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A canopy trimming experiment in Puerto Rico: The response of litter decomposition and nutrient release to canopy opening and debris deposition in a subtropical wet forest

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ABSTRACT

In this study, we used a replicated factorial design to separate the individual and interacting effects of two main components of a severe hurricane – canopy opening and green debris deposition on leaf litter decay in the tabonuco forest in the Luquillo Mountains of Puerto Rico. We quantify changes in percent mass remaining (PMR), the concentration and absolute amounts of various chemical elements using fresh (green) and senesced leaf litter contained in litterbags of two different mesh sizes. Mass loss was significantly slowed by canopy trimming. There was no significant effect of debris treatment on the PMR of the litter. Canopy trimming increased the percent of initial N, Al, Ca, Fe, and Mg remaining and decreased the percent of initial Mn remaining compared with not trimmed plots. Debris addition increased the percent of initial N and P remaining and decreased the percent of initial Al, and Fe remaining in the decomposing litter compared to no debris added plots. Of the elements studied, only Al and Fe accumulated above 100% of initial. Accumulation of Al and Fe in the canopy trimmed and no debris plots is most likely dominated by the adsorption of these ions onto the surfaces of the decaying litter. Overall, P showed a rapid initial loss during the first 0.2 yr followed by steady loss. Nitrogen was lost steadily from leaf litter. The PMR of fresh and senesced litter was significantly affected by mesh size, with a higher mass remaining in small mesh bags. Fresh litter decayed faster than senesced litter; following patterns of initial N and P concentrations (higher in the former litter type). We found a significantly negative correlation between the Margalef index of diversity for the litter arthropods contained in the litterbags and the PMR, suggesting functional complexity is an important determinant of decay in this forest. Our results imply hurricanes can differentially impact litter decomposition and associated nutrient release via canopy opening and litter inputs.

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1. Introduction

The release of nutrients from decomposing litter is an important pathway of nutrient flux in forested ecosystems (Blair, 1988). Resource quality, decomposer organisms, and physico-chemical conditions influence the decomposition of litter residues and hence the recycling of nutrients. Resource quality is defined by the chemical composition of the plant residues such as C:N ratio, lignin and polyphenol contents (Melillo et al., 1982; Palm and Sanchez, 1991; Tian et al., 1997). Physico-chemical conditions include both climate and parent material, and help determine abiotic soil characteristics that in turn influence litter quality and, ultimately, the activity and composition of microbial and invertebrate communities (Wardle and Lavelle, 1997). Although decomposition is mainly the result of microbial activities, invertebrate fauna are important in shredding and consuming litter, and producing frass, therefore stimulating microbial actions (Coleman and Crossley, 1996). Conversely, microbiovores such as Collembola and Psocoptera, specialist grazers of microfungi on litter surfaces, may potentially reduce microbial activity. Thus, the rate at which nutrients are released depends on various factors, including the initial amounts of nutrients in the litter, the structural (molecular) nature of the nutrients in the litter matrix, the microbial demand for the nutrient, the availability of exogenous sources of the nutrient (Seastedt, 1984; Blair, 1988) and the faunal community composition.

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Hurricanes defoliate canopy species and deposit large amounts of canopy biomass (debris) onto the forest floor (Walker et al., 1991; Everham and Brokaw, 1996). Such disturbance may increase nutrient losses from the forest depending upon how the debris is managed, how the microbiota responds to the disturbance and the chemical and physical characteristics of the soil (Miller and Lodge, 2007). Canopy disturbances associated with severe hurricane storms dramatically alter patterns in litterfall and associated nutrient cycling (Scatena and Lugo, 1995; Lugo and Scatena, 1996). For example, leaf litterfall in the Luquillo Mountains of Puerto Rico from Hurricanes Hugo (1989) and Georges (1998) was 0.55–0.93 times the annual rate, resulting in a 120–250% increase in forest floor standing stocks (Lodge et al., 1991; Ostertag et al., 2003). Unlike regular litter, hurricane litter contains a high proportion of green leaves from which nutrients have not been translocated, thus altering litter quality in the forest floor (Richardson et al., 2010). Canopy openings also increase the amount of solar radiation reaching the forest floor, ultimately altering the forest floor temperature and moisture conditions (Richardson et al., 2010).

Some studies, particularly in northern hardwoods, on forest ecosystem recovery in clear-cut watersheds have demonstrated, or at least implied, that decomposition rates accelerate after the disturbance (Aber et al., 1978; Covington, 1981). In contrast, studies on decomposition of leaf litter and woody debris in a clear-cut watershed at Coweeta Hydrological Laboratory, North Carolina, USA, have indicated that decomposition rates were lower than in an adjacent undisturbed control watershed (Seastedt, 1979; Abbott and Crossley, 1982; Blair and Crossley, 1988). Similarly in tropical forests, studies of litter decomposition associated with canopy openings (either via hurricanes or treefall gaps) have shown varied results. For example, Ostertag et al. (2003) found rapid disappearance of hurricane inputs in tropical forests representing three lifezones in Puerto Rico after the passage of Hurricane Georges. They found short-term increases in the concentrations of nitrogen, phosphorus, calcium, and magnesium in litter in a moist forest, but nutrient concentrations generally decreasing in palm (*Prestoea montana*) and tabonuco (*Dacryodes excelsa*) forests. These results led them to suggest decomposition rates were not accelerated by the hurricane as relatively high decomposition rates are typical of tropical forests (Anderson and Swift, 1983). In contrast, Sullivan et al. (1999) found mass loss of tabonuco and *Cyrilla racemiflora* leaves were lower after Hurricane Hugo than before the hurricane while conducting a short term experiment (<0.5 yr) in Puerto Rico. Meanwhile, both Denslow et al. (1998) and Luizão et al. (1998) found the decomposition of litter material was not accelerated in canopy openings created by tree fall gaps as compared to intact forests in Costa Rica and Brazil, respectively. Thus, to establish whether or not disturbance immediately accelerates or decreases litter decay rates in a tropical forest, and influences differentially the dynamics of associated nutrients in the litter, we used a replicated factorial design to separate the individual and interacting effects of two main components of a severe hurricane – canopy opening and green debris deposition, in the tabonuco forest in the Luquillo Mountains of Puerto Rico. This was part of a large-scale experiment, the first of its type (the canopy trimming experiment, CTE), designed to decouple the abiotic and biotic effects of hurricane-type disturbance in a subtropical wet forest and investigate their effects on forest recovery, in a multi-disciplinary approach.

The practical objectives of this present study were to quantify changes through time in percent mass remaining (PMR), the concentration and absolute amounts of nitrogen, phosphorus, aluminum, calcium, iron, potassium, magnesium, manganese, sodium and sulfur using fresh (green) or senesced leaf litter contained in litterbags of two different mesh sizes. Fresh or senesced leaf litter (high vs. lower quality litter, respectively) was used to study the effects of litter types and differences in initial elemental concentration on PMR associated nutrient dynamics. Although the decomposition of green leaves has undergone extensive study in highly managed forest systems, the influence of natural greenfall deposition in forest ecosystems has received relatively little attention (Fonte and Schowalter, 2004). Furthermore, using litterbags with different mesh sizes allows access of particular organisms, which can help elucidate the effects of litter microarthropods on PMR-associated nutrient dynamics. In this study, we study the impacts of disturbance on a broad array of nutrients to document the effects on the various pools and rates process. Details of the diversity, abundance, and community composition of micro- and mesoarthropods extracted from these litterbags before chemical analysis, and the microclimate changes associated with canopy opening, including litter and soil moisture in the plots, are already published (Richardson et al., 2010). The data are not, therefore, repeated in this paper. However, in this study, for the first time in the CTE, we correlate characteristics of litter microarthropod community with litter decay and the associated nitrogen remaining.

2. Methods

2.1. Study site

The Luquillo Experimental Forest (LEF) (also known as El Yunque National Forest), is located in hurricane-prone northeastern Puerto Rico (Fig. 1). The canopy trimming experiment (CTE) plots are within mature tabonuco (*D. excelsa* Vahl) forest (subtropical wet forest in the Holdridge System; Ewel and Whitmore, 1973), near El Verde Field Station (EVFS, 18.321°N, 65.820°W) at 340–485 m a.s.l. Annual rainfall is approx. 3.5 m (García-Martinó et al., 1996), with about 97 rainless d/yr. Rainfall is weakly seasonal, with a 'dryer' season between December and March (most commonly March) (http://lternet.edu/data/lterdb14/data/). Litterfall has a main peak from March–June, a secondary peak in September, and minima from December–February (Zou et al., 1995; Lawrence, 1996; Zalamea and González, 2008). Annual mean monthly temperatures (1975–2004) range between 20.6 and 25.8 °C, with an annual mean of 23.0 °C (SD = 1.9 °C) (http://lternet.edu/data/lterdb16/data/).

