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Woody debris characterization along an elevation gradient in northeastern Puerto Rico

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Woody debris is an ecologically important component of forests as well as a potentially large contributor to the carbon pool of forested terrestrial ecosystems. We characterized coarse woody debris, fine woody debris, litter, and duff biomass at 24 sites along an elevation gradient in northeastern Puerto Rico. These sites are representative of eight mature forest types that include Elfin woodland, Sierra palm *Prestoea montana*, Palo Colorado *Cyrilla racemosa*, Tabonuco *Dacryodes excelsa*, lowland moist, lowland dry, fresh water *Pterocarpus* swamps, and flooded mangrove forests. We expected the amount and composition of both woody debris and forest floor components to vary by forest type. We hypothesized mid- to upper-elevation forests, exhibiting the greatest basal area and amount of aboveground biomass, would have the greatest amounts of woody debris. In addition we expected the fine woody debris (wood < 7.60 cm diameter), litter, and duff fractions to be an important source of organic matter in some forest types, representing a significant percentage of total woody debris. We found significant differences in mean total woody debris, coarse woody debris, and fine woody debris among forest types along the elevation gradient. The mean total woody debris was significantly greater in the Palo Colorado forest, than the low-elevation Dry (14.79 Mg ha^{-1}) and highest elevation Elfin (17.38 Mg ha^{-1}) forests, with the other forest types containing intermediate amounts of woody debris. In addition, the total fine woody debris fraction was an important component of total carbon storage, representing 22–56% of total carbon stored in each forest.

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Woody debris is an ecologically important component of forests; providing habitat for animals and germinating plants, as well as contributing to soil moisture regulation and nutrient cycling (Harmon et al. 1986, Santiago 2000). Decaying woody debris serves as a water and nutrient reservoir, providing nutrients to the soil directly underneath in the form of dissolved organic matter (Yavitt and Fahey 1985, Harmon and Hua 1991, Hart 1999, Spears et al. 2003, Spears and Lajtha 2005, Zalamea et al. 2007). Nutrients are also harvested from woody debris through fungal sporocarp formation (Harmon et al. 1994), mycorrhizal and root absorption, or insect ingestion and transport.

Woody debris is an important component of the carbon pool and a potential carbon sink in terrestrial ecosystems globally (Harmon and Hua 1991, Torres 1994, Creed et al. 2004). Persisting for centuries, woody debris may represent a significant portion of total carbon storage in a system (Harmon and Sexton 1996). Global comparative studies have found positive correlation between temperature, precipitation, and rates of decomposition of litter and woody debris (Meentemeyer 1978, Yatskov et al. 2003). As temperatures and climates shift globally, rates of decomposition and amounts of woody debris may be affected resulting in increased release or storage of carbon. The exact contribution of woody debris to global carbon storage is unknown (Harmon et al. 1986), necessitating more research in this area.

While surveys of amounts and properties of woody debris have been performed within temperate systems as well as the mainland tropics, these collections are often limited to few forest types encompassing large land areas (Delaney et al. 1998, Nascimento and Laurance 2002). Temperate, tropical, and island ecosystems vary in climate, species composition, decomposer community structure and rates of biomass production, resulting in variable amounts of carbon stored in persistent downed woody debris. Of the studies conducted in the tropics, many have focused solely on reporting total mass, and only the coarse fraction of woody debris (Clark et al. 2002, Baker et. al. 2007, Palace et. al. 2007). Detailed surveys including all size classes of woody debris within a variety of tropical forest types are important for better understanding of the complexity and uncertainty associated to global carbon pools; particularly, given the importance of both natural and anthropogenic disturbances in Puerto Rico. Disturbances (e.g. hurricanes) can transfer large amounts of woody debris to the forest floor and ultimately have long term consequences in the functioning of these forested ecosystems.

The main objective of this study was to characterize the amounts of woody debris including: coarse woody debris, fine woody debris, duff, and litter for eight different forest types along the elevation gradient in northeastern Puerto Rico (Fig. 1, Table 1). Coarse woody debris attributes were also measured, including: diameter, length, volume, decay class, the presence of cavities, and occurrence of brown rot fungi, white rot fungi, and termites. We expected the amount and composition of both woody debris and forest floor biomass to vary by forest type. In addition we hypothesized the mid-elevation forests, exhibiting the greatest basal area and amounts of aboveground biomass, would have the greatest amounts of woody debris. We expected the fine woody debris, litter, and duff fractions to be an important source of organic matter in these forest types, representing a significant percentage of total woody debris. Within forest types populated by small-diameter tree species, we expected the coarse woody debris fraction to represent a smaller proportion of total debris encountered.

Data generated by this survey contributes to development and improvement of existing woody debris management plans, addressing increased fire risk in northeastern Puerto Rico. Factors such as growing population and shifting climate in Puerto Rico have resulted in both increased amounts of urban–wildland interface as well as greater potential for harmful forest fires (US Fire Administration 2002, Cochrane and Laurence 2008). Fire frequency is increasing and fires are occurring in humid forests – like these forest types within the Luquillo Mountains, for the first time (Burney et al. 1994, Robbins et al. 2008). Fuel loads, or the distribution of woody debris and other carbon sources in forests, is the only key element of the fire behavior triangle that can be effectively managed (Gould et al. 2008). Our detailed survey of fuel loads within these forest types will also aid in development of more effective management practices.

