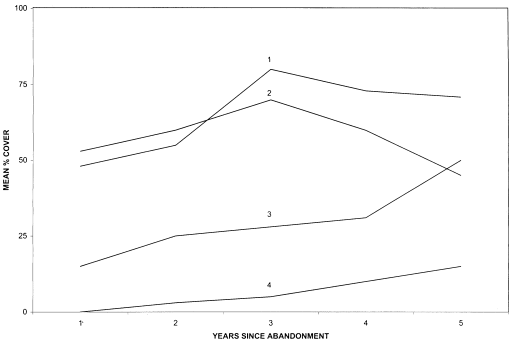

FIGURE 1. Mean percent cover per subplot through time of major plant species groups. Standard errors are not graphed for readability. Species groups are: (1) grasses, (2) forbs, (3) ferns, and (4) woody species including trees, shrubs, and vines.

stems over 50 cm in height were tagged, identified to species, and measured for height and basal diameter. After five years, the spatial location (within 1 m) of each pasture tree stem was also mapped. Because temperate land-use studies have shown the critical need for comparison of recovery from areas that differ in previous land use (review in Myster 1993), I also used the same plot design and sampling regime in an abandoned sun coffee (*Coffea arabica*) plantation and sampled it for two years. The plantation, located within 8 km of the pasture site, also bordered the LEF and had very similar soils and elevation compared to the pasture plot.

I tabulated tree stem and cover totals, mean height of all tree stems, total basal area, tree/shrub richness and evenness (Simpson's index of diversity; Myster & Walker 1997), turnover of tree species (Myster & Pickett 1994), and productivity (summing over the plot using species-specific allometric equations in Myster [2002] relating aboveground biomass to height and basal diameter of tree stems; Uhl *et al.* 1988). The equation for turnover at year t is (number of tree species present in year 1 but not present in year t + number of tree species present in year t but not present in year 1)/(number of tree species present in year 1 + number of tree species present in year t − number of tree species present in year t that had been successfully introduced between year 1 and year t; Diamond 1969). Lack of replication precluded further statistical analysis.

Grass dominated early in the pasture, increased to a peak in year 3 and then declined in years 4 and 5 (Fig. 1), with *Panicum* spp. more common than *Brachiaria subquadripara*. The same trend but at lower cover levels was also true for dicotyledonous herbs (dominated by *Dieffenbachia seguine* and *Colocasia esculenta*, with *Desmodium ascendens* common). The ferns (*Nephrolepsis* sp. and *Thelypteris deltoidea*) gradually increased along with the woody species (*e.g.*, the vines *Ipomea* spp. and *Passiflora* spp.). For the trees and shrubs, *Syzygium jambos* dominated and peaked in year 3; *Miconia impetiolaris* and *M. prasina* dominated but did not decline; *Citrus* spp. trees maintained low cover; both *Calophyllum calaba* and *Piper* spp. peaked in year 3 and *Clidemia hirta* was still increasing in cover and dominating after 5 years (Table 1), with a rare bimodal cover curve. After these trees, species more common in other LEF seres (see Myster & Walker [1997] for landslide species and temporal patterns) such as *Piper* spp., *Guarea guidonia*, and *Inga vera* were observed in the sere. Other species (*Tabebuia heterophylla*, *Eugenia pseudopsidium*, and *Andira inermis*) maintained a low level of cover over the entire sere. Total counts of tree and shrub stems over time in the large plot showed the increase, peak, and decline of the cover by these species (Table 1).