2.2. The canopy trimming experiment

The experiment has been described in detail by Zalamea and González (2008), Richardson et al. (2010), Shiels et al. (2010), and Shiels and González (2014). Three blocks (A, B and C) were established in the research area (see Fig. 1), each with four 30×30 m plots. A factorial 2×2 experimental design was used with two levels of canopy trimming and two levels of debris manipulation in all combinations as follows

(1) **Canopy not trimmed and no canopy debris added** to the forest floor **(No Trim + No Debris; NT + ND)**: This represents the "reference" or "background" condition without any disturbance.
(2) **Canopy not trimmed and canopy debris** from a trimmed plot added on the forest floor **(No Trim + Debris; NT + D)**: This simulates the changes in redistribution of biomass created by a hurricane without canopy disturbance.
(3) **Canopy trimmed and no canopy debris added** to the forest floor **(Trim + No Debris; T + ND)**: This simulates the changes in canopy openness created by a hurricane without the associated redistribution of biomass.
(4) **Canopy trimmed and debris added** to the forest floor **(Trim + Debris; T + D)**: These are two of the main variables

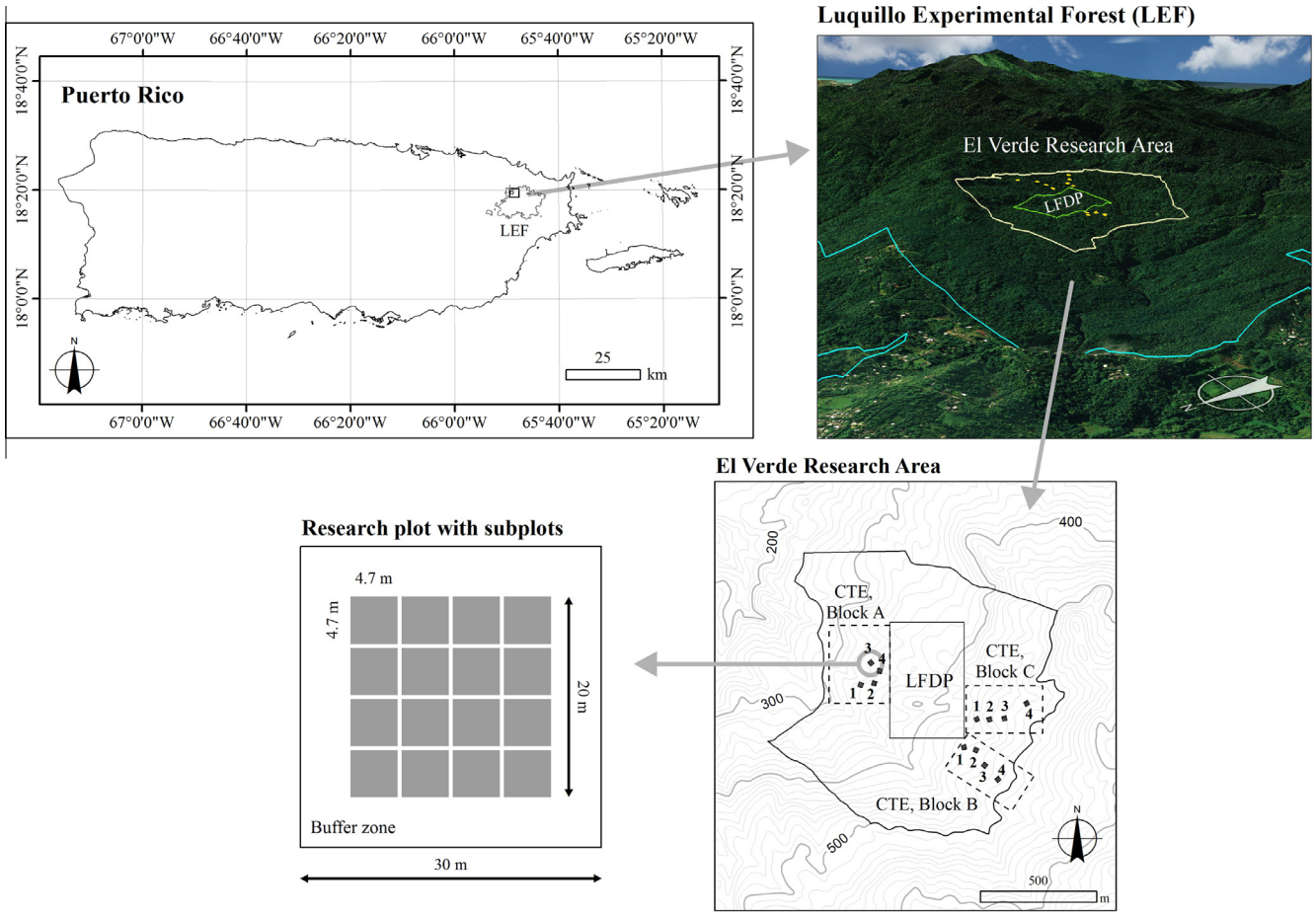

Fig. 1. Location and details of the CTE site in the Luquillo Experimental Forest, NE Puerto Rico.

affected by a hurricane; changes in canopy openness and redistribution of biomass from the canopy into the forest floor.

Treatment combinations were randomly assigned to plots within each block established in tabonuco forest with similar land-use history, soil type and vegetation (>80% cover in 1936; Foster et al., 1999; Thompson et al., 2002). In all plots existing litter was left in place. The interior 20 × 20 m of each plot was used for measurements.

2.3. Canopy Trimming and debris redistribution

Professional arborists carried out the canopy trimming. The trimming, weighing and application of debris lasted from 26 October 2004 to 16 June 2005. Two plots in each block were trimmed and two were not trimmed. Treatment implementation was slowed by adverse weather, and the extremely large amount of material that had to be collected, weighed and redistributed manually. All trees larger than 15 cm dbh had limbs and stems smaller than 10 cm diameter removed. All trees between 10 and 15 cm dbh were trimmed at 3 m height. Palms (*P. montana*) had leaves reaching above 3 m trimmed, and the apical meristem was preserved. All material removed from the canopy of each trimmed plot (debris) was collected, segregated as leafy twigs, wood and palm, and weighed. Subsamples of each debris category were dried at 45 °C, and reweighed to establish wet/dry weight ratios. In each block, after weighing, debris from one trimmed plot was returned to that plot, and evenly distributed. Debris from the other trimmed plot was removed and redistributed to one of the two not trimmed plots. Where there were large differences in amounts of material from the two trimmed plots in a block, the amount of debris returned to the two with-debris plots was evened out. Approximately 10 t fresh weight of vegetation was removed from each plot (ca. 111 t per ha), weighed and redistributed (approximately 39% leafy twigs, 55% wood and 6% palm fronds initially, by fresh weight). Mass losses that occurred between trimming and redistribution were consistent across blocks for wood (11.6%) and palm (16.1%). Green leaves suffered some herbivory but, as material had been stored and moved on tarpaulins, nutrients in the form of frass were returned to the plots. The amount of debris added to each of the six debris-addition plots was approximately 5.4 t dry weight, equivalent to 60 t per ha, composed of approximately 34% leafy twigs, 60% wood and 6% palm fronds (by fresh weight).

2.4. Litterbags and Invertebrate Collection

Litterbags (14.5 × 14.5 cm) were of large (1.8 mm) or small mesh (0.47 mm). They contained air-dried pre-weighed green (fresh) or senescent leaves (approx. 6.0 g per bag), composed of a mixture of plant species that were collected to match the same proportion as their representation in natural litterfall (Zalamea and González, 2008). The leaves were stored in the laboratory for several months prior to litterbag construction. The contents of the each litterbag (on a dry mass basis) were individually weighed out and were represented by: 51% of the most common species (*D. excelsa*, *Manilkara bidentata*, *P. montana*, and *Buchenavia tetraphylla*), 20% were the seven next most frequent species, and the remaining

29% were 19 less frequent species (see Table 1). Fresh leaves are considered higher quality than the senesced litter given significantly higher concentrations of nitrogen (N), and phosphorus (P). Senesced litter consistently had significantly higher concentration of Carbon (C), C:N ratio, and C:P ratio (Table 2) than fresh litter. In addition, fresh leaves had a significantly higher concentration of potassium (K), magnesium (Mg), sodium (Na), and sulfur (S) (Table 2). Litterbags were placed in all 12 CTE plots on 20–23 June 2005, and recovered after 0, 2, 4, 7, 10, 13, 16 and 19 months in the field. The litterbags were put out at the same start period, after all canopy trimming was completed, to avoid confounding results with seasonal variations in replicate blocks that were treated at different times. At the beginning, and at each of 7 subsequent sampling dates, a litterbag for each litter treatment and mesh size was collected from each of five sub-plots (sub-plots are 4.7 × 4.7 m; 1920 litterbags total). The initial subset of litterbags was collected and returned to the laboratory immediately after placement in the field. These bags (240 total, 20 litterbags per site representing the two litter types and mesh sizes) were oven-dried at 60 °C to establish handling loss and dry mass relations (e.g., González and Seastedt, 2001). At the 7 sampling dates invertebrates were extracted from three of the five bags (litterbags collected from three of the five subplots) using Tullgren funnels (see findings reported in Richardson et al. (2010)). After microarthropod extractions, the litter samples were retained for further mass loss and chemistry analysis.

2.5. Chemistry analysis

Litter samples were re-dried at 65 °C and ground to pass through an 18-mesh sieve. Total C and N for the plant tissue samples were determined using the macro dry combustion method by means of the LECO TruSpec CN Analyzer. The ground litter samples were digested using a modification of the method recommended by Chao-Yong and Schulte (1985). This wet oxidation uses concentrated HNO_3, 30 percent H_2O_2 and concentrated HCl and was achieved using a digestion block with automatic temperature control. The digests were analyzed in a Spectro SpectroBlue ICP Emission Spectrometer, for P, aluminum (Al), calcium (Ca), iron (Fe), K, Mg, and manganese (Mn), Na and S. The results are reported as mg g^{-1} on a dry basis at 105 °C. A blank and a certified reference material were analyzed in each batch to ensure the completeness of elemental recovery. A moisture factor correction at 105 °C was determined by the LECO Thermogravimetric Analyzer, model TGA 701 and applied to all reported values. Ash content of the samples at 490 °C was also determined using the LECO TGA 701 Analyzer and reported as a percentage. Litter chemistry was measured in litterbags collected at 0, 2,7,13 and 19 months in the field.

Table 1
Composition of litter species contained in the litterbags. The fraction of total litterfall is based on Zalamea and González (2008).

