Effects of post-hurricane fertilization and debris removal on earthworm abundance and biomass in subtropical forests in Puerto Rico

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Abstract

Hurricanes are a common disturbance in the Caribbean, striking the island of Puerto Rico on average every 21 years. Hurricane Hugo (1989) distributed the canopy litter onto the forest floor changing the chemistry and quantity of litter inputs to the soil. In this study, we determined the effect of inorganic fertilization on earthworm abundance, biomass, and species composition in hurricane-damaged subtropical wet (tabonuco) and elfin forests. In addition, the effects of the removal of hurricane-generated litter on earthworm populations were studied in the tabonuco (wet) forest. We found that earthworms were more abundant in tabonuco (El Verde) than in elfin forest (Pico del Este). There was no effect of fertilization on the abundance and biomass of earthworms in the elfin forest. In the tabonuco forest, the density and biomass (fresh and dry) of total and endogeic earthworms was significantly greater in the control than in the fertilization treatments. The removal of hurricane-generated debris significantly increased the density of total and endogeic earthworms in the tabonuco forest. The results from the subtropical wet forest (tabonuco) in this study support the contention that earthworm density and biomass can be decreased by fertilization via changes in soil acidity. Available N, higher soil pH and reduction of the litter fauna might explain differences in abundance in litter removal treatments as compared to fertilized and control plots at this site.

Resumen

Los huracanes son un disturbio común en el Caribe, golpeando la isla de Puerto Rico en promedio cada 21 años. El huracán Hugo (1989) distribuyó la hojarasca del dosel al piso del bosque, cambiando así la química y la cantidad de entrada de hojarasca al suelo. En este estudio, se determinó el efecto de la fertilización inorgánica sobre la abundancia, biomasa y la composición de especies de lombrices de tierra en bosques subtropicales húmedos y elfinos (nubloso) impactados por el huracán. Además, se estudiaron los efectos de la eliminación de la hojarasca generada por el huracán en las poblaciones de las lombrices de tierra en el bosque de tabonuco (bosque húmedo). Las lombrices de tierra fueron más abundantes en el bosque de tabonuco (El Verde) que en el bosque elfino (Pico del Este). No hubo efecto de fertilización sobre la abundancia y la biomasa de las lombrices de tierra en el bosque elfino. En el bosque de tabonuco, la densidad y la biomasa (fresca y seca) total de las lombrices y de las lombrices endogeas fue apreciablemente mayor en los tratamientos control que en aquellos con fertilización inorgánica. La eliminación de la hojarasca generada por el huracán aumentó apreciablemente la densidad total de las lombrices de tierra, así como también de las especies endogeas en el bosque de tabonuco. Los resultados del bosque húmedo subtropical (tabonuco) en este estudio apoyan la tesis de que la densidad y biomasa de lombrices de tierra pueden ser disminuidas por la fertilización inorgánica vía cambios en la acidez del suelo. La disponibilidad de nitrógeno, un pH de suelo más alto y la reducción de la fauna asociada a la hojarasca quizás expliquen las diferencias en la abundancia de lombrices en tratamientos donde se eliminó la hojarasca generada por el huracán, en comparación con los tratamientos control y de fertilización en este sitio (tabonuco).

Introduction

Natural disturbance is an important element of ecosystems influencing plant and animal community structure and function. Caribbean forests are subject to periodic, large-scale disturbance by hurricanes (Reilly, 1991). On average, the island of Puerto Rico is exposed to the direct impact of hurricanes once every 21 years (Salivia, 1972). In September 1989, Hurricane Hugo defoliated extensive areas of the Luquillo Experimental Forest in northeastern Puerto Rico. It distributed the canopy litter and increased the amount of light reaching the forest floor (Photo 3.1). It also changed the chemistry and quantity of litter inputs to the soil. In heavily damaged areas, the amount of fine litterfall and associated nutrients reaching the forest floor during this single storm event was more than a year's normal input (Lodge et al., 1991). Subsequently, there was a reorganization of most terrestrial and aquatic communities largely due to changes in the microclimate and food sources (Waide, 1991). Nevertheless, the controls affecting a biotic response following disturbance can vary depending on the physical characteristics of a site, in addition to the species–specific characteristics (Walker et al., 1996).