In the coffee plots, the coffee trees themselves continued after abandonment, with a cover of 30 percent in the first year and 23 percent in the second year, on average. Like the pasture plots, grass dominated (94% in yr 1, 90% in yr 2; *Ichnanthus pallens* was most common), with dicotyledonous herbs (45% in yr 1, 50% in yr 2; *Phytolacca icosandra* and planted *Musa* spp. were common) and vines (64% in yr 1, 67% in yr 2; same species as in pasture) as subdominants, and ferns (5% in yr 1, 6% in yr 2; same species as in the pasture) at a low cover; however, these nonwoody plants attained greater cover here than in the pasture, with vines at greater levels than herbs. The tree species in the coffee plantation

TABLE 1. *Number of tree (T) or scrub (S) stems at least 50 cm in height per species in a 250 m² plot during the first five years of post-abandonment after pasture in Puerto Rico.*

Species	Year 1	Year 2	Year 3	Year 4	Year 5
Syzygium jambos (T)	18	80	76	70	65
Calophyllum calaba (T)	5	45	31	18	8
Clidemia hirta (S)	1	39	29	17	9
Tabebuia heterophylla (T)	4	11	10	12	5
Miconia impetiolaris (S)	4	24	22	21	20
Miconia prasina (S)	3	39	29	22	19
Citrus spp. (T)	2	3	3	3	3
Guarea guidonia (T)	1	4	3	5	2
Eugenia pseudopsidium (T)	2	7	6	8	7
Myrcia splendens (T)	0	2	3	1	1
Presotea montana (T)	0	1	2	2	2
Inga laurina (T)	2	5	4	5	3
Ocotea leucoxylon (T)	0	0	1	2	1
Andira inermis (T)	0	2	5	8	6
Inga vera (T)	2	9	11	12	10
Casearia sylvestris (T)	1	3	1	4	4
Miconia racemosa (S)	3	12	13	7	5
Psychotria berteriana (S)	0	2	1	2	2
Piper hisperdium (S)	2	23	10	3	3

were much reduced under a combination of shading from the remnant coffee trees and competition from the grasses and herbs. None of the woody plants dominant in pasture (*Syzygium*, *Calophyllum*, and *Clidemia*) were present here; however, important species such as *Tabebuia*, *Miconia*, and remnant fruit trees (*Citrus* spp.) attained similar cover levels as in pasture. The species *A. inermis* and *G. guidonia* (which may have been planted with the coffee; Garcia-Montiel 1991) attained greater cover levels compared to the pasture plots, but no *Inga* spp. (also often planted with coffee) were present. *Myrcia splendens* and *Casearia sylvestris* were the only other tree species found in both plots. Tree and scrub species unique to the coffee plots were *Homalium racemosum*, *Pouteria sapota*, *Ocotea* spp., *Trichilia pallida*, *Roystonea borinquena*, *Casearia decandra*, *Meliosma herbertii*, *Psychotria* spp., *Myrcia leptoclada*, *Gonzalagunia spicata*, *Margaritaria nobilis*, *Cordia sulcata*, and *Spondias mombin*, but none attained much cover (1–3% range) in the first two years of this sampling. Unlike the pasture, *Schefflera morototoni* was found in the coffee plots, but *Cecropia schreberiana* was not found either in coffee or pasture.

Large tree/shrub stems were more common near the forest where they would be expected to invade first (Fig. 2a). Also, the temporal species replacement sequences of Figure 1 were reflected spatially because subplots closer to the forest had more mid- and later-successional species (Fig. 2a,b; Table 1) compared to subplots away from the forest (Myster 1993). Aboveground productivity increased to *ca* 500 g/m²/yr and then leveled off to *ca* 100 g/m²/yr (Fig. 3a), and may be a good indicator of the rate of forest regeneration after pasture abandonment (similar to forest aboveground levels in 100 yrs; Uhl *et al.* 1988). Total stems also peaked early at 289 and then gradually declined (Fig. 3b). Mean height increased monotonically through time to approach 250 cm (Fig. 3c) and basal area seemed to stabilize at *ca* 800 cm² (Fig. 3d). Total cover, an indicator of stratification and developing structure, showed a rapid increase to two or three strata (200–300% cover per subplot; Fig. 4a) and then maintained a tree/shrub layer, a sapling layer, and a grass/herb/fern layer. Percent tree turnover decreased significantly and then returned to 50 percent (Fig. 4b). Tree richness rose to 20 species and then remained constant (Fig. 4c). Tree evenness increased slightly then decreased slightly, always *ca* 0.8 (Fig. 4d).