Species	Fraction of total litterfall	Amount in litterbags (g)
Dacryodes excelsa Vahl	0.24	1.47
Manilkara bidentata (A. DC.) A. Chev.	0.12	0.72
Prestoea montana (Graham) G. Nicholson	0.09	0.55
Buchenavia tetraphylla (Aubl.) R.A. Howard	0.06	0.39
Homalium racemosum Jacq.	0.06	0.34
Rourea surinamensis Miq.	0.03	0.15
Sloanea berteriana Choisy ex DC.	0.02	0.14
Cyrilla racemiflora L.	0.02	0.13
Tetragastris balsamifera (Sw.) Kuntze	0.02	0.13
Schlegelia brachyantha Griseb.	0.02	0.13
Matayba domingensis Radlk.	0.02	0.12
Subtotal	**0.71**	**4.27**
Mix, composed of the following species:	**0.29**	**1.74**
Marcgravia sintenisii Urb.		
Tabebuia heterophylla Britton		
Alchorneopsis floribunda Müll.Arg.		
Inga fagifolia Willd. ex Benth.		
Ficus citrifolia Mill.		
Cecropia schreberiana Miq.		
Guarea guidonia (L.) Sleumer		
Byrsonima spicata Rich. ex Juss.		
Croton poecilanthus Urb.		
Laetia procera (Poepp.) Eichler		
Hirtella rugosa Pers.		
Drypetes glauca Vahl		
Eugenia stahlii (Kiaersk.) Krug & Urb.		
Casearia arborea (Rich.) Urb.		
Micropholis garciniifolia Pierre		
Pinzona coriacea Mart. & Zucc.		
Coccoloba swartzii Meisn.		
Sapium laurocerasum Desf.		
Heteropterys laurifolia Gardn.		

2.6. Calculations and statistical analysis

The maximum amount of N and P accumulated per unit of initial litter mass during the immobilization phase was calculated from the slope and intercept of the linear regression equation between N or P concentration and dry mass remaining. Data of initial points, where lixiviation of soluble compounds occurred, were previously excluded (Aber and Melillo, 1980, 1982; Aerts and de Caluwe, 1997). The slope of the regressions is a measure of the increase in nutrient concentration per unit of C mineralized. From the slope and the intercept of the regression lines and the initial N (or P) concentration of the litter, we calculated the amount of N (or P) immobilized (mg of immobilized nutrient per gram litter) and the percentage mass remaining (PMR) at the point where immobilization changes to mineralization (cf. Aber and Melillo, 1982; Aerts and de Caluwe, 1997).

All data were tested for homogeneity of variance by using the Levene's test of equality of error variances, and skewness (PASW Statistics 17.0). Log transformations were employed when the data did not meet the assumptions of normality. Differences in the initial concentration, the percent of initial element remaining in the litter, and final elemental concentration in the litter between fresh and senesced litter were analyzed by one-way analysis of variance (AOVs). Multiple analysis of variance (MANOVAs) were used to test for differences in the main effects of (1) canopy opening (trim vs. no trimmed canopy), debris manipulation (debris vs. no debris added to the plot) and days in the field (DIF, to determine effects through time) and (2) litter type and mesh size on the PMR, the concentration of elements in the litter, percent of initial element remaining, and final content of elements in the litter. The SNK (Student–Neuman–Keuls) test was used to compare the concentration and absolute amounts of the individual element means ($\alpha = 0.05$) through time (PASW Statistics 17.0).

3. Results

3.1. Percent mass remaining (PMR)

Overall, we found PMR differed among treatments (Fig. 2), and significantly declined over time (Table 3, DIF, $p < 0.001$). There was a significant effect of canopy (C) treatment on the PMR of the litter (Table 3, $p < 0.001$). Overall, the PMR was greater in trim (T) than in no trim (NT) plots (Fig. 3). There was no significant effect of debris (D) treatment on the PMR (Table 3). However, there was a significant interaction of canopy and debris treatments on litter decay (Table 3). The PMR was higher in plots with no debris (ND) than in plots with debris (D) when canopy was NT (Fig. 3, 1-AOV, $p < 0.001$). There was no difference in PMR between

Table 2
Initial elemental concentration (±standard error) (n = 120) of fresh and senesced litter contained in litterbags. Carbon (C), and nitrogen (N) as %. All other elements (mg/g). Ratios are expressed as g/g. Bold font represents significant differences in elemental concentration between litter types at $p < 0.05$.

Initial chemistry	Litter type		p	Power	R
	Fresh	Senesced			
Carbon (C)	52.35 (0.45)	**53.26 (0.12)**	0.004	0.82	0.03
Nitrogen (N)	**1.71 (0.02)**	0.98 (0.01)	0.000	1.00	0.86
C:N	30.89 (0.32)	**54.64 (0.46)**	0.000	1.00	0.88
Phosphorus (P)	**0.84 (0.01)**	0.28 (0.01)	0.000	1.00	0.81
C:P	636.99 (10.64)	**2046.87 (41.92)**	0.000	1.00	0.82
N:P	20.57 (0.24)	37.35 (0.63)	0.000	1.00	0.72
Aluminum (Al)	0.17 (0.01)	0.20 (0.01)	0.095	0.39	0.01
Calcium (Ca)	8.01 (0.11)	8.13 (0.14)	0.551	0.09	0.02
Iron (Fe)	0.47 (0.13)	0.52 (0.14)	0.809	0.06	0.00
Potassium (K)	**6.11 (0.12)**	1.85 (0.04)	0.000	1.00	0.83
Magnesium (Mg)	**2.43 (0.03)**	2.20 (0.03)	0.000	1.00	0.11
Manganese (Mn)	**0.43 (0.01)**	0.56 (0.02)	0.000	1.00	0.14
Sodium (Na)	**1.78 (0.04)**	1.21 (0.04)	0.000	1.00	0.32
Sulfur (S)	**2.87 (0.03)**	1.74 (0.03)	0.000	1.00	0.72
C:Ca	66.75 (1.09)	99.77 (32.94)	0.328	0.16	0.00
C:Mg	218.72 (3.21)	**248.81 (3.68)**	0.000	1.00	0.14
C:Mn	**1276.35 (27.01)**	1025.22 (24.97)	0.000	1.00	0.19
C:Fe	3341.06 (103.37)	3650.26 (110.38)	0.060	0.47	0.01
C:Al	**4117.84 (156.14)**	3071.8 (92.84)	0.000	1.00	0.13

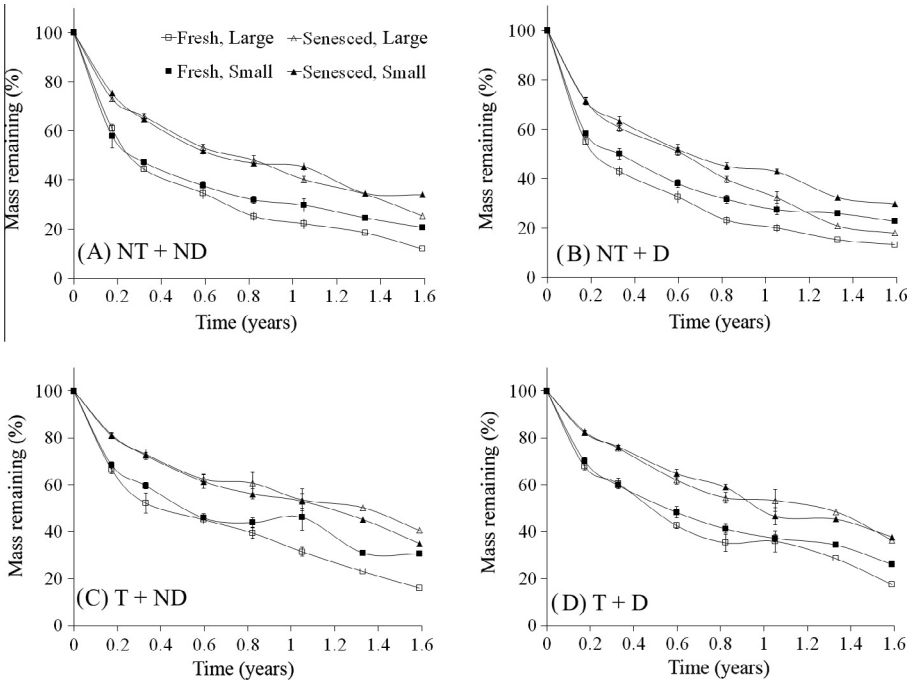

Fig. 2. Changes in mean percent of initial mass remaining in small and large mesh litterbags containing fresh and senesced leaf litter in the CTE over 1.6 yr. Bars represent ± SE.

ND and D in T plots (Fig. 3, 1-AOV, p = 0.47). Considering all treatments, the PMR was significantly different and the lowest in the NT + D plots (20.90% mass remained at the end of the experiment, Fig. 2B) followed by NT + ND (Fig. 2A) although not significantly different between these treatments. The PMR was highest in T + D plots (Fig. 2D) but that was not significantly different from PMR values in T + ND plots (Fig. 2C). At the end of the experiment, 29.4 and 27.2% mass remained in T + D vs. T + ND plots, respectively (Fig. 2).

There was a significant effect of litter type (fresh vs. senesced litter) and the size of the mesh of the litterbags on the PMR ($p < 0.001$, Power = 1.0 for both effects). Overall, fresh litter decayed faster than senesced litter (Fig. 4). Litter contained in litterbags constructed with large mesh decayed faster than in small meshed litterbags (Figs. 2 and 4).

3.2. Nutrient concentration

Time (as days in the field, DIF) had a significant effect on all elemental concentrations in the litterbags (Fig. 5). The temporal patterns of nutrient concentrations in residual leaf litters were generally similar (Fig. 5). Overall, N, Al, Fe, Mn, and Ash concentration increased significantly over the time of the experiment (Fig. 5A, C, E, G, and H). Mg concentration and the C:N ratio decreased significantly over the time of the study (Figs. 5F and 6A). On average, P concentration decreased during the first 0.2 yr

Table 3
Results of the Significance and (Power) of MANOVA on the effects of canopy (C, NT vs. T), debris (D, ND vs. D), and days in the field (DIF) on PMR, and percent of initial element remaining (PMR) of N, P, Al, Ca, Fe, K, Mg, Mn, Na and S. Bold font represents significant main effects on the dependent variables.

