



CHANGES IN EARTHWORM DENSITY AND COMMUNITY STRUCTURE DURING SECONDARY SUCCESSION IN ABANDONED TROPICAL PASTURES

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Summary—Plant community succession alters the quantity and chemistry of organic inputs to soils. These differences in organic input may trigger changes in soil fertility and faunal activity. We examined earthworm density and community structure along a successional sequence of plant communities in abandoned tropical pastures in Puerto Rico. The chronological sequence of these plant communities were pasture, grass–vine–fern, shrub–small tree, and forest. Earthworm density was the highest in pasture (831 worms m^{-2} in top 0.25 m soil), decreased as secondary succession proceeded, and reached the lowest (32 worms m^{-2}) in the forest. Whereas only soil feeding *Pontoscolex corethrurus* was present in the pasture and grass–vine–fern communities, both soil and litter feeding worm species were found in the shrub–small tree and forest communities. Ground litter biomass correlated negatively with earthworm density. Soil water content differed slightly among the successional communities, but was unlikely to play an important role in triggering differences in worm density among these abandoned lands. Soil pH values did not differ along the successional changes. These results suggest that decrease in earthworm density and increase in worm community diversity during secondary succession may result from changes in the chemistry of organic inputs, rather than in soil properties and litter quantity. We conclude that successional development from grass-dominated pastures to woody species-dominated forests reduces earthworm density and diversifies worm community structure in humid tropical soils. © 1997 Elsevier Science Ltd

INTRODUCTION

Plant and animal communities change during secondary succession in disturbed lands (Horn, 1974). These changes can alter the quantity and chemistry of litter input to soils. Differences in litter quality and chemistry may trigger changes in the abundance and community structure of earthworms. While 1.9 billion ha of tropical forest have been disturbed by human activities (Grainger, 1988), much of these lands have been converted into cattle pasture (Skole and Tucker, 1993). With the growing concern about losing biodiversity, researchers are evaluating various strategies to rehabilitate vegetation in deforested tropical lands (Brown and Lugo, 1994). One of these strategies is to allow secondary succession to proceed under natural conditions after removal of human stress. Earthworms compose the highest biomass among tropical soil macrofauna (Odum and Pigeon, 1970; Fragoso and Lavelle, 1992), and they play important roles in regulating soil processes. Understanding interactions between earthworm communities and secondary succession would aid in designing forest rehabilitation programs.

In Puerto Rico, deforestation occurred extensively during the late nineteenth century and the beginning of this century. Forest cover of the whole island declined from 67% in 1830 to a minimum of about 7% in 1947 (Birdsey and Weaver, 1987). Much of the deforested area on montane slopes was converted to cattle pastures. The subsequent development of an industrial economy released about 200,000 ha of agricultural lands, and forest cover had returned to 31% by 1989. While most of these lands were not managed, invasion and natural regeneration of tree species have rehabilitated many of these abandoned cattle pastures back to secondary forests. This rehabilitation process includes four secondary succession stages (Aide *et al.*, 1995): the initial grass community (< 3 y after abandonment), grass–vine–fern community (3–15 y), shrub–small tree community (15–40 y), and forest (> 40 y). We developed this project to examine changes in earthworm density and community structure during secondary succession in abandoned tropical pastures in Puerto Rico.

MATERIALS AND METHODS

This study was conducted at Sabana (18°18'N, 65°50'W) in the northeastern Luquillo Mountains

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of Puerto Rico. Native forest is described as subtropical wet forest (Ewel and Whitmore, 1973) dominated by tabonuco trees (*Dacryodes excelsa*). Elevation is about 420 m above sea level, and the mean monthly temperatures vary from 22 to 26°C. Annual precipitation is approximately 3500 mm (Scatena, 1989).

Using air photos taken in 1936, 1951, 1964, 1971, 1977, 1983, 1988, 1991 and 1993, we were able to locate four sites adjacent to each other on a single hill slope north of the Rio Sabana. Three sites were deforested and converted to pastures prior to 1936. Two of those were abandoned by 1971 and 1988, and one has been maintained as pasture. The fourth site has been forest since 1936. The site abandoned in 1971 has developed into a shrub-small tree community (Aide *et al.*, 1995) dominated by species in the Melastomataceae (*Miconia prasina*, *M. impetio-larias*, *M. racemosa*) and Rubiaceae (*Palicourea riparia*, *Psychotria brachiata*). The more recently abandoned site has developed into a grass-vine-fern community. Soils in all the study sites are Oxisols, belonging to the Zarzal series with high clay content.

Earthworms were sampled between 21 June and 28 July 1993. Three 0.25 m² (pasture and grass-vine-fern communities) or 0.5 m² (shrub-small tree and forest communities) plots were located 15 m apart in each site along the slope. Ground litter (leaves and twigs <2 mm dia) were collected in each plot and stored in plastic bags. Soils in the upper 250 mm were then removed onto a cloth sheet. Earthworms were hand-sorted and stored in plastic bags in a cooler with ice. A soil sample was taken from each plot and placed in a plastic bag for measuring pH and water content. Ground litter biomass was obtained after drying twigs and leaves at 60°C for at least 72 h. Fresh weight of earthworms was acquired after the worms were rinsed with water and dried with paper towels on the same day of sampling. Soil moisture content was calculated for each site by oven-drying 15 g of fresh sample at 105°C for 48 h. Soil pH was measured using a paste of 1:1 ratio of fresh soil and deionized water. Analyses of variance and Scheffe's multiple range test were employed to examine differences among successional communities. The significance level was set at $\alpha = 0.10$.