Species patterns in this young pasture showed an individualistic succession, composed of broadly overlapping population curves through time. Most species had persistent tails indicating that they had been present through most of the five-year sere (Egler 1954), becoming dominant at different and unique times (seen also in temperate old fields in New Jersey; Pickett 1982). This result implies that species-specific strategies and mechanisms were driving these patterns, which may have included different uses of resources, tolerance niches, dispersal, predation (Myster 2003), and competitive ability (Nepstad *et al.*

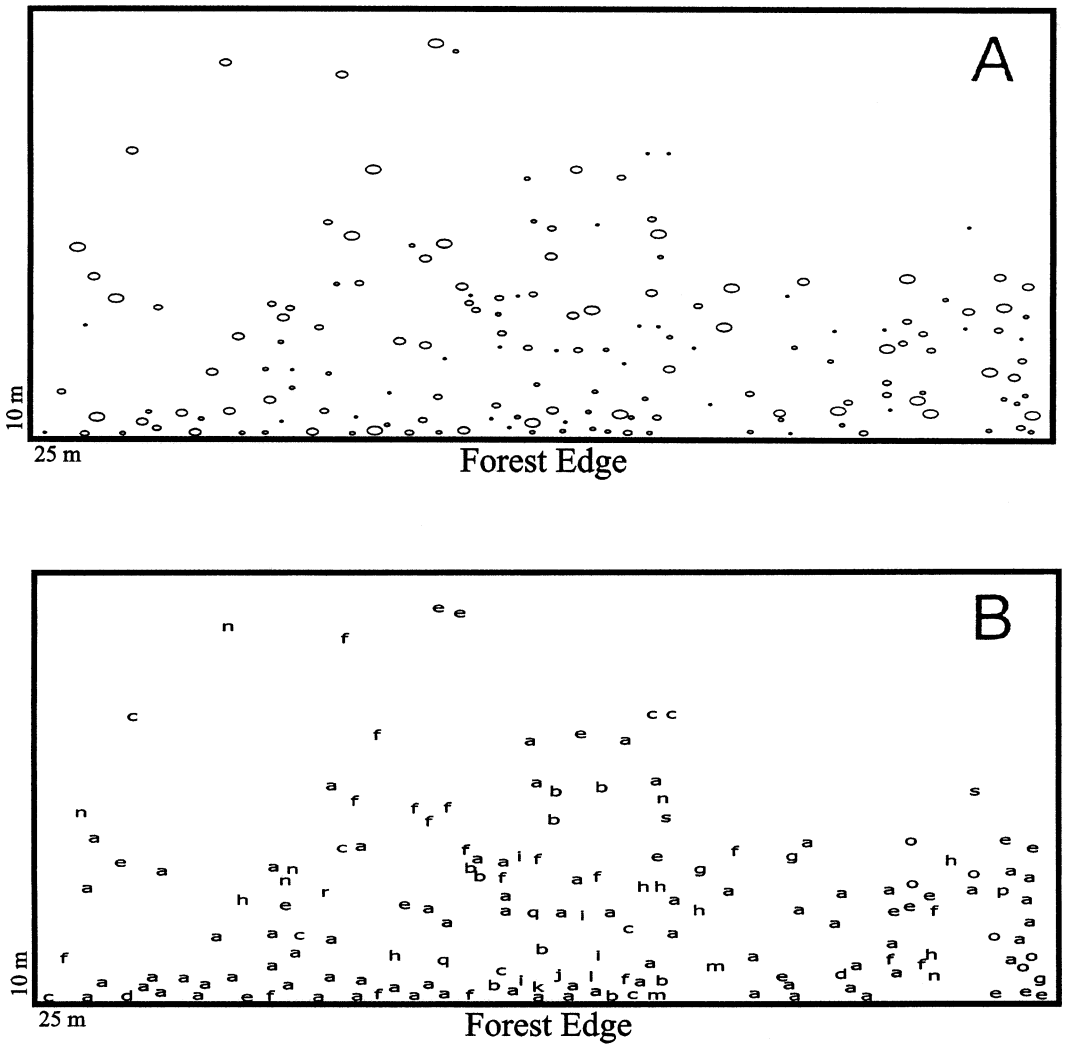

FIGURE 2. Spatial location of all tree stems in the large plot in year 5 of the sampling. (a) Stems are indicated by increasingly larger circles representing their basal diameters, some smaller than 1 cm. (b) Stems are indicated by species from Table 1 using the first letter of their name.

1996, Myster in press) that led to inhibition, facilitation, and differences in ecophysiology among the species.

Perhaps the most surprising thing about this pasture sere was the lack of early-successional trees thought to be characteristic of LEF disturbances (*e.g., Cecropia* spp. and *Shefflera* spp.; Devoe 