Source	Main effects				
	Canopy	Debris	DIF	C × D	Other interactions
PMR	**0.00 (1.00)**	0.25 (0.21)	**<0.01 (0.93)**	**<0.01 (0.93)**	C × DIF
PMR – N	**<0.01 (1.00)**	**0.01 (0.80)**	**<0.01 (1.00)**	0.55 (0.09)	None
PMR – P	0.80 (0.06)	**<0.01 (0.98)**	**<0.01 (1.00)**	0.07 (0.43)	None
PMR – Al	**<0.01 (1.00)**	**<0.01 (1.00)**	**<0.01 (1.00)**	**<0.01 (0.82)**	C × DIF; D × DIF
PMR – Ca	**<0.01 (1.00)**	0.01 (0.70)	**<0.01 (1.00)**	0.06 (0.47)	None
PMR – Fe	**<0.01 (1.00)**	**<0.01 (1.00)**	**<0.01 (1.00)**	**<0.01 (0.90)**	C × DIF; D × DIF
PMR – K	0.09 (0.40)	0.46 (0.11)	**<0.01 (1.00)**	0.04 (0.52)	C × DIF
PMR – Mg	**<0.01 (0.95)**	0.46 (0.11)	**<0.01 (1.00)**	0.05 (0.50)	None
PMR – Mn	**<0.01 (0.95)**	0.07 (0.43)	**<0.01 (1.00)**	0.01 (0.73)	None
PMR – Na	0.93 (0.05)	0.24 (0.22)	**<0.01 (1.00)**	0.07 (0.44)	None
PMR – S	0.01 (0.72)	0.01 (0.74)	**<0.01 (1.00)**	0.92 (0.05)	None

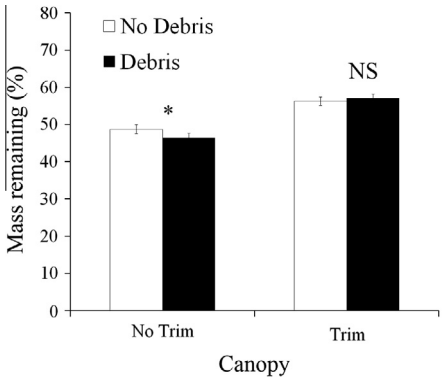

Fig. 3. Overall mean percent of initial mass remaining in the CTE. Asterisks represent a significant difference between D and ND plots.

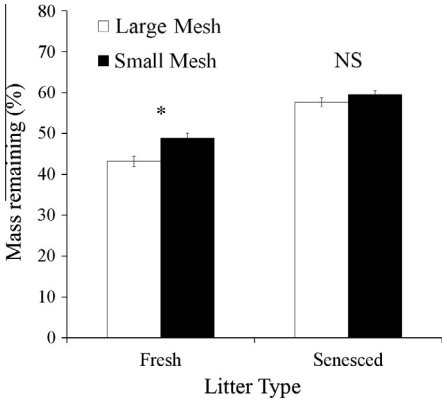

Fig. 4. Mean percent mass of fresh and senesced leaf litter in small and large mesh litterbags. Asterisks represent a significant difference in decay between small and large mesh litterbags within each litter type.

but later increased and remained constant through time (Fig. 5B). Ca concentration and the C:P ratio increased during the first 0.2 yr then declined (Figs. 5D and 6B). Meanwhile, the N:P ratio increased during the first 0.2 yr and stayed higher than initial for the course of the study (Fig. 6C).

Overall, there were significant effects of canopy, debris and canopy × debris interactions on elemental concentrations in the litterbags (2-MANOVA, Pillai's Trace, df = 1008, $p < 0.001$, Power = 1.0 for all effects). From all the elemental concentrations studied, canopy treatment had a significant effect on P, Al, Ca, Fe, Mg, Mn, N:P and Ash (df = 1, $p < 0.001$, Power > 0.95 for all tests of between-subjects effects). On average, P, Ca, Mg, and Mn concentrations were higher in NT than T plots whereas, Al, Fe, N:P, and Ash concentrations were significantly higher in T than in NT plots (df = 1, $p < 0.001$, Power > 0.99 for all tests of between-subjects effects; Figs. 5 and 6). The final C:P and N:P ratios were significantly higher in T than in NT plots (Fig. 6B and C; Table 4). Similarly, the final Mn, Na, and S concentrations of the leaf litters were significantly affected by the canopy treatment (Table 4). From all the elemental concentrations studied, debris treatment had a significant effect on N, P, Al, Ca, Fe, C:P, N:P and Ash concentration. On average, N, P, and Ca concentrations were higher in D than ND plots. The final concentrations of N and P were significantly higher D than in ND plots. Meanwhile, on average, Al, Fe, C:P, N:P, and Ash concentrations were significantly higher in ND than in D plots (df = 1, $p < 0.001$, Power > 0.80 for all tests of between-subjects effects; Figs. 5 and 6). The N:P ratio was significantly different and the lowest in the NT + D as compared to all other plots (Fig. 6C). Ash concentrations differed significantly among treatments and followed the pattern: NT + D > T + D = NT + ND > T + D. P concentration was the highest in NT + D (Fig. 5B), while Al and Fe concentrations were highest in T + ND plots (Fig. 5C and E). The final Mn, Na, and S concentrations of the leaf litters were significantly affected by the canopy treatment (Table 4).

There was a significant influence of the effect of litter type on the concentration of N, C:N, P, C:P, Ca, S, and Ash (Table 5). The C and P concentration was higher in fresh than in senesced litter (Table 6). Meanwhile, C:N and C:P ratios were higher in senesced than in fresh litter (Table 6). There was a significant influence on the effect of mesh size on the concentration of N, C:N, P, C:P, N:P, Al, Ca, Fe, Mg, Mn, and S (Table 5). With the exception of Al and Fe, on average the single elemental concentration was consistently higher in small than in large size mesh litterbags (Tables 5 and 6).

3.3. Percent of initial element remaining

Overall, there were significant effects of canopy, debris and days in the field on elemental concentrations in the litterbags (MANOVA, Pillai's Trace, Hypothesis df = 11, 1, 33, $p < 0.001$, Power = 1.0 for all main effects) (see Table 3). Time (days in the field) had a significant effect on all percent of initial element remaining in the litterbags (Fig. 7, Table 3). The temporal patterns of percent of initial element remaining in residual leaf litters were generally similar for N, P, Ca, and Mg (Fig. 7), the values significantly decreased over time. The percent of initial Al and Fe remaining did not differ from the initial to the first collection (0.2 yr) but then significantly increases over time (Fig. 7C and E). The percent of initial Mn remaining decreased from the initial to the first collection

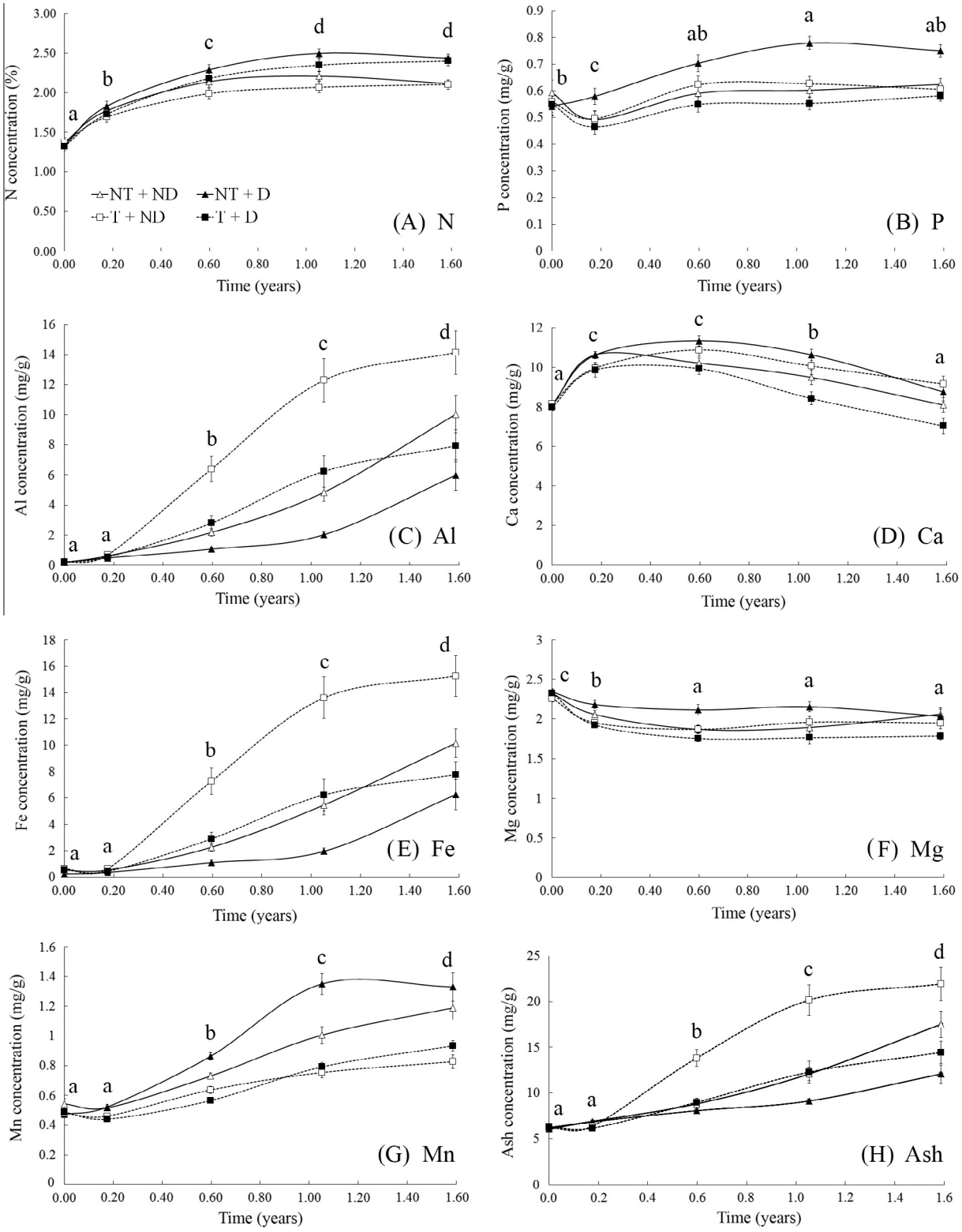

Fig. 5. (A–H) Changes in mean concentrations of elements in fresh and senesced leaf litter in the CTE over 1.6 yr. Bars represent ± SE. Lowercase letters indicate a significant difference among time periods for all treatments combined.