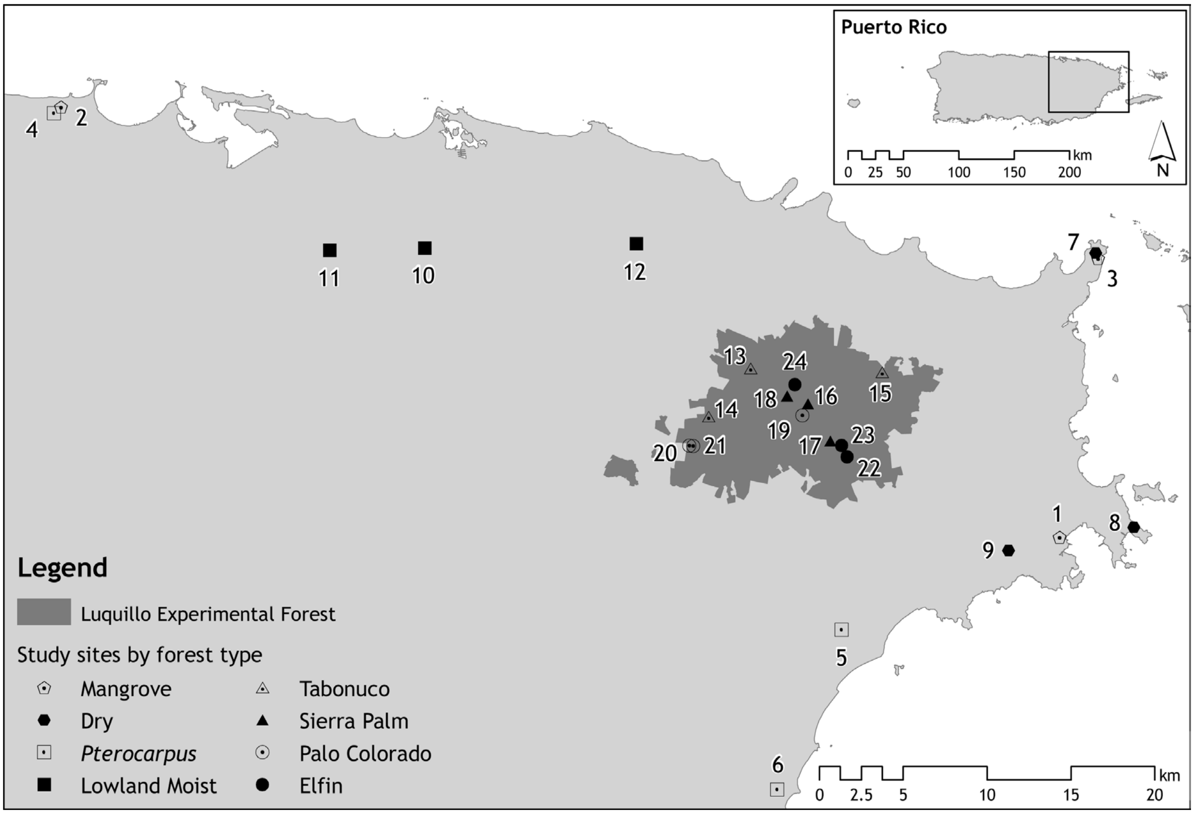

Figure 1. Map of locations of all sites used in this study.

Table 1. Elevation (m), mean annual precipitation (MAP, mm) (±SE), mean annual temperature (MAT, °C) (±SE) (2002–2011), and plant community for each of the eight forest types characterized in the study.

Forest type	Site locations[1]	Elevation	MAP	MAT	Dominant Holdridge Life Zone	Plant community
Mangrove	1–3	0.4	1482.0 (91.98)	27.4 (0.68)	Subtropical dry	*Avicennia germinans–Laguncularia racemosa*
Pterocarpus	4–6	1.3	1809.1 (270.9)	26.5 (0.25)	Subtropical moist	*Pterocarpus officinalis–Acrostichum aureum*
Dry	7–9	23.5	1412.1 (291.1)	27.5 (0.44)	Subtropical dry	*Bucida bucera–Guapira fragans*
Moist	10–12	58.4	1849.5 (272.7)	26.3 (0.16)	Subtropical moist	*Manilkara bidentata–Ocotea leucoxylon*
Tabonuco	13–15	417.3	3176.0 (409.3)	23.0 (0.91)	Subtropical wet	*Dacroydes excelsa–Manilkara bidentata*
Sierra palm	16–18	797.4	4201.4 (380.5)	21.1 (0.42	Lower montane wet	*Prestoea montana–Cecropia schreberiana*
Palo Colorado	19–21	790.1	3142.5 (398.8)	20.5 (0.13)	Lower montane wet	*Cyrilla racemiflora–Micropholis garciniifolia*
Elfin	22–24	1008.9	4146.0 (427.2)	19.8 (0.18)	Lower montane rain	*Tabebuia rigida–Eugenia borinquensis*

[1]Numbers correspond to site locations of Fig. 1.

Methods

Site description

Puerto Rico is within the geographic tropics and the global frost-free zone and it falls within the subtropical belt of the Holdridge Life Zone System because of its temperature regime (Lugo et al. 2012). Puerto Rico also has a rich history of both natural and human caused large-scale disturbance (Zimmerman et al. 1995, Foster et al. 1999). The island is subject to both large hurricanes and historically almost all of the accessible primary forest was converted to farmland. Less than one percent of primary forest remains, and these study sites are representative of most mature secondary forest types on the island, resulting from the disturbance regime and land use history (Birdsey and Weaver 1982).

The Luquillo Mountains of northeastern Puerto Rico are characterized by steep and highly dissected topography, with distinct gradients in plant community composition and forest structure. The geology is characterized by non-calcareous material derived from volcanic bedrock (montane and lowland sites) or Quarternary deposits (coastal sites) (Gould et al. 2006). Soils range from shallow to deep, poorly to well-drained clayey (Huffaker 2001).

We characterized woody debris in the Luquillo Experimental Forest (18°18′N, 65°50′W) as well as on federal, state, and private managed and unmanaged lands of Puerto Rico (Fig. 1). The 24 sites ranged in elevation from sea level to 1010 m, encompassing five Holdridge Life Zones: subtropical dry, subtropical moist, subtropical wet, lower montane wet, and lower montane rain forests. Eight mature forest types within Puerto Rico were represented, including: Elfin woodland, Sierra palm *Prestoea montana*, Palo Colorado *Cyrilla racemiflora*, Tabonuco *Dacryodes excelsa*, lowland moist, lowland dry, fresh water *Pterocarpus* swamps, and flooded mangrove forests (Gould et al. 2006, González et al. 2007). A detailed description of the plant communities of each forest type can be found at Gould et al. (2006), and Weaver and Gould (2013).

Mean annual temperature (MAT) measured at the sites (from 2002 to 2011) ranged from 19.75 to 27.43°C, and mean annual precipitation (MAP) ranged 1412–4146 mm (González unpubl.). The elevation gradient encompasses eight different forest types with three previously established permanent plots within each forest type, for a total of 24 plots. As elevation increases, annual precipitation increases whereas average air temperature decreases (Fig. 2) (Richardson et al. 2005, González et al. 2007). The sites experience a weakly seasonal rainfall regime in which a typically dry season occurs between February and April and a typically rainy season from August to November (Zalamea and González 2008). Along the elevation gradient of the Luquillo Mountains, soil oxygen decreases with increasing annual rainfall (Silver et al. 1999). Wind velocity increases with elevation from 0.42–0.83 to 2.22–5.00 m s^{-1}, and wind direction is more constant at higher elevations (Waide et al. 2013). Wind direction is generally from the northeast at high elevations but tends to the southeast at lower elevation stations (Brown et al. 1983), perhaps because of a leeward pressure trough (Odum et al. 1970). The cloud condensation level is around 600 m, which means that the whole aboveground structure of the forests above this elevation is immersed frequently in clouds. This