1989, Myster & Walker 1997). The complete absence of these species may have been due to the lack of seed input, dominance of competition by grass, or other mechanisms. Grass competition was also implicated as a dominant mechanism in LEF landslides because *Cecropia* and *Shefflera* do not establish when extensive grass cover is present (Myster & Walker 1997; Myster, pers. obs.). This situation may be temporary, however, because these species are found in 25-year-old LEF pastures (Aide *et al.* 1995). Tree species that do establish early may share characteristics with *Cecropia* spp., which are thought to be important in determining their placement in Neotropical seres (Myster & Walker 1997, Brokaw 1998). These include seed size and its correlates (*Cecropia* spp. have small seeds that are bird- or bat-dispersed, have long viability in the soil, and germinate easily; Everham *et al.* 1996), VA mychorrizae association strategy

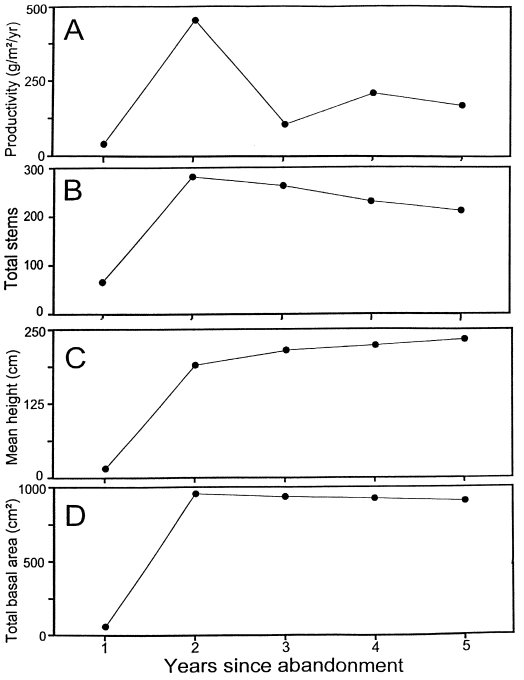

FIGURE 3. (A) Productivity, (B) total stems, (C) mean height, and (D) total basal area, in the large plot (250 m^2) through time.

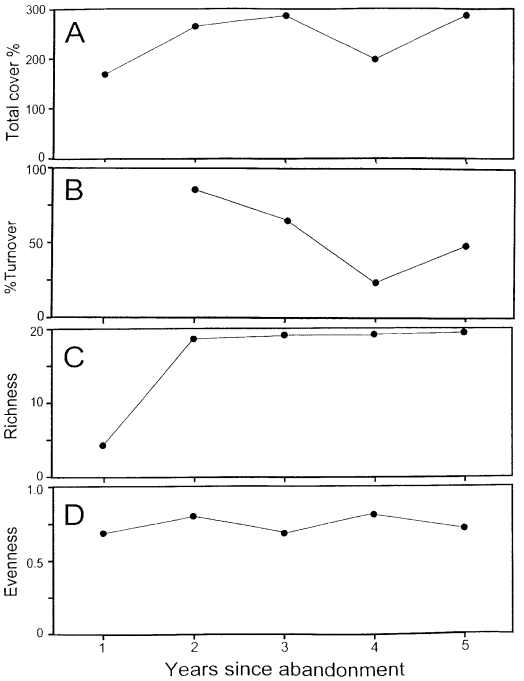

FIGURE 4. (A) Total % cover, (B) % turnover, (C) richness, and (D) evenness, in the large plot through time.