Photo 3.1. Hurricanes distribute the canopy litter and increase the amount of light reaching the forest floor. (Photo C. Estrada)

Earthworms are among the most important macro-decomposers in tropical wet forests (Anderson & Swift, 1983), where they are important regulators of soil processes (e.g., Lee 1985; Edwards & Bohlen, 1996; González, 2002). Indeed, faunal effects on litter breakdown can reach up to 66% of the total in the wet tropics, mainly due to earthworms (González & Seastedt, 2001). Previous research in Puerto Rico indicated that the density, biomass and community structure of earthworms is affected by anthropogenic disturbances (Zou & González, 1997; González et al., 1996). Forest management practices (e.g., site preparation, tree species selection, fertilization, harvesting or allowing natural succession to proceed) can affect the abundance and community structure of earthworms differently via pathways that involve changes in soil properties and plant litter quantity and quality (González et al., 1996; Zou & González, 2001).

Very little information has been gathered on the effects of natural disturbances (in particular, hurricanes) on earthworm populations in tropical regions. Given that: 1) hurricane intensity is predicted to increase due to global climate change (Knutson et al., 1998; Goldenberg et al., 2001); 2) available data indicate that earthworms are important drivers of complex ecological processes in the tropics; and 3) organismal responses can depend on site characteristics (Walker et al., 1996), it is important to understand how nutrients and hurricane associated-debris inputs into the soil can affect earthworm abundance, biomass and community structure. Therefore, in this study we determined the effect of inorganic fertilization on earthworm abundance, biomass and species composition in two hurricane-damaged forests: a subtropical wet and an elfin (cloud or dwarf) forest. In addition, the effects of the removal of hurricane-generated litter on earthworm dynamics was examined in the tabonuco (wet) forest.

Methods

Study sites

This study was part of an extensive long-term project focusing on the recovery of subtropical forests from hurricane damage. It was conducted in a subtropical wet (tabonuco) and a subtropical rain (elfin) forest within the Luquillo Experimental Forest in Northeastern Puerto Rico (18°18'N, 65°50'W). The subtropical wet forest is located near El Verde Field Station at an elevation of 350-500 m. Mean annual air temperature near this site (Luquillo) is 22.3°C (Brown et al., 1983), and mean annual precipitation 3524 mm (García-Martinó et al., 1996), with rainfall distributed more or less evenly throughout the year. The vegetation in the wet forest was dominated by tabonuco trees (*Dacryodes excelsa* Vahl) (Zimmerman et al., 1995). The soils are classified as very fine, kaolinitic, isohyperthermic Typic Kandiudox, belonging to the Zarzal series (Soil Survey Staff, 1995). The elfin forest study site was located in Pico del Este. The vegetation is closed broadleaf evergreen (FAO, 1998; Ahern et al., 1999), classified as the elfin woodland forest type or alliance (Weaver, 1994) and montane subtropical cloud forest formation (Gould et al., 2006). It is a gnarled, epiphyte laden, and dense forest type characterized by closely spaced, stunted trees with a high percentage of endemics (Gould et al., 2006). Located at an elevation of about 1051 m, the forest receives a mean annual precipitation of 4200 mm. Mean monthly temperatures range between 17 and 20°C (Brown et al., 1983). The soils are silty loams, in the Ultisol order and the Guayabota series, commonly saturated with low permeability (Brown et al., 1983).

Experimental design

The main experimental design of this study follows that already described by Zimmerman et al. (1995), Walker et al. (1996), and Halleck et al. (2004). In general terms, field plots were established within 4 wk after the passage of Hurricane Hugo. In El Verde (tabonuco, wet forest), four randomized blocks were established and each block included three treatments: control, fertilization and litter removal. The blocks were located along ridges < 30° slope, and within blocks the plots were located < 100 m apart. Each of the 12 plots was 20 x 20 m with a central 10 x 10 m-plot where measurements were taken. All organic debris (woody debris, branches and pre- and post-hurricane leaf litter) was removed from the litter removal plots once, at the beginning of the experiment. No woody or litter debris was removed from the fertilization and control plots. Inorganic fertilization treatments were applied to the ground surface of the fertilization plots in October 1989 and subsequently at approximately every three months. Nutrients were added at an annual rate of 300 kg ha^{-1} N, 100 kg ha^{-1} P, 100 kg ha^{-1} K, 19 kg ha^{-1} Mg, 25 kg ha^{-1} Mn, 26 kg ha^{-1} Zn, 15.4 kg ha^{-1} Cu, 2.2 kg ha^{-1} Fe, and 8 kg ha^{-1} B.