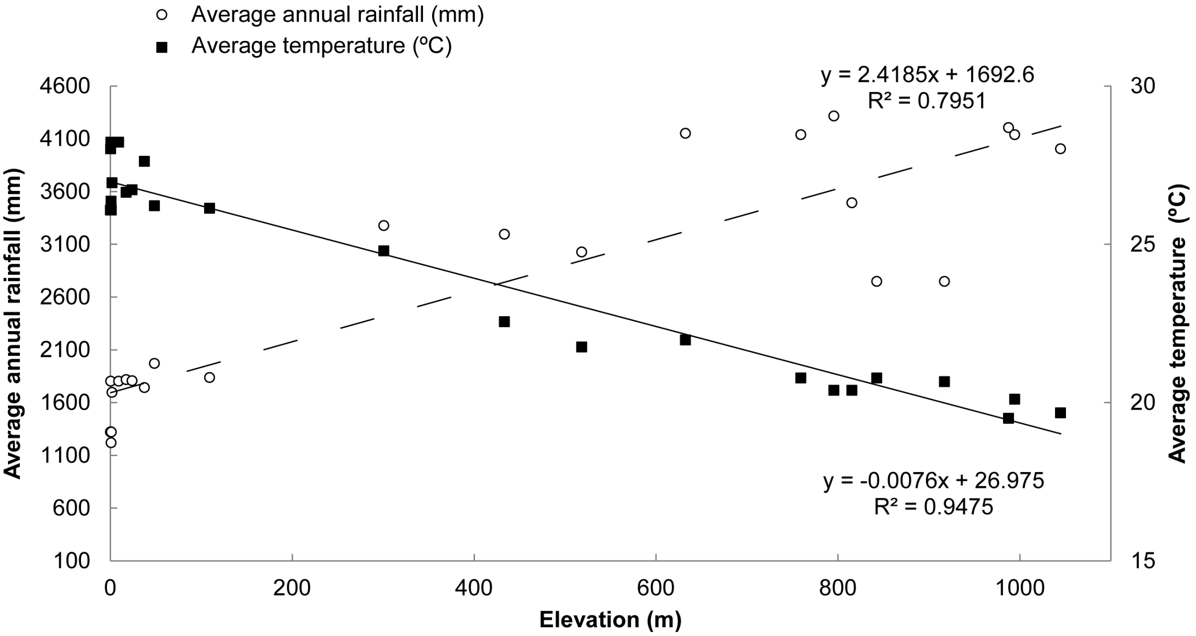

Figure 2. The monthly rainfall (mm) and temperature (°C) data arranged by elevation (m) along the elevation gradient in northeastern Puerto Rico. Values averaged from data collected monthly (rain) and daily (temperature–data loggers) during 2002–2011.

increased humidity, decreases radiation input, and saturates all plants and soil surfaces (Lugo et al. 2012).

Transect design

During the summer of 2010, we systematically installed three woody debris transect units at each of the previously established plots for a total of 72 transect units (nine replicates per forest type). Care was taken during transect installation to remain within the targeted forest type.

Transect design and sampling protocols were adapted from methods currently employed by the USDA Forest Service Forest Inventory Analysis (FIA) (Woodall and Williams 2005); allowing for comparison with existing woody debris data, while improving the resolution of fuels data to include all the main forest types within our area of interest. Each transect unit consists of three 33 m long transects radiating from a center point at 0°, 120°, and 240° degrees. Slope angle was also recorded used to correct for a final Horizontal Transect Length of at least 90 m (Harmon and Sexton 1996). Transect unit replicate 1 was centered over the existing permanent plot, and replicates 2 and 3 were positioned in a systematic, flexible fashion, to allow for small or narrow forest patches (Fig. 3). All measurements were performed on each transect leg. Total horizontal transect length of > 90 m for each replicate was chosen based on standards set within the literature (Brown 1974, Harmon and Sexton 1996).

Woody debris size classes and measurements

Woody debris in this study was defined as dead, downed or leaning at an angle greater than 45° from vertical, and not attached to any living sprouts or sections (Brown 1974, Harmon and Sexton 1996, Woodall and Williams 2005). We did not include any portion that was buried below litter or soil. Woody debris was split into 1, 10, 100, and > 1000-h size classes using fuels moisture time lag values (Table 2). Fuel moisture time lag indicates the amount of time

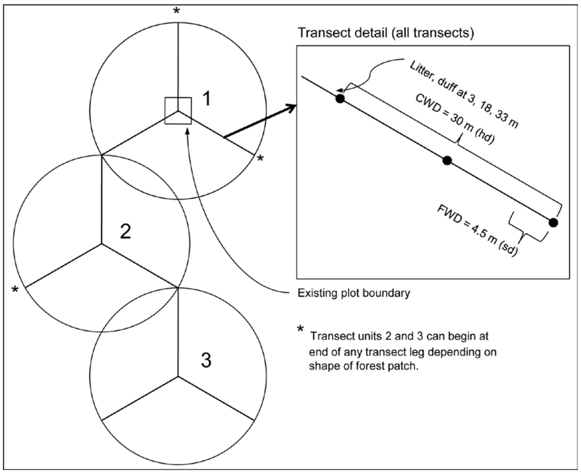

Figure 3. Layout of the three transect units per plot with transect leg detail showing location of all measurements.

Table 2. Woody debris categories based on diameter of each woody category and fuel moisture time-lag values. Modified from Woodall and Monleon (2008).

Woody debris category	Diameter of wood (cm)	Fuel moisture time-lag (hour)
1 h FWD	< 0.60	1
10 h FWD	0.61–2.54	10
100 h FWD	2.55–7.59	100
1000 h CWD	> 7.60	1000+

required by an individual piece of woody debris to reach moisture equilibrium with the surrounding environment (Pyne et al. 1996, Woodall and Williams 2005). These categories are standard, used across the United States, and allow us to make comparisons with data previously gathered throughout Puerto Rico by the FIA.

Each piece of coarse woody debris (CWD) had a minimum diameter of 7.60 cm and a minimum length of 1 m. CWD was sampled using a line-intercept method. This widely used method allows for quick data collection and provides an acceptably accurate measure of woody debris on a mass per volume basis within a forested stand (Harmon and Sexton 1996, Woodall and Williams 2005). The CWD transect began 3 m from the center to at least 33 m (for a total of 30 horizontal distance). Several attributes were measured for each piece of CWD including: transect, large-end, and small-end diameter; length; decay class; cavities; presence of termites; and occurrence of brown or white rot. Groups of fungi were determined based on observed color changes and appearances of the decayed woods (sensu Harmon and Sexton 1996, Shimada et al. 1997).