(0.2 yr), staying constant for about a year, then significantly decreased at the end of the study (Fig. 7G).

Canopy treatment had a significant effect on the percent of initial N, Al, Ca, Fe, Mg and Mn remaining (Table 3). The percent of initial N, Al, Ca, Fe, and Mg remaining were greater in T than in NT plots. The percent of initial Mn remaining was greater in NT than in T plots (Fig. 7). The debris treatment had a significant effect on the percent of initial N, P, Al, and Fe remaining in the leaf litter from the litterbags (Table 3, Fig. 7). The percent of initial Al and Fe remaining was higher in ND than in D plots (Fig. 7).

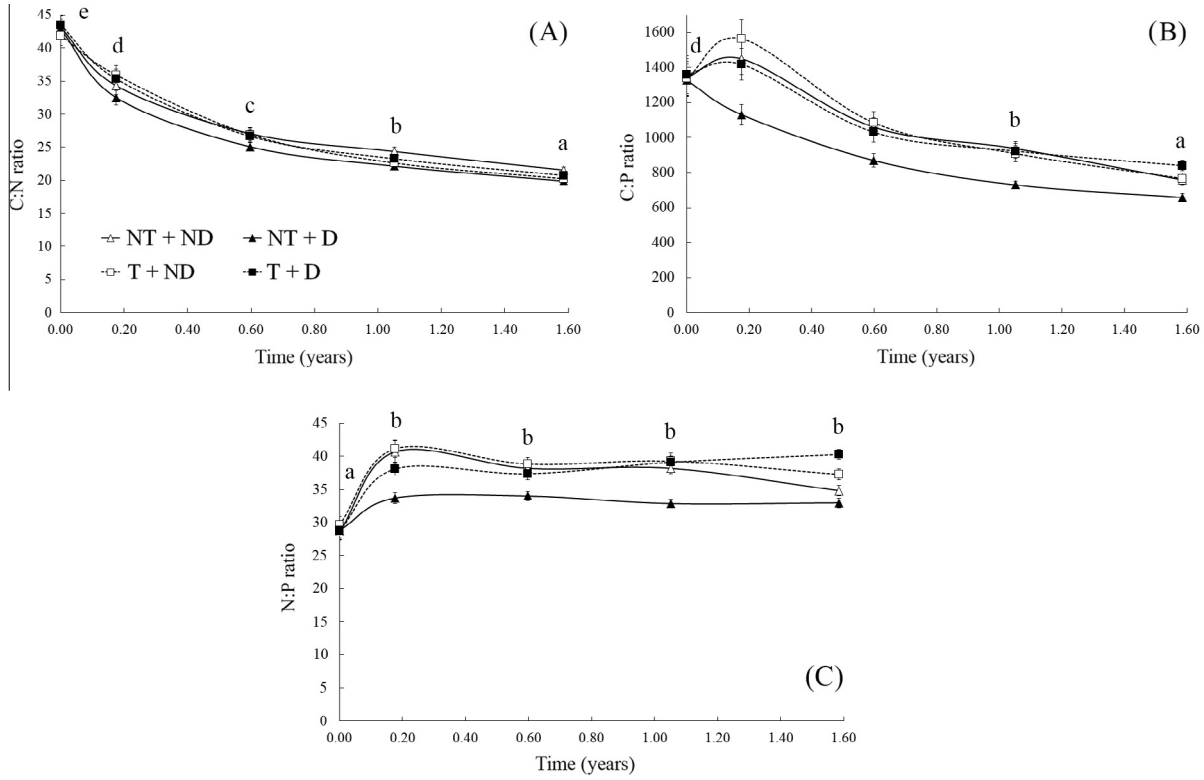

Fig. 6. (A–C) Overall mean ratios of (A) C:N, (B) C:P, and (C) N:P in decomposing leaf litter in the CTE over 1.6 yr. Ratios are expressed as g/g. Bars represent ± SE. Lowercase letters indicate a significant difference among time periods for all treatments combined.

Table 4
Results of the Significance and (Power) of MANOVA on the effects of canopy (C, NT vs. T), debris (D, ND vs. D) on the final content of various elements in the litterbags. Bold font represents significant main effects on the dependent variables.

Source	Main effects		
	Canopy	Debris	C × D
C	0.20 (0.25)	**<0.01 (0.99)**	0.04 (0.54)
N	0.81 (0.06)	**<0.01 (0.99)**	0.77 (0.06)
C:N	0.68 (0.07)	0.15 (0.30)	0.03 (0.60)
P	**<0.01 (0.99)**	**<0.01 (0.95)**	0.01 (0.70)
C:P	**<0.01 (0.92)**	0.64 (0.07)	**<0.01 (0.86)**
N:P	**<0.01 (1.00)**	0.44 (0.12)	**<0.01 (0.88)**
Al	0.01 (0.68)	**<0.01 (0.99)**	0.37 (0.14)
Ca	0.41 (0.13)	**<0.01 (0.93)**	0.09 (0.39)
Fe	0.01 (0.76)	**<0.01 (1.00)**	0.14 (0.32)
K	0.05 (0.51)	0.79 (0.06)	0.30 (0.82)
Mg	0.01 (0.72)	0.23 (0.23)	0.32 (0.17)
Mn	**<0.01 (1.00)**	0.05 (0.50)	0.70 (0.07)
Na	**<0.01 (1.00)**	0.39 (0.14)	0.65 (0.07)
S	**<0.01 (0.94)**	**<0.01 (0.99)**	0.12 (0.34)
C:Al	0.07 (0.45)	**<0.01 (1.00)**	0.82 (0.06)
C:Ca	0.54 (0.09)	0.07 (0.43)	0.08 (0.41)
C:Fe	0.02 (0.62)	**<0.01 (1.00)**	0.91 (0.05)
C:Mg	0.09 (0.40)	**<0.01 (0.87)**	0.14 (0.32)
C:Mn	**<0.01 (0.81)**	0.93 (0.05)	0.33 (0.16)

Table 5
Results of the Significance and (Power) of MANOVA on the effects of Litter type (L), and Mesh size (M) on the final content of various elements in the litterbags. Bold font represents significant main effects on the dependent variables.

Source	Main effects		
	Litter type	Mesh	L × M
C	0.15 (0.30)	0.01 (0.71)	0.94 (0.05)
N	**<0.01 (1.00)**	**<0.01 (1.00)**	0.69 (0.07)
C:N	**<0.01 (1.00)**	**<0.01 (1.00)**	0.37 (0.14)
P	**<0.01 (1.00)**	**<0.01 (1.00)**	0.04 (0.53)
C:P	**<0.01 (1.00)**	**<0.01 (1.00)**	0.82 (0.06)
N:P	0.46 (0.11)	**<0.01 (0.99)**	0.09 (0.40)
Al	0.72 (0.06)	**<0.01 (0.99)**	0.14 (0.32)
Ca	**<0.01 (0.78)**	**<0.01 (1.00)**	0.24 (0.22)
Fe	0.12 (0.34)	**<0.01 (0.99)**	0.49 (0.10)
K	0.74 (0.06)	0.03 (0.61)	0.11 (0.35)
Mg	0.23 (0.22)	**<0.01 (0.96)**	0.01 (0.73)
Mn	0.41 (0.13)	**<0.01 (1.00)**	0.21 (0.24)
Na	0.89 (0.05)	0.29 (0.18)	0.72 (0.06)
S	**<0.01 (1.00)**	**<0.01 (1.00)**	0.02 (0.62)
C:Al	0.27 (0.20)	**<0.01 (0.90)**	0.90 (0.05)
C:Ca	0.01 (0.73)	**<0.01 (1.00)**	0.09 (0.40)
C:Fe	0.07 (0.07)	**<0.01 (0.75)**	0.65 (0.70)
C:Mg	0.52 (0.10)	0.04 (0.52)	0.01 (0.72)
C:Mn	0.49 (0.11)	**<0.01 (1.00)**	0.41 (0.13)
Ash	**<0.01 (0.94)**	0.52 (0.10)	0.46 (0.11)

Meanwhile, percent of initial P remaining was higher in D than in ND plots (Fig. 7). The percent of initial Al and Fe remaining was the highest in the T + ND plots as compared to all plots (Fig. 7C and E).

There was a significant influence on the effect of litter type on the percent of initial N, P, Ca, K, Mg, Mn, Na, S, and Ash remaining (Table 7). These were all significantly greater in the senesced than in the fresh litter (Table 8). Mesh size had a significant effect on the percent of initial remaining for N, P, Ca, Mn and S (Table 7). Consistently, litter in small mesh bags had significantly greater percent of initial N, P, Mn, and S remaining than large mesh litterbags (Table 8). Consistently, N immobilization occurred in litterbags with senesced litter and small mesh size across all plots at about 68–77% of the initial biomass remaining (Table 9 A). From those litterbags, the immobilized nitrogen at the NT + ND was the lowest (0.03 mg N/g initial litter) as compared to all plots. Meanwhile, the immobilized nitrogen at the NT + D was the highest (0.96 mg N/g initial litter) as compared to all plots. Calcium also

Table 6
Final elemental concentration (±standard error) (n = 120) of fresh and senesced litter contained in litterbags. Carbon (C), and nitrogen (N) as %. All other elements as (mg/g). Ratios are expressed as g/g. Asterisks (*) represent significant differences of litter type within each element (1-AOV, $\alpha \leqslant 0.05$). Bold font represents significant differences in elemental concentration between mesh sizes within a litter type.