The experimental design in Pico del Este (elfin forest) resembled that of El Verde without the litter removal treatment (Figure 3.1). Twelve 9 x 14 m-plots (samples taken on a central 5 x 5 m plot) were located along a slope near a ridge top at least 5 m apart. Adjacent pairs of plots (blocks) were assigned randomly to two treatments: control and fertilization. Nutrients in Pico del Este were added at the same rate as at El Verde and starting in April 1990. The N added in the fertilization treatments represents three times the normal leaf litter inputs in El Verde and about 15 times that in Pico del Este (Lodge et al., 1991).

Measurements

Earthworms were sampled three times from the El Verde and Pico del Este plots in April and July 1996, and in January 1997. On each sampling date, earthworms were collected from four 25 x 25 cm subplots within each plot, located along a transect across the plots parallel to its slope, with an interval of about 2.5 m in El Verde and 1.5 m in Pico del Este. Although earthworm samples could be auto-correlated if taken within 5-10 m distance (Rossi, 2003), there is a highly clumped spatial pattern of earthworms in these forests (González et al., 1999) showing a high variability in earthworm abundance that includes many zero values. Thus, 48 subplots per forest type (2) were sampled during each of the three collecting dates; for a total of 288 subplots sampled. Earthworms were collected by hand-sorting the soils to a depth of 25 cm and stored in a cooler with ice. After returning to the laboratory, worms were grouped by species, recorded in numbers per subplot, and weighed for fresh biomass determinations after being rinsed with water and dried with paper towel on the same date of collection. All worm specimens were preserved in 10% formaldehyde. Worms were classified according to Bouché (1977) into three categories: epigeic, anecic, and endogeic. Soil water content was determined for each subplot by oven drying 10 g of fresh sample at 105°C for 48 hrs and reported on the oven-dry basis. Soil pH was measured using a paste of 1:1 ratio of fresh soil and deionized water. Litter production was monitored in litter baskets (1.6 m^2 total surface area; at 1 m height from the ground floor) randomly placed within the inner plots (10 baskets within 10 x 10 m at El Verde and 6 baskets within 5 x 9 m at Pico del Este). Litterfall was collected every two weeks, dried at 60°C to constant mass, sorted into leaves, wood, and miscellaneous and weighed. Litterfall rates were calculated in g m^{-2} d^{-1} for the months when earthworms were sampled.

Statistical analyses

All statistical analyses were performed using the software SPSS© (SPSS 11.5, Windows 2002). The significance level was set at $\alpha = 0.05$. Data were tested for homogeneity of variance by