Decay class ranged from freshly fallen to almost completely decayed. A complete description of decay class can be found at Woodall and Williams (2005). Fine woody debris (FWD) was tallied along a 4.5 m (slope distance) section at the end of each transect leg. Each piece of FWD that was encountered was tallied and based on size, placed in the category of: small, medium, or large based on diameter at intersection with transect. Litter was defined as fresh, fallen, easily recognizable plant material. Duff consisted of partially or highly decomposed plant material (Brown 1974). We recorded litter, duff, and fuel-bed depths at three points along each transect: 3, 18, and 33 m (slope distance). To compute litter and duff weights per unit area, the depth was multiplied by the bulk density for tropical hardwoods and a unit-conversion factor (sensu Woodall and Williams 2005).

Data analyses

All line-intercept CWD data were converted to reported values following Harmon and Sexton (1996). Due to the high diversity of our forest types, the difficulty in determining species of highly decayed material, and lack of density information for decayed material, we chose to use decay values from Harmon and Sexton (1996) for the conversion from volume to mass. The values are as follows: (0.775, 0.696, 0.671, 0.639, 0.220) ranging from least to most decayed. Fine woody debris tallies were converted to volume and then mass following Harmon and Sexton (1996) and Woodall and Williams (2005).

All statistical analysis were performed using the software SPSS (SPSS 11.5, Windows 2002). The significance level was set $\alpha = 0.05$. Data were tested for homogeneity of variance by using the Levene's test of equality of error variances, and skewness. Log transformations were employed when the data did not meet the assumptions of normality. Differences in the mean mass of woody debris among forest sites, for each woody debris category, were determined by mean analysis of variance (MANOVA). Woody debris categories included: 1, 10, 100, > 1000-h size classes, total mass of fine woody debris, litter biomass, and duff biomass. Analysis of variance (ANOVA) and Student–Neuman–Keuls (SNK) tests were used to determine significant differences and compare the means ($\alpha = 0.05$) of different woody debris categories, forest floor litter and duff, and occurrence of white rot fungi, brown rot fungi, and termites among forest types (SPSS 2002). A simple linear correlation analysis (Pearson's coefficient) was performed among woody debris categories and elevation, MAP, and MAT. Similarly, simple linear correlation analysis (Pearson's coefficient) was performed among and elevation, MAP, MAT, and decay class, and the occurrence of brown rot fungi, white rot fungi, and termites.

Results

There were significant differences in mean total woody debris (WD) among forest types along the elevation gradient (Table 3). The mean total WD in the Dry (14.79 Mg ha^{-1}) and Elfin (17.38 Mg ha^{-1}) forests were significantly less than the mean total WD in the Palo Colorado (73.24 Mg ha^{-1}) forest. The remaining forest types had intermediate amounts (23.23–54.52 Mg ha^{-1}) of mean total WD. The trend shown in mean coarse woody debris (CWD) was similar (Table 3). The mean CWD in the Mangrove (10.28 Mg ha^{-1}), Dry (5.81 Mg ha^{-1}), and Elfin (7.99 Mg ha^{-1}) forests were significantly lower than the mean CWD in the Palo Colorado (55.53 Mg ha^{-1}). The remaining forest types had intermediate amounts (16.06–40.60 Mg ha^{-1}) of CWD. Elevation and mean annual precipitation (MAP) were significantly and positively correlated at our sites, and both of these were negatively correlated with mean annual temperature (Fig. 2). There were significant positive relationships between CWD and both elevation ($r = 0.27$, $p = 0.02$) and MAP ($r = 0.28$, $p = 0.02$). CWD amounts increased and MAP

Table 3. Mean mass of litter, duff, and all categories of woody debris (Mg ha^{-1}) in eight forest types along an elevation gradient in northeastern Puerto Rico. Common letters within a category of debris represent significant differences among forest types (based on 2-MANOVAs, for the effect of forest type on 1) litter and duff and 2) all categories of woody debris as dependent variables. Student–Newman–Keuls Post Hoc Tests, $\alpha = 0.05$).

Category	R^2 (p value)	Mangrove	Dry	*Pterocarpus*	Moist	Tabonuco	Sierra palm	Palo Colorado	Elfin
Litter	0.22 (< 0.001)	0.12^{d}	0.91^{c}	1.12^{c}	1.29^{c}	2.59^{a}	1.90^{b}	1.44^{c}	1.19^{c}
Duff	0.10 (< 0.001)	0.00^{d}	0.68^{cb}	0.44^{c}	1.03^{a}	0.47^{c}	0.31^{c}	0.88^{ab}	0.52^{c}
1 h FWD	0.38 (< 0.001)	0.20^{bc}	0.35^{ab}	0.44^{a}	0.28^{bc}	0.31^{ab}	0.13^{c}	0.27^{bc}	0.18^{bc}
10 h FWD	0.31 (< 0.001)	2.63^{bc}	2.56^{bc}	4.91^{a}	3.07^{bc}	2.42^{bc}	2.39^{bc}	3.86^{ab}	1.52c
100 h FWD	0.26 (< 0.01)	10.12^{ab}	4.49^{b}	13.57^{a}	12.71^{a}	6.00^{ab}	9.19^{ab}	11.27^{ab}	5.99^{ab}
FWD – total	0.29 (< 0.01)	12.95^{ab}	7.39^{b}	18.91^{a}	16.06^{ab}	8.73^{b}	11.70^{ab}	15.39^{ab}	7.68^{b}
1000 h CWD	0.27 (< 0.01)	10.28^{b}	5.81^{b}	16.06^{ab}	21.75^{ab}	25.96^{ab}	40.60^{ab}	55.53^{a}	7.99^{b}
WD – total	0.30 (0.001)	23.23^{b}	13.2^{b}	34.97^{ab}	37.81^{ab}	34.69^{ab}	52.31^{ab}	70.92^{a}	15.67^{b}
Grand total (DWM)	0.31 (0.001)	23.35^{ab}	14.79^{b}	36.53^{ab}	40.13^{ab}	37.75^{ab}	54.52^{ab}	73.24^{a}	17.38^{b}

increased. Contrarily, CWD amounts decreased as MAT increased (Table 4).