RESULTS

Earthworm density was the highest in the active pasture, decreased steadily after abandonment, and was the lowest in the forest (Table 1). Worm biomass in the active pasture was nine-fold that in the mature forest. Whereas the anecic species *Amyntas rodericensis* and *Estherella gatesi* were present only in the shrub-small tree and forest communities, the endogeic species *Pontoscolex corethrurus* occurred in all successional stages, and it was the only worm species in the pasture and grass-vine-fern communities (Table 1).

Biomass of ground litter differed among the successional communities (Table 1) and correlated negatively with earthworm density and biomass (Table 2). Litter biomass in the shrub-small tree and forest communities were 10–30 times those of pasture and grass-vine-fern communities. Soil water content differed slightly ($P = 0.07$) among successional communities, but did not correlate with worm density or biomass. Soil pH did not differ among the communities (Table 1), nor did it correlate with earthworm density (Table 2).

DISCUSSION

Earthworm density decreased to one fifth of its original level after pastures had undergone succession to shrub-small tree community (Table 1). Factors contributing to the decline may include alteration in soil moisture content, soil pH, and the quantity and chemistry of litter input. Despite changes in plant species composition and above-ground biomass (Aide *et al.*, 1995), soil pH did not differ across the successional stages. Although soil water content was lower in the shrub-small tree community than in other successional stages, this might have resulted from different sampling dates. Soils in the shrub-small tree community were sampled in late July which was the beginning of a dry summer, whereas other soil samples were taken in late June and early July that were in a relatively wet season. It is unlikely that the variation in soil water content (61–83%) might have played an important role in explaining the large differences in worm density and biomass among these plant communities. However, large differences in the biomass of ground twigs and leaves were observed between

Table 1. Changes in earthworm density, biomass, soil pH and water content, and ground litter biomass during secondary succession in abandoned tropical pastures in Puerto Rico. Common letters within a column indicate no significant difference (Scheffe's multi-range test, $\alpha = 0.10$) between successional communities

Successional community	Density(No. m ⁻²)	Biomass (g m ⁻²)		Soil H ₂ O%	Soil pH	Ground litter (g m ⁻²)
		Total	% Anecic worm			
Pasture	831 a	175 a	0 a	73 a	4.8 a	14 a
Grass-vine-fern	403 a	110 ab	0 a	83 a	5.1 a	26 a
Shrub-small tree	141 b	41 ab	15 ab	61 b	4.7 a	524 b
Forest	32 b	19 b	52 b	70 ab	5.0 a	335 b

Table 2. Correlation coefficients (significance level) between earthworm density and biomass with soil variables and litter biomass. Data were collected in a secondary successional sequence in abandoned pastures in Puerto Rico

Variable	Soil H ₂ O%	Soil pH	Litter biomass
Earthworm density	0.17 (0.60)	0.31 (0.33)	-0.62 (0.03)
Earthworm biomass	0.22 (0.48)	0.34 (0.28)	-0.59 (0.04)

active or recently abandoned pastures and woody-species communities (Table 1). Greater litter biomass on the forest floor than on pasture soil suggests that changes in the chemistry, rather than in the quantity, of litter input along successional gradients reduced earthworm density. This supports the observation by Zou (1993) that differences in tree litter chemistry, rather than litter quantity, altered the density of *P. corethrurus* in Hawaiian tree plantations. Higher earthworm density was also found in a meadow field than in a forest of late succession in Czechoslovakia (Pizl, 1992). Results from a ¹⁴C tracer study implied that earthworms may eat live roots as one of their food sources (Cortez and Bouche (1992). The shift from grass-dominated vegetation to woody-species-dominated forest during secondary succession may have drastically reduced the quality of roots and leaf litter upon which worms feed.

Although worm density decreased during secondary succession, the diversity of the worm community increased. Whereas there was only one endogeic worm species in the pasture and grass-vine-fern communities, both endogeic and anecic species were found in the shrub-small tree and forest communities (Table 1). This change in worm community structure is probably related to the changes in organic input from a below-ground dominated pattern to a balanced pattern of both below- and above-ground litter inputs. There was relatively little above-ground litter input in the active pasture and grass-vine-fern community compared with the woody-species-dominated shrub-small tree and forest communities. This change in organic input pattern can affect nutrient status (e.g. N, Ca and Mg) in soils. Decrease in the availability of these soil nutrients was reported to be favored by the epigeic-anecic worm community both in tropical (Fragoso and Lavelle, 1992) and temperate conditions (Muys *et al.*, 1992). The increased above-ground litter input associated with the late successional stages may have triggered the colonization of anecic worm species in these communities. Pizl (1992) also observed that a higher proportion of endogeic worms were observed in meadow than

in forest soils. Controlled experiments are needed to examine the specific mechanisms associated with litter input that trigger the decline in earthworm density and the change in worm community structure during secondary succession in the humid tropics.

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