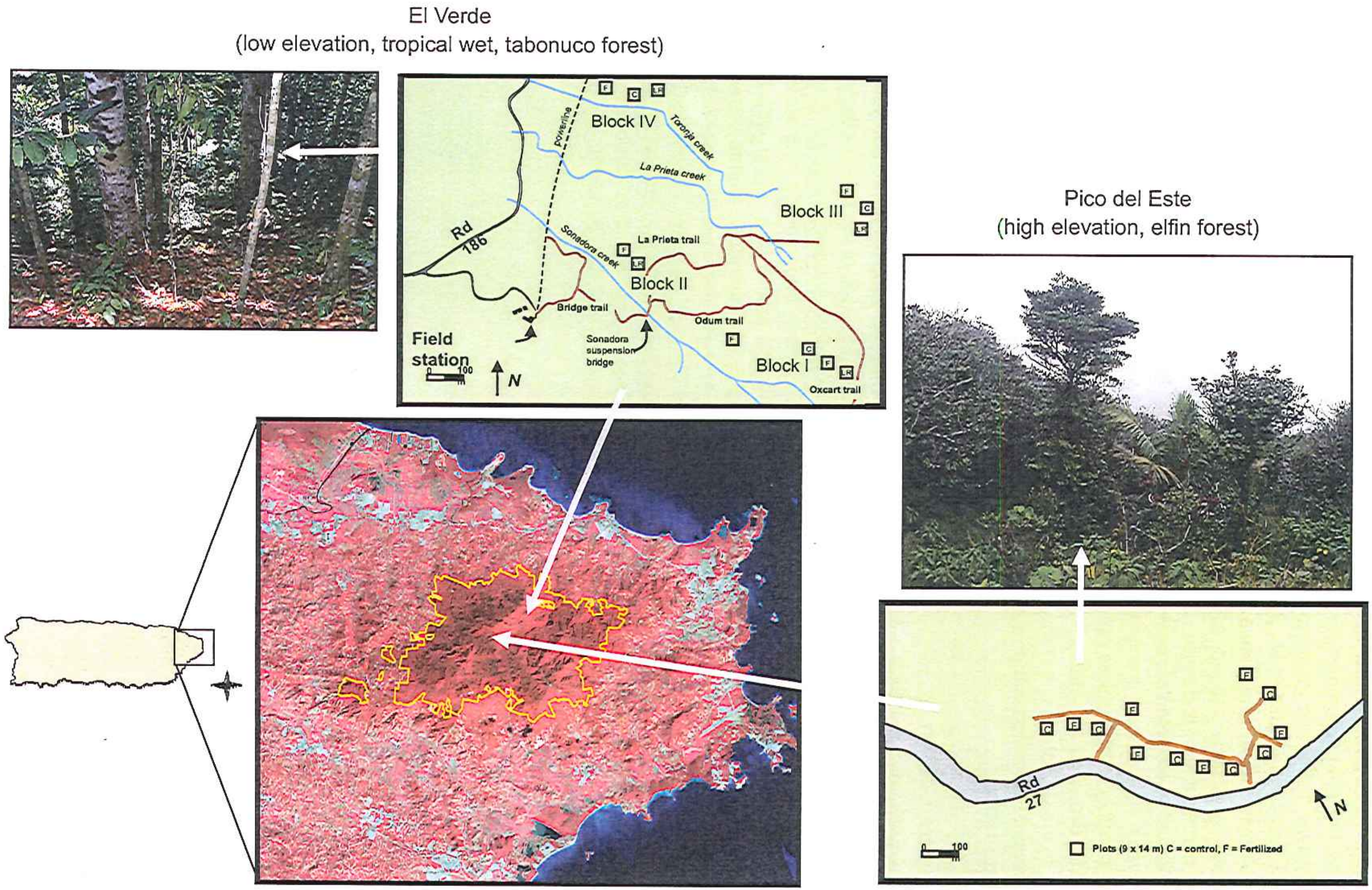

Figure 3.1. Map and plot layout of the study sites, El Verde and Pico del Este located in the Luquillo Mountains, Northeastern Puerto Rico. Scale in meters. (Photos G. González)

using Levene's test of equality of error variances, and skewness. A multivariate analysis of variance (MANOVA) was performed to examine the effects of forest type (El Verde and Pico del Este), treatment (Control *vs.* Fertilization) and date of collection (independent variables) on the density and biomass (fresh and dry) of total, endogeic, and anecic earthworms (dependent variables). One-way ANOVAs were performed to observe differences in earthworm density and biomass (fresh and dry), mean litterfall, soil pH and water content for treatments within each forest type. A simple linear correlation analysis was performed among the abundance, and biomass (fresh and dry) of total, endogeic, and anecic earthworms and litterfall, soil pH and water content.