There were significant differences in mean total fine woody debris (FWD) among forest types along the elevation gradient (Table 3). The mean total FWD in the Dry forests (7.39 Mg ha^{-1}) was significantly lower than the Moist (16.06 Mg ha^{-1}) and Palo Colorado (15.39 Mg ha^{-1}) forests. The remaining forest types had intermediate amounts (7.68–18.91 Mg ha^{-1}) of mean total FWD. The trend shown in 10 h FWD and 100 h FWD was similar. The Dry forest had a significantly lower amount of 100 h FWD (4.49 Mg ha^{-1}) than both the Moist (12.71 Mg ha^{-1}) and Palo Colorado (11.27 Mg ha^{-1}) forests. The Elfin forest had a significantly lower amount of 10 h FWD (1.52 Mg ha^{-1}) than both the *Pterocarpus* (4.91 Mg ha^{-1}) and Palo Colorado (3.86 Mg ha^{-1}) forests. However, the mean total 1hr FWD category did not follow the above trends. In this case, the Sierra palm forest had the least of all forest types (0.13 Mg ha^{-1}) and significantly less than the Dry forest (0.35 Mg ha^{-1}). There were significant negative relationships between FWD and both elevation ($r = -0.14$, $p = 0.04$) and MAP ($r = -0.14$, $p = 0.03$) (Table 4). Overall, forests at lower elevations had greater amounts of total FWD. Total FWD decreased as MAP increased (Table 4). There was no correlation between FWD and MAT ($r = 0.10$, $p = 0.14$) (Table 4).

There were significant differences in mean forest floor biomass (FF) (including litter and duff layers) among forest types along the elevation gradient (Table 3). The mean FF in the Mangrove (0.12 Mg ha^{-1}) and *Pterocarpus* (1.56 Mg ha^{-1}) forests were significantly lower than the mean total FF in the Tabonuco (3.06 Mg ha^{-1}) forests. The remaining forest types had intermediate amounts (1.59–2.32 Mg ha^{-1}) of mean total FF. All forest types showed significantly larger amounts of litter than duff except for the moist forest where the difference was not significant (Fig. 4). There were significant positive relationships between FF biomass and both elevation ($r = 0.24$, $p < 0.001$) and MAP ($r = 0.25$, $p < 0.001$). Amounts of FF biomass increased as both elevation and MAP increased (Table 4). An opposite trend was found for FF biomass and MAT, where FF increased and MAT decreased ($r = -0.29$, $p < 0.001$; Table 4).

There were significant differences in average number of occurrences of brown rot, white rot, and termites per piece of CWD encountered among the forest types (Table 5). Tabonuco and Palo Colorado forests had the greatest occurrence of brown rot (Fig. 5). The Elfin forest had the greatest occurrence of white rot. While, the dry forest had the greatest average number of termite occurrences (Fig. 5).

When we compared within each forest type, the average occurrence of brown rot, white rot and termites per

Table 4. Pearson correlation coefficients (r) for the elevation (m), mean annual precipitation (MAP) (mm), and mean annual temperature (MAT) (°C); and litter (Mg ha^{-1}), forest floor (Mg ha^{-1}), 1–100 h FWD (Mg ha^{-1}), total FWD (Mg ha^{-1}), and CWD (Mg ha^{-1}). Numbers in bold font represent correlation coefficients with a significant two-tailed probability value < 0.05 (n = 216).

Variable	Litter	Forest floor	1 h FWD	10 h FWD	100 h FWD	Total FWD	CWD
Elevation (m)	**0.28**	**0.24**	**–0.34**	**–0.19**	–0.10	**–0.14**	**0.27**
MAP (mm)	**0.35**	**0.25**	**–0.32**	**–0.21**	–0.10	**–0.14**	**0.28**
MAT (°C)	**–0.33**	**–0.29**	**0.28**	**0.15**	0.07	0.10	**–0.30**

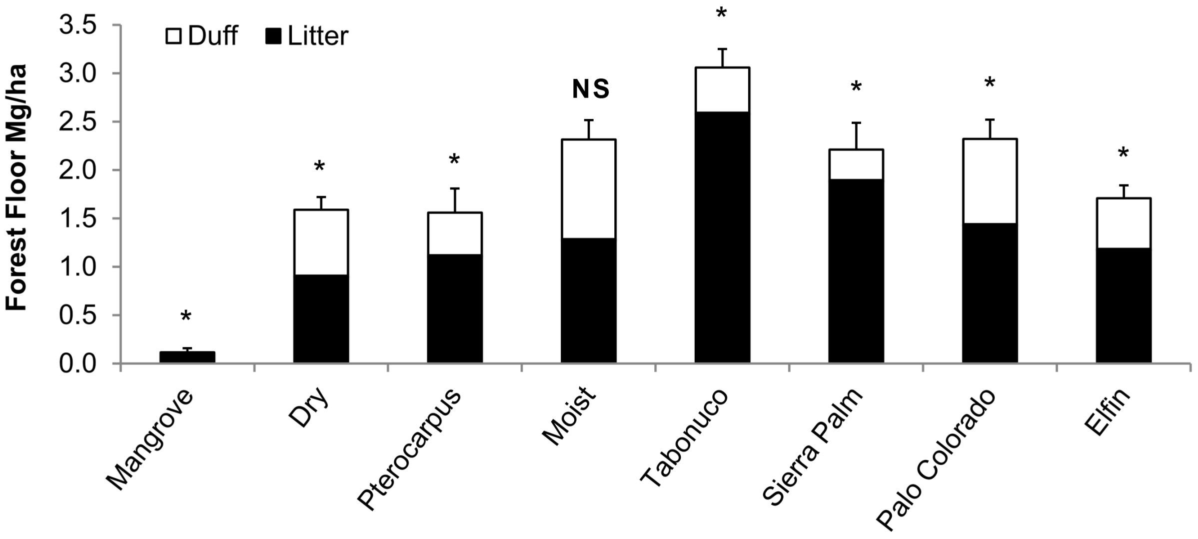

Figure 4. Forest floor litter and duff (Mg ha^{-1}) (±SE total forest floor; n = 81) for eight forest types along elevation gradient in northeastern Puerto Rico. Asterisks indicate significant difference between litter and duff biomass within forest type.

piece of CWD, we found that Palo Colorado and Tabonuco forests had significantly greater numbers of occurrence of brown rot than both white rot and termites (Table 5, Fig. 5). The Sierra palm forest had the lowest occurrence of termites as compared to brown and white rots (Fig. 5). The occurrence of termites on CWD was greatest in the dry forest (Table 5). Overall, there was a significant positive relationship between decay class and the occurrence of brown rot (Table 6, Fig. 6). White rot was significantly positively correlated with decay class in the Elfin forest solely. The occurrence of white rot was significantly positively correlated to both elevation and MAP (Table 6). While inversely, MAT was negatively correlated with the occurrence of white rot. Termites correlated negatively with elevation and MAP (Table 6).