(*Cecropia* spp. is weakly facultative; Myster, pers. obs.), and shade tolerance (*Cecropia* spp. are intolerant of shade; Brokaw 1998). Also, *S. jambos* is an introduced exotic species (Francis & Liogier 1991), which often does well in agricultural fields by outcompeting the resident plants (Myster & Pickett 1992).

Lack of information about tropical tree biology makes interpreting many of these patterns difficult. Whereas a few early successional trees may regenerate from the seed bank, for many trees, seeds may be lost largely through seed predation (Myster 2003, in press); thus, species variation in levels of predation may be a key mechanism determining position in the sere. Another important mechanism may be competition, especially for light, when availability seems to be a key factor in determining species composition and abundance in seres that were once rain forest. Indeed, cover patterns suggest light as a key factor because of the correspondence between the pasture's temporal and spatial species sequences (light decreases through time and into the forest) and abundance patterns seen in LEF gaps that differ by light levels (*Tabebuia* at highest light levels, then *Miconia* at high levels, *Piper* at moderate levels, and *Inga* at low levels; Devoe 1989). Finally, the ability of *Miconia* spp., *Piper*, and *Clidemia* to sprout from broken or bent stems (M. Aponte, pers. comm.) may have helped them achieve their abundance levels.

Comparison with equivalent plots in a recently abandoned coffee (*C. arabica*) plantation showed how different LEF successions could be after different crops, emphasizing the importance of both land use in determining LEF successional dynamics and forest structure, and the individual permanent plots to examine them. Although pastures usually have had crops growing in them previously, they have a distinct recovery that may be due to the presence of cattle. Effects of cattle include trampling of vegetation, which compacts the soil to increase soil bulk density and lead to more resistance to penetration, the creation of hummocks, and deposition of dung.

Past studies in other pastures have suggested that key mechanisms controlling species replacements include competition for soil nutrients with grasses, drought stress, high levels of predation on seeds and seedlings, low seed rain, or the seed bank (Nepstad *et al.* 1996; Myster 2003, in press). Amazonian pasture plots on the mainland Neotropics (Uhl *et al.* 1988) differ from this Puerto Rican pasture, in that the Amazon plots show: (1) *Cecropia* spp. and sprouting are common; (2) 1.5 times more aboveground production for an equal-sized area of lightly grazed pasture; and (3) the same number of tree species for an area 2.5 times as smaller than the study plot. The effects of previous crops in general and grass species in particular on post-abandonment successional patterns and processes are illustrated in this pasture as well as in the abandonment of temperate hay fields planted with *Dactylis glomerata* (Myster & Pickett 1994). The effects of *Dactylis* in New Jersey fields included: (1) persistence of the species itself for at least five years after abandonment (attaining cover levels similar to the pasture grasses seen in this study over the same time period); (2) reduction of herbaceous cover (Myster & Pickett 1988); (3) alteration of successional pathways compared to other fields for at least eight years; (4) competitive inhibition of numerous woody species for at least six years (Myster & Pickett 1992); and (5) a reduction in both initial species richness and rate of succession in which turnover did not decrease as sharply as in other fields (*i.e., Dactylis* reduced new species invasion or invisibility; Myster & Pickett 1994). I expect that many of these same effects of grass will be seen in this pasture later in succession, and that these data, in general, will stimulate further research on regeneration in abandoned tropical pastures.

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