Results

Overall, there was a significant effect of forest type, fertilization, and of the interaction of forest and fertilization on the density and biomass of earthworms (Table 3.1). We found earthworms were more abundant in El Verde (tabonuco) than in Pico del Este (elfin forest) (Table 3.2, Figure 3.2A). In El Verde, the density and biomass (fresh and dry) of total and endogeic earthworms was significantly greater in the control than in the fertilization treatments (Figure 3.2). However, there was no treatment effect on the density and biomass of earthworms in Pico del Este. Endogeic earthworms, mainly *Pontoscolex corethrurus*, dominated the density and biomass of total earthworms in El Verde but not in Pico del Este (Figure 3.2). At El Verde (tabonuco forest), total and endogeic earthworm abundance was significantly higher in the litter removal plot and lower in the fertilization treatment when compared to the control plots (Figure 3.3A). The fresh and dry biomass of total earthworms was not significantly different in the litter removal and the control treatments but was lowest in the fertilization treatment in El Verde (Figure 3.3B and C); a similar pattern was found for the fresh biomass of anecic and endogeic earthworms.

Overall, there was a significant effect of sampling date on earthworm populations, as well as a significant date x treatment and date x forest interaction (Table 3.1). In general, the abundance of earthworms was lowest in July (23 individuals m^{-2} *vs.* 38 individuals m^{-2} in April and 43 individuals m^{-2} in January). Yet, when the data on earthworm

Table 3.1. Effects of forest type (Pico del Este and El Verde), treatment (Control *vs.* Fertilization) and sampling date (April, July 1996, and January 1997) on the density and biomass (fresh and dry) of total, endogeic, and anecic earthworms in the Luquillo Mountains of Puerto Rico.

Source	df	*F*	*P*	Power
Forest (F)	9	11.94	0.000	1.00
Treatment (T)	9	4.81	0.000	0.99
Date (D)	18	3.08	0.000	0.99
F x T	9	3.24	0.001	0.98
F x D	18	2.69	0.000	0.99
T x D	18	1.66	0.045	0.94
F x T x D	18	1.37	0.145	0.87

Statistical values are based on 3-way MANOVA (n = 168) using a Pillai's Trace test.

Table 3.2. Partial results of test of between-subject effects for forest type (Pico del Este and El Verde) and treatment (Control *vs.* Fertilization) on the mean density and biomass of total, anecic, and endogeic earthworms (MANOVA, n = 168) for the three sampling dates. Numbers in bold font represent a significant probability value <0.05.

Source	Dependent variables	*P*	Power
Forest	Density		
	- Total	**0.00**	1.00
	- Anecic	0.20	0.25
	- Endogeic	**0.00**	1.00
	Fresh Biomass		
	- Total	0.50	0.10
	- Anecic	0.70	0.07
	- Endogeic	**0.00**	1.00
	Dry Biomass		
	- Total	0.52	0.10
	- Anecic	0.60	0.08
	- Endogeic	**0.00**	1.00
Treatment	Density		
	- Total	**0.00**	0.98
	- Anecic	0.09	0.40
	- Endogeic	**0.00**	0.82
	Fresh Biomass		
	- Total	0.87	0.05
	- Anecic	0.96	0.05
	- Endogeic	**0.04**	0.56
	Dry Biomass		
	- Total	0.77	0.06
	- Anecic	0.96	0.05
	- Endogeic	**0.02**	0.65