Table 5. Mean number of observed occurrences of the brown rot, white rot, and termites (±SE) per piece of CWD in eight forest types along an elevation gradient in northeastern Puerto Rico. F and significance value (p) are results of the MANOVA analysis for the effect of forest type on the dependent variables (brown rot, white rot, and termites). Common letters within a variable represent significant differences (1-AOVs, Student–Newman–Keuls Post Hoc Tests, α = 0.05) among forest types.

Forest types	Brown rot	White rot	Termites
Mangrove	0.17 (0.06)^{b}	0.07 (0.04)^{b}	0.17 (0.06)^{bcd}
Pterocarpus	0.30 (0.06)^{ab}	0.32 (0.06)^{ab}	0.38 (0.07)^{b}
Dry	0.37 (0.11)^{ab}	0.21 (0.09)^{b}	0.79 (0.09)^{a}
Moist	0.50 (0.09)^{ab}	0.27 (0.08)^{ab}	0.33 (0.09)^{bc}
Tabonuco	0.66 (0.09)^{a}	0.14 (0.06)^{b}	0.07 (0.05)^{d}
Sierra palm	0.31 (0.07)^{ab}	0.31 (0.07)^{ab}	0.02 (0.02)^{d}
Palo Colorado	0.55 (0.06)^{a}	0.30 (0.06)^{ab}	0.12 (0.04)^{cd}
Elfin	0.35 (0.12)^{ab}	0.53 (0.12)^{a}	0.06 (0.06)^{d}
F (p)	4.44 (< 0.001)	2.77 (0.008)	12.14 (< 0.001)

Discussion and conclusion

The main objective of the study was to characterize, by size class, total amounts of woody debris within eight different forest types along an elevation gradient in northeastern Puerto Rico. To thoroughly estimate total biomass stored in woody materials, this survey included: coarse woody debris, fine woody debris, duff, and litter biomass. Exact comparison of the values obtained in this study with those collected in other tropical WD surveys was difficult as many of these surveys were focused solely on CWD. Furthermore, the definition of CWD in these surveys was not consistent and varied from 2.5 to > 10 cm minimum diameter. We reviewed CWD reported values within Puerto Rico, the tropics, and some temperate forests (Table 7). We found mean total woody debris (DWM) ranged 14.8 to 73.2 Mg ha^{-1} as characterized in eight forest types in northeastern Puerto Rico. When compared to values reported for other tropical forests in Puerto Rico, the mean total DWM averaged across all forest types (37.21 Mg ha^{-1}) in this study appears to be high (Table 7). This difference could be explained by CWD values which in this study were 6–7 times more than the values reported by Gould et al. (2008) and Brandeis and Woodall (2008). Yet, the CWD values reported in this study are well within the range of values of other tropical wet and moist forests in South and Central America (Table 4); which is contrary to results found by Brandeis and Woodall (2008). Forest age and structural development of sites can explain the

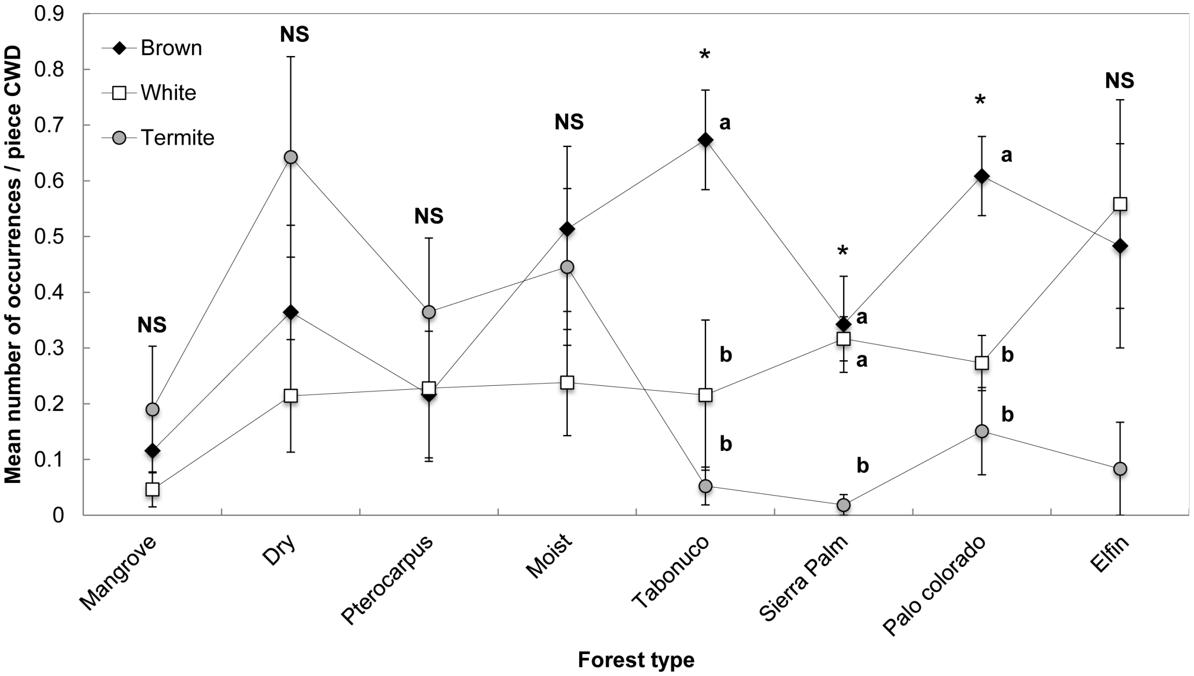

Figure 5. Number of observed occurrences of brown rot (black diamonds), white rot (white squares), or termites (grey circles) per piece of coarse woody debris for eight forest types along elevation gradient in northeastern Puerto Rico. Common letters within a forest type represent significant differences among categories (1-AOVs, α = 0.05).

difference in CWD values (Brandeis and Woodall 2008) between these two studies, particularly as the FIA plots are systematically located representing 121 points across the island (Brandeis and Woodall 2008) while this study was based on replicated mature forest stands within particular forest types in northeastern Puerto Rico. Another factor that can explain differences in CWD values between this study and Brandeis and Woodall (2008) is the timing of when the measurements were taken relative to the passage of last hurricane. The CWD values reported in Brandeis and Woodall (2008) were taken 3–8 yr subsequent to hurricane damage. While the in CWD values reported in this study are taken 12 yr since Hurricane Georges. Gould et al. (2008) found that age and forest structure had significant effects on forest floor fuels, downed woody debris, and live tree biomass. Thus, our study seems to support the contention that larger trees produce larger pieces of CWD and that perhaps over time FIA values would approach those values reported in this study as forests recover from hurricane damage and despite the fact that hurricane generated CWD will decay. When we examine the estimates within forest types for each woody material size class (Table 3), the values reported in this study fall within the expected range of values as previously reported in Puerto Rico. For example, mean total DWM reported for dry forests of NE Puerto Rico in this study (14.79 Mg ha^{-1}, Table 3) is very close to 15.0 Mg ha^{-1} estimated for the Guánica dry forest by Murphy and Lugo (1986)

Table 6. Pearson correlation coefficients (r) for elevation (m), mean annual precipitation (MAP), mean annual temperature (MAT), and decay class of CWD and mean number of observed occurrences of the brown rot, white rot, and termites per piece of CWD in eight forest types along an elevation gradient in northeastern Puerto Rico. Numbers in bold font represent correlation coefficients with a significant two-tailed probability value < 0.05.