Source	Fresh		Senesced	
	Large	Small	Large	Small
C	43.90 (1.12)	46.12 (0.80)	45.20 (0.98)	47.35 (0.53)
N	2.33 (0.02)	**2.68 (0.05)***	1.89 (0.04)	**2.14 (0.03)***
C:N	**18.93 (0.25)**	17.28 (0.20)*	**24.03 (0.43)**	22.28 (0.30)*
P	0.61 (0.02)	**0.79 (0.02)***	0.50 (0.01)	**0.62 (0.02)***
C:P	**722.35 (17.32)**	586.02 (12.37)*	**930.18 (31.11)**	804.88 (22.85)*
N:P	**39.05 (0.92)**	33.86 (0.64)*	38.24 (0.78)	35.88 (0.73)
Al	11.97 (1.53)	8.23 (1.06)	**13.15 (1.60)**	5.98 (0.64)*
Ca	5.72 (0.32)	**9.33 (0.34)***	**7.15 (0.41)**	9.90 (0.33)*
Fe	13.18 (1.64)	9.24 (1.27)	**11.90 (1.40)**	6.40 (0.72)*
K	0.54 (0.02)	0.63 (0.03)	0.59 (0.02)	0.60 (0.02)
Mg	1.66 (0.06)	**2.11 (0.07)***	1.92 (0.06)	2.01 (0.08)
Mn	0.79 (0.06)	**1.23 (0.07)***	0.93 (0.07)	**1.19 (0.06)***
Na	0.27 (0.02)	0.26 (0.01)	0.27 (0.01)	0.26 (0.01)
S	2.05 (0.06)	**2.58 (0.05)***	1.89 (0.05)	**2.20 (0.04)***
C:Al	85.50 (11.08)	134.39 (12.94)	101.08 (11.88)	153.72 (11.30)
C:Ca	**83.52 (3.27)**	52.54 (1.48)*	**71.54 (2.90)**	50.17 (0.99)*
C:Fe	79.17 (10.97)	129.84 (12.66)	115.99 (13.89)	151.88 (11.22)
C:Mg	**284.43 (13.27)**	232.95 (7.96)*	248.54 (8.21)	254.41 (6.80)
C:Mn	**695.93 (48.13)**	442.60 (21.18)*	**635.86 (40.50)**	447.34 (14.11)*

tends to get immobilized in small mesh size litterbags across all plots (Table 9 B). Immobilization of Calcium ranged from 34.2 to 81.6 mg Ca/g initial litter and occurred when about half of the initial biomass remained (Table 9 B).

3.4. Invertebrate density, biomass and diversity

Total invertebrate density, and the density and biomass of collembolans were significantly positively correlated with PMR and percent of initial N remaining (Table 10). Margalef's index of diversity of all litter arthropods was negatively correlated with both PMR and percent of initial N remaining (Table 10).

4. Discussion

4.1. Mass loss

In this study, we found mass loss was significantly slowed by canopy trimming. These results are consistent with other studies in the Southern Appalachians that have shown reduced litter decomposition rates associated with clear-cutting (Seastedt, 1979; Abbott and Crossley, 1982; Blair and Crossley, 1988; Heneghan et al., 2004). However, the results of this study differ from those at northern hardwood forest sites (Aber et al., 1978; Covington, 1981) and from a Ponderosa pine forest in central Arizona (Klemmedson et al., 1985), where clear-cutting caused increased decomposition rates. Previously, Blair and Crossley (1988) suggested that generalizations on decomposition rates after clear-cutting based from northern hardwood forests would not apply to southern hardwood forests. This study implies that generalizations on decomposition rates after canopy opening due to clear-cutting based from northern hardwood forests or more xeric landscapes would not apply to subtropical wet forests in Puerto Rico. Thus, as previously suggested by Blair and Crossley (1988) the effects of canopy removal may depend on both the nature of pre-disturbance processes and on the site-specific effects of disturbance on the processes studied.

Other studies have emphasized the large amount of green leaf litter on the forest floor following hurricanes and the implications of this for subsequent nutrient cycling (Lodge et al., 1991; Steudler et al., 1991; Whigham et al., 1991; Zimmerman et al., 1995). Yet, few available studies focused on litter decomposition dynamics after hurricane in subtropical wet forests. As previously mentioned, the results from those studies available suggest that hurricanes and associated canopy openings do not increase decomposition in these forests (Herbert et al., 1999; Ostertag et al., 2003; Sullivan et al., 1999). For example, Ostertag et al. (2003) studied forest floor mass changes following Hurricane Georges in Puerto Rico, and found it rapidly returned (ca. 6 months) to pre-storm forest floor mass levels potentially due to the higher nutrient concentrations in green leaves in the hurricane debris. However, Sanford et al. (1991) described the tabonuco forest version of CENTURY model and predicted the decomposition of hurricane-generated debris would cause a suppression of forest productivity for a period of time following a hurricane. Results from Zimmerman et al. (1995) confirm that prediction as they found experimental removal of litter and woody debris generated by Hurricane Hugo increased soil nitrogen availability and above ground productivity in this forest. The results from our study are consistent with Sanford et al. (1991) predictions as well, as we found the percent of mass remaining was decreased and the percent of initial N remaining in the litter was increased in the hurricane simulated plots as compared to the control. Ultimately, the recovery of the forest floor mass after a hurricane (and differences observed among the various studies above described) will depend on the level of structural damage to the forests, the magnitude of both leaf and woody debris inputs, and the plant community composition (Ostertag et al., 2003; Zimmerman et al., 1995; Shiels and González, 2014).

In this study, the slow decay found in the trimmed plots can be attributed to a combination of factors that include the observed decrease in litter moisture (as presented in Richardson et al. (2010) and Shiels and González (2014)), the inferred shift in fungal community dominance from basidiomycetes to microfungi (details in Lodge et al. (2014)) and the associated changes in the faunal community (Richardson et al., 2010 and correlation analysis presented here). Although the litter moisture data are not presented in this study, Richardson et al. (2010) and Shiels and González (2014) showed that canopy opening resulted in increased throughfall, soil moisture and light levels, but decreased litter moisture in the CTE. Those results are consistent with Sullivan et al., 1999 who showed that litter decay seemed to be affected by variability in the timing and intensity of weather events where differences in litter mass disappearance between different study years is attributed to differential initial leaching that may have been related to differences in precipitation. Another factor that might explain the decreased litter decay under hurricane-like conditions is a shift in the fungal community composition in the CTE. In microcosms, white rot basidiomycetes have been shown to cause more leaf mass loss than microfungi (Santana et al., 2005), and the abundance of basidiomycetes was also associated with a greater mass loss of leaves in the field (Lodge et al., 2008). The shift in fungal communities from basidiomycetes to microfungal dominance was associated with changes in faunal community composition in the CTE (Richardson et al., 2010), with higher populations of the specialist fungivore groups – mites, collembola, and psocoptera, and lower abundance of larger organisms, such as isopods and millipedes in trimmed plots. These larger organisms are strongly light aversive, but major comminuters of litter, so their absence could reduce litter decomposition based on both direct (e.g., fragmentation) and the indirect losses through interaction with microorganisms (González, 2002). In the CTE, invertebrate diversity was significantly lower in trimmed than not trimmed plots (Richardson et al., 2010). In this study, we found there was a significantly negative correlation between the Margalef index of diversity for the

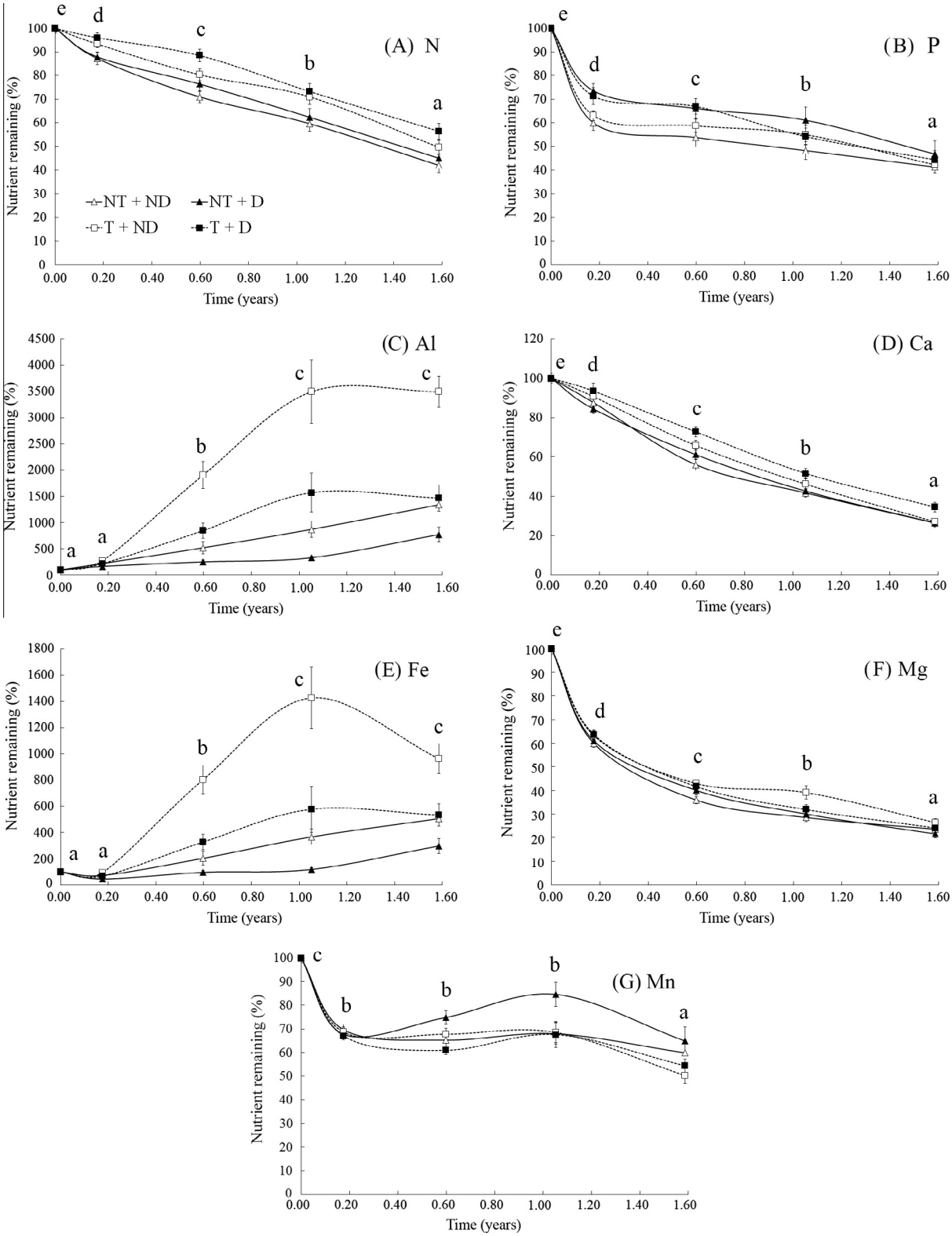

Fig. 7. (A–G) Changes in absolute amounts of elements in fresh and senesced leaf litter in the CTE over 1.6 yr. Bars represent ± SE. Lowercase letters indicate a significant difference among time periods for all treatments combined.