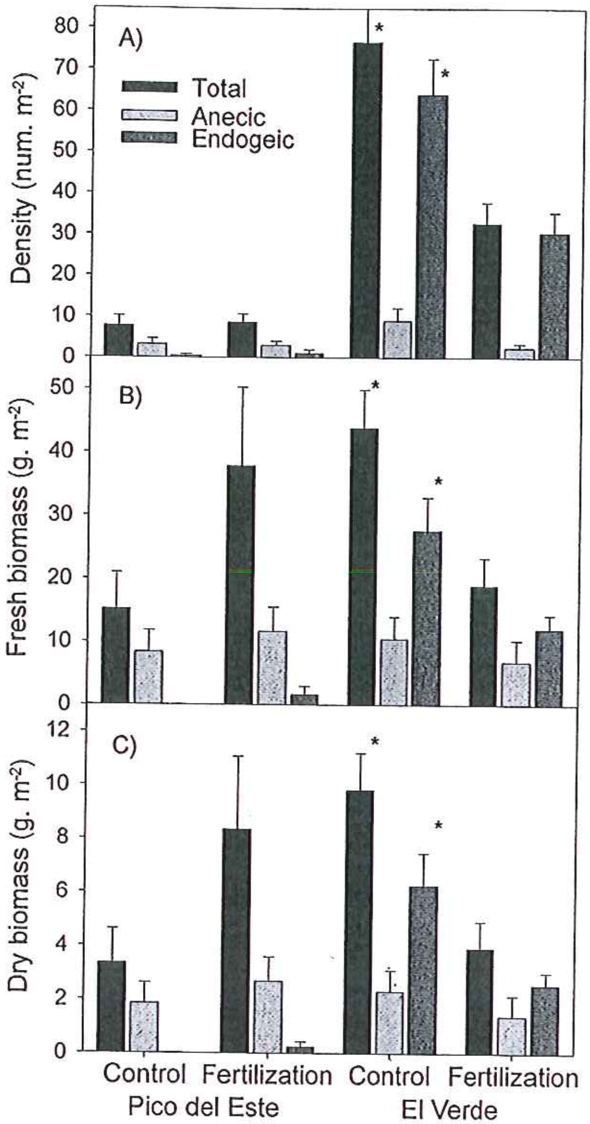

Figure 3.2. Mean A) Density, B) Fresh biomass and, C) Dry biomass of total, anecic and endogeic earthworms in Control and Fertilization treatments over three sampling dates in Pico del Este and El Verde. Asterisks (*) indicate significant differences between treatments within a forest and earthworm category (1-ANOVA's / GLM; ∝ = 0.05).

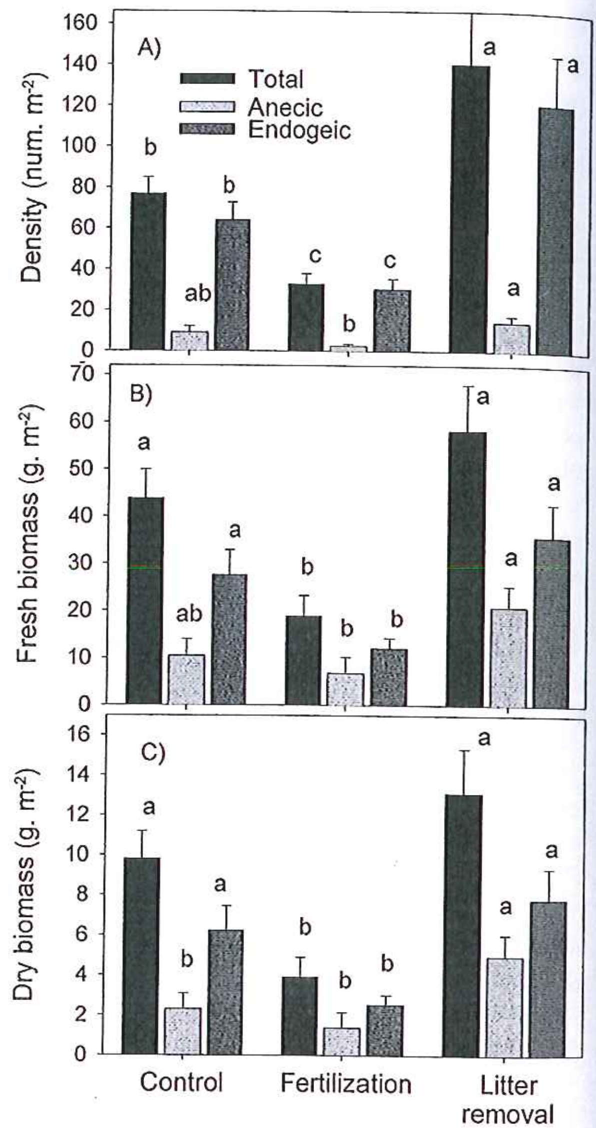

Figure 3.3. Mean A) Density, B) Fresh biomass and, C) Dry biomass of total, anecic and endogeic earthworms in Control, Fertilization and Litter removal treatments over three sampling dates in El Verde. Common letters within an earthworm category indicate no significant differences between treatments (MANOVA / SNK; ∝ = 0.05; n = 48).