Variable	Brown rot per piece CWD	White rot per piece CWD	Termite per piece CWD	Decay class
Elevation (m)	0.25	**0.33**	**–0.42**	**–0.31**
MAP (mm)	0.24	**0.34**	**–0.44**	**–0.37**
MAT (°C)	–0.32	**–0.35**	**0.42**	**0.26**
Decay class	**0.23**	0.03	0.03	–

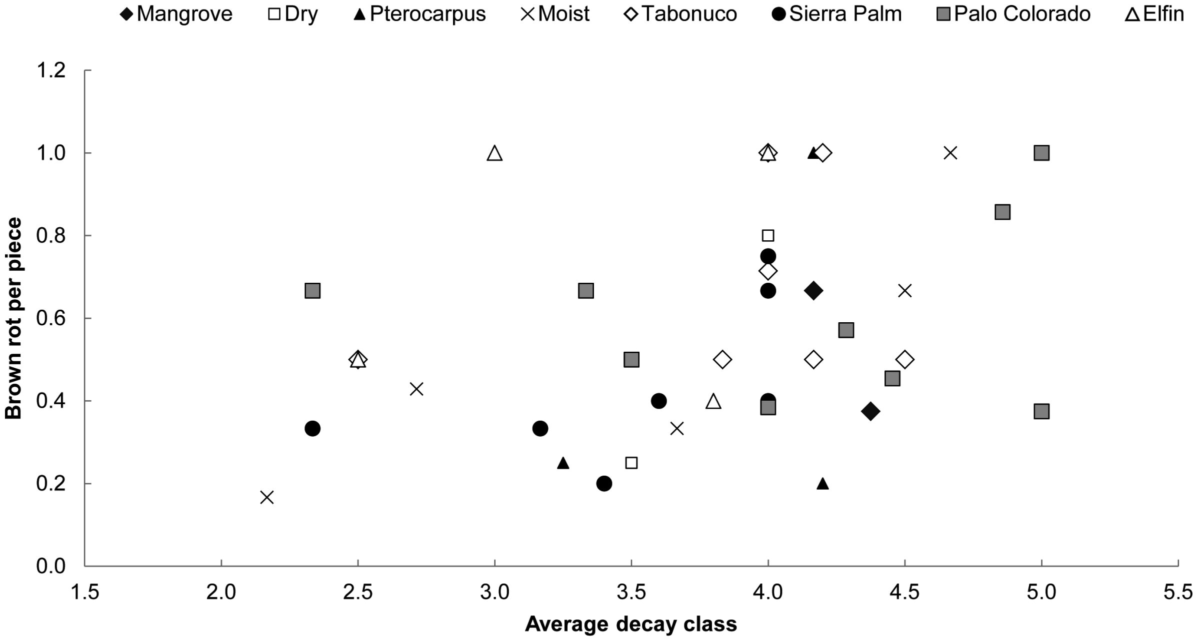

Figure 6. Correlation of average decay class and number of occurrences of brown rot per piece coarse woody debris.

(Table 7). In addition, mean total DWM we reported in the Elfin forest (15.67 Mg ha^{-1}, Table 3) was well within the range of 11.0–16.0 Mg ha^{-1} reported by Lugo et al. (1999) (Table 7).

The forests of Puerto Rico vary in terms of age, plant community, and woody debris amount and composition. In some cases, differences between current reported and historic values may be explained by factors such as time since disturbance, the land use history of a particular site, or seasonality. We reported a mean total DWM of 37.75 Mg ha^{-1} in our mature Tabonuco forest stands. This is much greater than the mean total DWM value reported by Li et al. (2005) (5.9 Mg ha^{-1}) for sites located within a recovering, post-agriculture, immature Tabonuco stand in the Luquillo Experimental Forest. Time since disturbance may partially explain the difference in reported values in this case.

Variability of the measurements within the landscape can also explain differences in reported values among studies. For example, in this study, the average size of individual pieces of coarse woody debris among all sites ranged from 0.10 to 1.05 m^3 (data not shown); however, we occasionally encountered individual pieces of woody debris up to 5.7 m^3 in size, increasing both variability and average size of CWD within a forest type. These pieces were large downed trees and were most often encountered in the mid-elevation forest types including: Lowland Moist, Tabonuco, Sierra palm, and Palo Colorado.

Reported values for litter, duff, and total forest floor in this study tended to be lower than other studies in Puerto Rico and many other forested ecosystems. For example, Murphy and Lugo (1986) reported 12.3 Mg ha^{-1} litter volume in a dry forest; in this study, the value (1.59 Mg ha^{-1}) was much lower and may be explained by seasonal peaks in litter fall within the dry forest. Cuevas et al. (1991) reported 4.54–9.53 Mg ha^{-1} forest floor for stands within Caribbean pine and broadleaf forests; this value was higher than we reported in any of the eight forest types in NE Puerto Rico. Time since disturbance or seasonality may explain these differences.

In this study, we expected that the amount and composition of both woody debris and forest floor would vary by forest type, and we found this to be true. Mean total amounts of DWM, CWD, FWD and FF varied among forest types. Similarly, the occurrence of particular categories of decomposer organisms varied among forests. We found that mid- to upper-elevation forests, which have been described by Gould et al. (2006) as exhibiting the greatest basal area and amounts of aboveground biomass, did have significantly larger amounts of mean total DWM than other forests in this study. The Palo Colorado forest (571–811 m) dominated by *Cyrilla racemiflora* and *Micropholis garciniifolia* have an average basal area of 61 ± 8.6 m^2 ha^{-1} and average aboveground biomass of 364 ± 62 Mg ha^{-1} (Gould et al. 2006). Meanwhile the Elfin forest, which occurs on the NE aspect of higher elevation sites (953–1000 m) in the Luquillo Mountains, and is dominated by *Tabebuia rigida* and *Eugenia borinquensis,* has low average basal area of 27 ± 4.8 m^2 ha^{-1} (Gould et al. 2006) as well as very low aboveground biomass particularly than the most productive forest, Palo Colorado. The dominant species of the Elfin forest, *T. rigida*, rarely pro-

Table 7. Values (Mg ha^{-1}) of coarse woody debris (CWD), fine woody debris (FWD), sum of coarse and fine woody debris (Total WD), sum of litter and duff (Forest floor), and sum of all categories (Total DWM) reported in this study and comparable tropical and temperate studies located across the region. Values reported from this study are the averages of each category across the 8 forest types.