litter arthropods in the litterbags and the PMR (Pearson's bivariate correlate, $r = -0.29$ (two-tailed probability value), $p < 0.01$, $N = 1180$). Thus, the results of this study are consistent with others in that exposure of plant litter to increased faunal functional complexity in litterbags has been shown to increase litter mass loss (González and Seastedt, 2000; Bradford et al., 2002).

In this study, mass loss was stimulated by debris addition only in untrimmed plots. The litterbags used in this experiment were placed on top of the debris. Fungal connectivity between litter layers, putatively by basidiomycetes was shown to be highest in untrimmed plots, especially in the NT + D plots (Lodge et al., 2014). Thus greater fungal activity, increased rates of delignification

Table 7
Results of the Significance and (Power) of MANOVA on the effects of Litter type (L), and Mesh size (M) on the percent of initial nutrient remaining of various elements. Bold font represents significant main effects on the dependent variables.

Source	Main effects		
	Litter type	Mesh	L × M
PMR – C	**<0.01 (1.00)**	0.09 (0.40)	0.79 (0.06)
PMR – N	**<0.01 (1.00)**	**<0.01 (1.00)**	0.38 (0.14)
PMR – P	**<0.01 (1.00)**	**<0.01 (1.00)**	0.22 (0.23)
PMR – Al	0.34 (0.15)	0.10 (0.38)	0.93 (0.05)
PMR – Ca	**<0.01 (1.00)**	**<0.01 (0.93)**	0.53 (0.09)
PMR – Fe	0.31 (0.17)	0.14 (0.31)	0.42 (0.13)
PMR – K	**<0.01 (1.00)**	0.56 (0.09)	0.23 (0.22)
PMR – Mg	**<0.01 (1.00)**	0.39 (0.14)	0.03 (0.59)
PMR – Mn	**<0.01 (0.89)**	**<0.01 (1.00)**	0.68 (0.07)
PMR – Na	**<0.01 (1.00)**	0.64 (0.07)	0.02 (0.62)
PMR – S	**<0.01 (1.00)**	**<0.01 (1.00)**	0.92 (0.05)

by basidiomycetes and/or greater nutrient translocation from the decomposed debris to the litter in our bags could have contributed to higher rates of mass loss in NT + D plots. Results of mass loss in this study are similar to those of the litterbasket decomposition experiment carried out in the same subplots (Lodge et al., 2014) except that debris addition accelerated mass loss in both trimmed and untrimmed plots in the litterbaskets. Differences in the effects of debris addition to mass loss in the litterbag and litterbasket decomposition experiments in the CTE can be explained by differences in experimental design. The experimental designs of these two studies differ in that additional green leaves were added on top of the senesced leaves in the litterbasket experiment, which could have accelerated mass loss of the senesced litter cohort below by supplying nutrients in leachates and maintaining moisture needed for fungal activity.

The relative control of climate and substrate quality on decomposition processes has been pondered in the literature (for example, see review of literature in González (2002)). Coûteaux et al. (1995) have suggested that climate is the dominant factor in areas subject to unfavorable (dry and cold) weather conditions, whereas litter quality is the dominant factor under favorable (wet and warm) conditions. Berg et al. (1998) have suggested that if climate and site conditions are constant then the chemical composition and physical structure of the organic matter regulate decomposition rates. Nitrogen has been described as good predictor of plant litter decomposition (e.g., Melillo et al., 1982; Coûteaux et al., 1991). Berg and Staaf (1980) and Sangha et al. (2006) suggested that early decomposition is regulated by nutrient concentrations, especially N and P. The above contentions seem to be supported by this study as we found mass loss of fresh (green) litter was greater than senesced litter, and the initial N and P concentrations were higher in fresh than in the senesced litterbags. In this study, differences in the decay rates of fresh (green) and senesced litter remained after 1.5 yr. More transient differences in the decay rates of leaves of differing age since abscission have also been reported. Herbert et al. (1999) showed *Metrosideros polymorpha* green leaves associated with Hurricane Iniki in Hawaii decayed faster than senesced leaves over a short period (1 month). Bloomfield (1993) looked at mass loss after six months in green and senesced leaves of *Cecropia schreberiana* and *Inga vera* within the tabonuco forest in Puerto Rico. She found green leaves to experience greater mass loss, but differences were small. Fonte and Schowalter (2004) found decomposition rates of green leaves of four dominant tree species in the tabonuco forest be significantly greater than the senesced leaves; but demonstrated convergence of decay rates after two months. Still, it has been argued that these short term aberrations (<2 yr) in nutrient cycles can have substantial long-term effects on ecosystem dynamics (Lodge et al., 1994; Zimmerman et al., 1995; Fonte and Schowalter, 2004).

4.2. Nutrient immobilization and mineralization patterns

Litter decay is a complex process with marked differences among nutrients in their rates of release (Goya et al., 2008). Calcium, magnesium and manganese are associated with plant cell structures and are usually lost through litter decomposition (Baker and Attiwill, 1985; Rustad and Cronan, 1988; O'Connell and Grove, 1996). In this study, we found only Al and Fe accumulated above 100% of initial. High values for Al and Fe in the T + ND treatment compared to other treatments likely resulted from soil contamination as there was little forest floor separating the litterbags from mineral soil, and earthworm activity was especially high in that treatment. Although accumulation of Fe between 0.6 and 1 yr in some treatments could be related to fungal siderophores, which are low molecular weight iron chelating ligands produced by microorganisms that function in iron transport and nutrient exchange (Renshaw et al., 2002), the abundance of fungal connections that are capable of translocating nutrients was inversely related to Fe accumulation. This suggests that accumulation of Fe (and Al, which paralleled patterns for Fe) is most likely dominated by the adsorption of these ions onto the surfaces of the decaying litter. The amount of the forest floor material separating our litterbags from the mineral soil was least in the trimmed plots and greatest in the NT + D treatment, which is concordant with Fe and Al accumulation results. In addition, we observed more litter mixed by earthworm soil casts in the trimmed plots. These observations of increased castings in the trimmed plots are consistent with Chauvel et al. (1999) and Barros et al. (2001) which reported an invasion of *Pontoscolex corethrurus* after forest clearing and

Table 8
Mean (±SE) of the percent of initial element remaining (PMR) of C, N, P, Al, Ca, Fe, K, Mg, Mn, Na and S in litterbags of different litter type (Fresh and Senesced) and Mesh Size. Bold numbers represent significant differences in mesh size within a litter type. Asterisks (*) represent significant differences of litter type within each element (1-AOVs, $\alpha \leqslant 0.05$). Significant immobilization (positive) values are bolded.

Source	Fresh		Senesced	
	Large	Small	Large	Small
PMR – C	36.30 (1.43)	41.66 (1.20)	51.23 (1.48)	53.01 (1.26)*
PMR – N	51.02 (1.67)	**61.44 (1.34)**	82.43 (1.61)	**91.67 (1.28)***
PMR – P	33.53 (1.18)	**38.27 (0.90)**	72.02 (1.72)	**83.42 (1.50)***
PMR – Al	1116.67 (130.98)	1063.14 (164.30)	1152.16 (124.32)	786.79 (72.94)
PMR – Ca	44.09 (1.82)	49.86 (1.39)	64.84 (2.14)	**71.50 (1.90)***
PMR – Fe	449.99 (9.87)	407.97 (60.64)	429.96 (47.58)	323.32 (34.91)
PMR – K	4.89 (0.27)	4.97 (0.19)	16.92 (0.61)	16.41 (0.46)*
PMR – Mg	31.25 (1.20)	33.66 (0.97)	47.74 (1.52)	47.50 (1.27)*
PMR – Mn	55.57 (2.14)	**71.36 (1.74)**	64.81 (1.50)	**73.17 (1.59)***
PMR – Na	5.94 (0.28)	5.92 (0.22)	10.74 (0.40)	11.17 (0.72)*
PMR – S	28.67 (0.88)	**32.90 (0.65)**	48.09 (0.99)	**52.82 (0.75)***

Table 9
Results of the regression of percent mass remaining vs. (A) N and (B) Ca concentration in the remaining residue, the maximum amount of immobilized N and Ca (Immob.) (concentration nutrient/g initial litter) and percentage of initial biomass remaining at this point (PMR^{Imm}) in litterbags placed in the different CTE plots by Litter type (Senesced vs. Fresh) and Mesh size (Small vs. Big). Calculations are based on methods of Aber and Melillo (1982).