abundance and biomass were analyzed by forests, there was no effect of date on earthworm populations in Pico del Este (data not shown). In El Verde, earthworm density and biomass was highest in January (Table 3.3). Overall, the density and biomass of endogeic earthworms did not differ among collecting dates. The density (ranging from 1 to 7 earthworms / m^{-2}) and biomass (ranging from 2.1 to 13 g / m^{-2}) of anecic worms was lowest in April. Litterfall rates were higher in El Verde than in Pico del Este at the time of this study (Table 3.4). Total litterfall, leaf fall and wood fall were significantly greater in the fertilization than in the control plots in Pico del Este. However, litterfall rates did not differ among the treatments at El Verde. On average, soils at El Verde were more acidic than in Pico del Este (Table 3.4). There was no effect of treatment on soil pH in Pico del Este nor soil water content at either site. In El Verde, soil pH was lower in the fertilization than in the control and litter removal plots (Table 3.4). The density of total and endogeic earthworms and the fresh and dry biomass of endogeic earthworms

Table 3.3. Mean density (individuals.m^{-2}), and fresh biomass ($g.m^{-2}$) (±1 SE in parenthesis) of earthworms in El Verde.

Variable	Treatment	Sampling date			Mean
		April 1996	July 1996	January 1997	
Density	Control	86.0 (11.8) bAB	42.0 (7.7) aA	102.0 (17.4) bB	76.67 (8.2)
	Fertilization	32.0 (8.5) aA	28.0 (8.7) aA	38.0 (9.7) aA	32.7 (5.1)
	Litter removal	160.0 (60.9) aB	121.0 (41.2) aB	140.0 (27.9) aB	140.3 (25.8)
Fresh Biomass	Control	44.2 (8.9) aA	27.9 (8.3) aA	59.4 (12.8) aB	43.8 (6.1)
	Fertilization	11.6 (5.0) aA	29.2 (11.4) aA	15.7 (4.0) aA	18.8 (4.4)
	Litter removal	38.4 (17.6) aA	65.1 (17.6) aA	71.1 (15.4) aB	58.3 (9.8)

Common capital letters within each column, variable and sampling date represent a non significant effect of treatment; common lower case letters within a row (treatment) represent a non significant effect of sampling dates on the density or fresh biomass of earthworms (n = 12, 1-AOVs; α = 0.05).

Table 3.4. Mean litterfall (±1 SE; $g.m^{-2}.d^{-1}$), soil pH and water content (WC, % ±1 SE in parentheses) in Control (C), Fertilization (F) and Litter Removal (LR) treatments in Pico del Este and El Verde forests in April and July 1996, and January of 1997.

Source	Pico del Este		El Verde		
	C	F	LR	C	F
Total litterfall	0.47 (0.07)b	0.64 (0.09)a	2.38 (0.42)	1.93 (0.28)	1.79 (0.20)
- Leaf fall	0.40 (0.06)b	0.53 (0.08)a	2.13 (0.39)	1.62 (0.24)	1.49 (0.19)
- Wood fall	0.03 (0.01)b	0.06 (0.02)a	0.17 (0.03)	0.16 (0.24)	0.19 (0.06)
- Misc. fall	0.04 (0.01)	0.06 (0.01)	0.08 (0.02)	1.15 (0.06)	0.10 (0.02)
pH	5.03 (0.07)	4.96 (0.12)	4.77 (0.03)a	4.92 (0.08)a	4.05 (0.06)b
WC	113.09 (7.58)	100.15 (9.17)	77.34 (4.03)	69.08 (3.45)	74.54 (4.03)

Note: Different letters within a forest indicate significant treatment effect (∝ = 0.05, ANOVA).

were significantly and positively correlated to the mean total litterfall, leaf fall and wood fall. Soil water content was negatively correlated to the density of total and endogeic earthworms (Table 3.5).