Location	CWD	FWD	Total WD	Forest floor	Total DWM	Author
Puerto Rico – This Study	23.0	12.35	35.35	1.86	37.21	González and Luce 2013
Puerto Rico – Dry Forest	–	–	2.7	12.3	15	Murphy and Lugo 1986
Puerto Rico – Car. Pine and Broadleaf	–	–	–	4.54–9.53	–	Cuevas et al. 1991
Puerto Rico – Wet Forest	–	–	–	–	11.0–16	Lugo et al. 1999
Puerto Rico – Wet Forest	–	–	–	–	5.9	Li et al. 2005
Puerto Rico – Closed Forest	3.0	9.4	12.4	8.3	20.7	Gould et al. 2008
Puerto Rico and US Virgin Islands	4.3	10.5	14.8	11.1	25.8	Brandeis and Woodall 2008
Venezuela – Dry Forest	2.4	5.2	7.6	–	–	Delaney et al. 1997
Venezuela – Dry/Moist Transition	3.3	2.7	6	–	–	Delaney et al. 1997
Venezuela – Lower Montane Moist	21.2	3.1	24.3	–	–	Delaney et al. 1997
Venezuela – Lower Montane Wet	17.2	2.7	19.9	–	–	Delaney et al. 1997
Venezuela – Moist Forest	16.7	2.4	19.1	–	–	Delaney et al. 1997
Mexico – Dry Forest	5.3–31.5	3.5–6.0	–	–	–	Eaton and Lawrence 2006
Mexico – Dry Forest	15.7	–	–	–	–	Stephens et al. 2007
Brazil – Amazon	28.9	9.6	38.5	–	–	Cummings et al. 2002
Brazil – Amazon	24.7	3.2	27.9	7.6	63.4	Nascimento and Laurance 2002
Brazil – Cauaxi and Tapajós	–	–	50.7–55.2	–	–	Keller et al. 2004
Brazil – Juruena and Mato Grosso	44.9	–	–	–	–	Palace et al. 2007
Peru – Amazon	24.4	–	–	–	–	Baker et al. 2007
Guyana – Rain Forest	21.5–22.6	2.9	–	–	–	ter Steege 2001
Micronesia – Mangrove	20.9	–	–	–	–	Allen et al. 2000
USA – All Forest	–	–	–	–	10.2–88.8	Birdsey 1992
USA – Temperate Forest	4.4	7.3	11.7	17.9	32	Chojnacky and Schuler 2004
USA – Tropical Wet Everglades	0.65	1.64	2.29	18.51	21	Smith et al. 2010
USA Temperate Marine West Coast	18.32	4.16	22.48	33.95	56.39	Smith et al. 2010

duces large enough trees to generate measurable amounts of coarse woody debris. Additionally, within this forest type we found very little dead downed debris, as downed trees tended to sprout new branches and roots where they fell.

Productivity and decomposition within forest types and along the elevation gradients vary as climatic conditions interact, creating more or less suitable growing conditions for both producers and decomposers (Meentemeyer 1978, González 2002). Productivity is affected by decreased temperature, increased rainfall, and prevalence of anoxic conditions. The presence of persistent woody debris within a forest is a product of both rates of production as well as rates of decomposition. In addition, growth habit, basal area and total aboveground biomass are all important in determining the amounts of woody debris encountered. In this study, across all forest types we found a significant correlation between decay class of CWD and MAP ($r = -0.37$, $p = 0.01$) and decay class of CWD and MAT ($r = 0.26$, $p = 0.04$, Table 6); indicating climate plays an important role on decay rates of CWD at these sites. As elevation and MAP increased, a trend of increasing amounts of woody debris (until the Elfin forest was encountered) and decreased decay of CWD was found. Interestingly, in the Elfin forest, the decay class of CWD was most strongly correlated with white rot (data not shown). Additionally, across all forest types in this study, the decay class of CWD also correlated well with the average occurrence of brown rot fungi (Table 6, Fig. 6).

We found brown rot frequency was greatest in the middle elevation moist forest type, whereas other studies in the tropics have found brown rot basidiomycete fungi diversity to peak in dry forests (Gilberston and Ryvarden 1986). However, the data presented here are consistent with the differential abundance of brown rot on large diameter CWD, especially boles with a lot of heartwood (Harmon et. al. 1994). In addition, white rot tends to precede brown rot in the decay of heartwood, supported in our study, as the occurrence of brown rot was associated with greater decay (Table 6, Fig. 6). Thus, these results suggest that decomposer organisms are also key determinants of decay in these forest types in NE Puerto Rico. Further it might suggest that the contribution of different groups of decomposers to the decay of CWD might vary among the different forest types located along elevation and environmental gradients. These two contentions of decreased decay as MAP increases and differential effects of organisms on decay would be consistent with results previously reported by Torres and González (2005) and González et al. (2008). Torres and González (2005) found that high moisture content, low animal abundance and the absence of groups of wood-inhabiting organisms can retard decay in wet forests. González et al. (2008) found moisture conditions to be an important control over wood decomposition over broad climatic gradients; and the presence of a particular group of organism (termites) can significantly alter the decay rates of wood more than what might be predicted based on climatic factors alone.

In this study, we also hypothesized that the FWD, litter, and duff layers be an important source of organic matter at these sites. We found the FWD fraction represented 54–56% of the biomass stored in woody debris in the Mangrove, Dry, and *Pterocarpus* forests. Tabonuco, Sierra palm, and Palo Colorado had a smaller fraction of FWD with 22–25% of total storage in these forests. Therefore, woody debris surveys focusing solely on CWD measurements can significantly underestimate woody debris contributions to the total carbon stored at some forest types.

As a future research direction, we propose surveying the presence and amount of palm fronds within different forests in Puerto Rico, to increase the understanding of the amounts of woody debris within and among forests types. Within the Sierra palm forest, palm fronds make up a significant portion of both litter and woody debris that cover the ground. Palm fronds fulfill a similar functional role to both woody debris and litter; providing, buffering of the soil surface temperature and moisture, nutrients and habitat for ground-dwelling decomposing organisms, soil stabilization, and carbon storage.

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