Treatment	Litter type	Mesh	Slope	Intercept	r^2	p	PMR^{Imm}	Immob.
(A) Nitrogen								
NT + ND	Senesced	S	−51.33	142.05	0.79	0.00	71.02	**0.028**
		L	−64.79	154.14	0.83	0.00	77.07	−0.630
	Fresh	S	−46.40	159.45	0.57	0.00	79.72	−3.403
		L	−44.70	148.30	0.47	0.00	74.15	−4.800
NT + D	Senesced	S	−43.33	136.58	0.83	0.00	68.29	**0.960**
		L	−42.29	124.64	0.51	0.00	62.32	−0.616
	Fresh	S	−45.99	166.19	0.81	0.00	83.09	−2.088
		L	−48.25	156.37	0.46	0.00	78.18	−4.430
T + ND	Senesced	S	−56.75	154.69	0.86	0.00	77.34	**0.740**
		L	−56.94	145.71	0.69	0.00	72.85	−0.480
	Fresh	S	−46.30	161.39	0.66	0.00	80.69	−3.040
		L	−24.49	107.22	0.13	0.00	53.61	−5.360
T + D	Senesced	S	−45.84	137.52	0.77	0.00	68.76	**0.514**
		L	−52.07	144.73	0.76	0.00	72.36	**0.260**
	Fresh	S	−37.94	151.14	0.71	0.00	75.57	−2.050
		L	−48.49	171.42	0.66	0.00	85.71	−1.950
(B) Calcium								
NT + ND	Senesced	S	−3.13	93.10	0.31	0.00	46.55	**52.13**
		L	0.49	54.64	0.04	0.71	–Ψ	–Ψ
	Fresh	S	−1.55	64.22	0.10	0.37	–Ψ	–Ψ
		L	2.67	29.04	0.19	0.13	–Ψ	–Ψ
NT + D	Senesced	S	−4.99	113.08	0.40	0.00	56.54	**46.96**
		L	−1.89	76.80	0.19	0.12	–Ψ	–Ψ
	Fresh	S	−3.85	88.89	0.29	0.01	44.44	**34.21**
		L	−1.08	56.46	0.08	0.52	–Ψ	–Ψ
T + ND	Senesced	S	−1.55	64.22	0.10	0.37	–Ψ	–Ψ
		L	2.45	45.55	0.26	0.03	22.77	−38.27
	Fresh	S	−3.33	86.54	0.29	0.01	43.27	**39.12**
		L	2.69	34.92	0.24	0.04	17.46	−28.43
T + D	Senesced	S	−1.88	86.15	0.26	0.03	43.07	**81.59**
		L	−2.30	88.53	0.23	0.05	44.26	**68.09**
	Fresh	S	−5.15	104.15	0.36	0.00	52.07	**35.56**
		L	−1.45	67.25	0.12	0.32	–Ψ	–Ψ

Ψ There was no significant relation between PMR and N concentration in the remaining residue, so the method of Aber and Melillo (1982) was not valid here.

Table 10
Pearson correlation coefficients (r) (and two-tailed probability values) for the percent of mass (PMR) and N remaining (PMR-N) of fresh and senesced litter and the density, biomass and diversity (Margalef) of all litter microarthropods, and density and biomass of collembolans in litterbags collected from the CTE ($N = 1007$). Bold font represents significant correlations.

Variable	PMR	PMR-N
Total Density	**0.28 (<0.01)**	**0.25 (<0.01)**
Total Biomass	−0.05 (0.14)	−0.07 (0.08)
Margalef	**−0.29 (<0.01)**	**−0.17 (<0.01)**
Density, collembolans	**0.20 (<0.01)**	**0.22 (<0.01)**
Biomass, collembolans	**0.16 (<0.01)**	**0.16 (<0.01)**

introduction of exotic grasses that resulted in a large increase in earthworm population density; consequently producing an impermeable crust (up to 20 cm thick) of compact castings. Disturbed forests and early plant successional communities in Puerto Rico were previously found to be dominated by *P. corethrurus* (González et al., 1996; Zou and González, 1997) as this exotic worm can thrive under harsh climatic conditions (González et al., 2006, 2008).

In this study, P showed a rapid initial loss during the first 0.2 yr followed by steady loss. Rapid initial losses of P from senesced rain forest leaf litter was recently shown to result from physical leaching of organic and inorganic forms of P (Cleveland et al., 2006; Schreeg et al., 2013). Phosphorus retention was significantly greater under closed canopy than in trimmed plots between 0.2 and 0.6 yr. Our results agree with those of Lodge et al. (2014); they suggested that higher fungal connectivity between litter cohorts in untrimmed plots resulted in more translocation of P into senesced litter. P content never exceeded 100% of initial in our study or in a previous study at El Verde that also used mixed leaves in proportion to litterfall ratios (Zou et al., 1995), but Lodge et al. (2014) found immobilization of P exceeded 100% of initial while using senesced leaves of only the dominant tree on ridges, *D. excelsa*, which had much higher C:P ratios than senesced leaf litter mixes (4200–6065 in Lodge et al. vs. 637–2047 in this experiment and 420 in Zou et al. (1995)). Yet, previously C:P < 200 had been reported as a threshold for mineralization to occur (Duchaufour, 1970).

Patterns of immobilization and mineralization are also influenced by the physical and biological microenvironments of the background litter on which litterbags are placed (Smith et al., 1998). Thus, differences in the physico-chemical environments among the studies could explain differences in the immobilization and mineralization patterns. In addition, in this study, we used air dried leaves that had been stored for months and could have lost a substantial portion of the resident fungi. Though Hudson (1968) emphasized the persistence of endophytic and epiphyllic fungi in freshly fallen leaves, and others have shown their frequent occurrence and possible importance during the early stages of decomposition in temperate forests (Osono, 2002), most of the fungal species on and in live leaves can be rapidly replaced in decomposing leaves by forest floor fungi at our site (Holler and Cowley, 1970). Regardless of the rapid replacement of endophytic and epiphyllic fungi once senesced leaves reach the forest floor, they might still play a role in immobilizing nutrients and early decomposition as hypothesized by Osono (2002, 2005) and others.

Still, the percent of initial P remaining at 0.2, 0.4 and 0.6 yr were significantly higher than those values reported by Lodge et al. (2014). A higher percent of initial P remaining in this study might suggest either P translocation from the debris below, less P mineralization in litterbags vs. litter baskets, or greater input of P in leachates from higher litterfall. This latter contention can be supported by Silver et al. (2014), who found that leaf litterfall N and P concentrations increased in the trimmed plots relative to those of intact canopy. Nutrient concentrations increased in some litter fractions following trimming, likely due to a combination of changes in the species and fractional composition of litterfall, and increased nutrient uptake from reduced competition for nutrients (Silver et al., 2014).

4.3. Effect of litter microarthropods on mass loss and nutrient dynamics

In this study, the PMR of fresh and senesced litter was significantly affected by mesh size, with a higher mass remaining in small mesh bags. The total abundance and biomass of microarthropods contained in the litterbags was also significantly affected by mesh size (Richardson et al., 2010), as only smaller species or instars were found in small mesh bags. In general, litterbags contained smaller individuals of the same taxonomic groups as found in bulk litter samples in the LEF (Richardson et al., 2005). Faunal effects on litter breakdown can be up to 66% in the tabonuco forest at LEF, a site of high abundance of macrofauna and diversity of functional groups (González and Seastedt, 2001). In fact, as previously mentioned, in this study the diversity of soil microarthropods was significantly negatively related to the PMR. This finding is also consistent with Heneghan et al. (1998) study of soil microarthropod community structure and litter decomposition dynamics in two tropical sites (LEF and Costa Rica) and a temperate forest in North Carolina. They found faster litter decomposition rates in the tropics than in the temperate forest, and suggested that in addition to climate, it was due to a higher diversity of soil fauna in the tropics in spite of higher soil fauna densities in the temperate forest (Heneghan et al., 1998). In this study, the small mesh size did not inhibit the activities of collembolans as they were significantly more abundant in the small mesh litterbags than in the large mesh litterbags. In trimmed plots, where collembola were at their highest abundance, PMR was high and predators were in lower abundance than in untrimmed plots until the last recording period (Richardson et al., 2010). Collembola grazing on microfungi could reduce their decompositional activity, which would support the findings of Hanlon and Anderson (1979), who reported inhibition of soil microbial respiration as the number of grazing collembolans was increased beyond an optimal number. The range of values for the contribution of soil fauna activities to litter decomposition varies widely because it is dependent on the confounding effects of the size, abundance, diversity, and functionality of the fauna (e.g., Hansen, 1999; Heneghan et al., 1999; Irmler, 2000; González and Seastedt, 2001). This study suggest that both litter microarthropods and macrofauna are important determinants of decay in the LEF and that canopy opening effects on litter fauna given hurricane disturbance can have a significant influence on the decay and nutrient cycling of litter materials at LEF.

5. Conclusions

In this study, we showed canopy opening can have a significant effect on the PMR of leaf litter in the tabonuco forest in the Luquillo Mountains. Trimming reduced litter mass loss. Overall, there was no significant effect of debris addition on the PMR. Canopy trimming increased the percent of initial N, Al, Ca, Fe, and Mg remaining and decreased the percent of initial Mn remaining compared with not trimmed plots. Debris addition increased the percent of initial N and P remaining and decreased the percent of initial Al, and Fe remaining in the decomposing litter compared to no debris added plots. Still after 1.6 yr, nitrogen mineralization from the decomposing litter was reduced by the hurricane-like treatment as compared to the control. Similarly, P and Ca were significantly immobilized in the decomposing litter in the hurricane-like treatment as compared to the control during the first 0.6 yr. The PMR of fresh and senesced litter was significantly affected by mesh size, with a higher mass remaining in small mesh bags. Fresh litter decayed faster than senesced litter; following patterns of initial N and P concentrations (higher in the former litter type). Thus, we conclude hurricanes can differentially impact litter decomposition and associated nutrient release via canopy opening and litter inputs. A significantly negative correlation between the Margalef index of diversity for the litter arthropods contained in the litterbags and the PMR suggests that functional complexity is an important determinant of decay in this forest. Our results highlight the complexity inherent to the understanding of hurricane effects on ecosystem processes as their associated confounding effects (canopy opening and debris deposition) can have differing effects on litter decomposition and associated nutrient cycling.

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