Discussion

The present study sought to understand how nutrient inputs affect earthworms in two hurricane-damaged forests. We found that inorganic fertilization significantly reduced earthworms in the tabonuco (subtropical wet) forest but had no effects on earthworms in the elfin forest. Research on the effects of forest fertilization on earthworm communities in tropical regions is lacking though it has been extensively studied in temperate regions, particularly in grasslands and agricultural ecosystems. From those studies, fertilization is thought to have a generally positively effect on earthworm populations indirectly, via an increase in plant production (Edwards & Bohlen, 1996). When organic fertilizers are applied alone (Marshall, 1977) or in combination with inorganic fertilizers (e.g., Tiwari, 1993), earthworm density and biomass can increase. However, chemical fertilization may either increase or decrease earthworm density and biomass. For instance, nitrogen additions without changes in soil pH can increase earthworm communities via increases in plant production and improvement in litter quality (Zou & González, 2001). Nevertheless, application of acidifying N-fertilizers for long periods in the absence of liming may have deleterious effects on earthworms due to changes in soil acidity (Ma et al., 1990). In the present experiment, soil pH was significantly lowered by fertilization in the tabonuco forest but was not different in both control and fertilized plots in the elfin forest. Soil pH has been shown to be an important factor determining the sensitivity and distribution of earthworm species (Laverack, 1961, 1963; Piearce, 1972; Standen, 1979). Thus, our results from the subtropical wet forest (tabonuco) are consistent with the contention that earthworm density and biomass can be decreased by inorganic fertilization via changes in soil acidity. However, the lack of fertilization

Table 3.5. Pearson correlation coefficients (*r*, n = 72) for the density and biomass of total, anecic and endogeic earthworms and mean total litterfall, leaf fall, wood fall, and miscellaneous fall ($g.m^{-2}.d^{-1}$), soil pH and water content (WC, %).

Variables	Density			Fresh biomass			Dry biomass		
	Total	Anecic	Endogeic	Total	Anecic	Endogeic	Total	Anecic	Endogeic
Total litterfall	**0.58**	0.12	**0.60**	0.16	0.01	**0.51**	0.16	0.17	**0.50**
- Leaf fall	**0.59**	0.11	**0.61**	0.14	-0.01	**0.50**	0.14	0.13	**0.49**
- Wood fall	**0.32**	0.14	**0.33**	0.18	0.22	**0.38**	0.18	0.37	**0.38**
- Misc. fall	0.09	-0.03	0.09	0.13	-0.05	0.14	0.13	0.08	0.15
pH	-0.21	0.02	-0.28	-0.07	0.11	-0.15	-0.07	0.02	-0.14
WC	**-0.35**	-0.26	**-0.38**	-0.09	-0.08	0.13	-0.12	-0.29	-0.31

Numbers in bold font represent correlation coefficients with a significant two-tailed probability value <0.05.

effect on earthworms in the elfin forest contradicts the general notion that fertilization can increase earthworm populations via increases in plant productivity, since litterfall rates where higher in the fertilization than in the control treatment in the elfin forest. Nonetheless, these results tend to support those of Walker et al. (1996), who found that the nature of the organismal response (earthworms in this case) was dependent on the species and also on site characteristics. Furthermore, we deduce that acidification via fertilization in this subtropical wet forest can deleteriously affect the density and biomass of euryoecic (exotic species best adapted to unsuitable edaphic conditions, Fragoso et al., 1999) endogeic species as *P. corethrurus*, that dominated the density and biomass of total and endogeic earthworms in the tabonuco forest.

Surprisingly, we found that the removal of hurricane-generated debris (mostly coarse woody material) significantly increased the density of total and endogeic earthworms. The possible reasons for the increased earthworm density in the litter removal treatment at El Verde may be due to: 1) increased nitrogen availability in the litter removal soils (Zimmerman et al., 1995); 2) less leaching of organic compounds from coarse wood (Zalamea-Bustillo, 2005), and consequently, increased soil pH; and 3) reduction of the litter fauna (e.g., frogs, ants, lizards) that function as both competitors for resources and predators. Regardless of the mechanisms that might explain the differences in earthworm density in the litter removal treatment as compared to the control or fertilization plots in El Verde, this study indicates that hurricanes can have persistent effect on earthworm communities over the long term (in this case lasting six years after litter manipulation).

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