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Review

Soil Biology Research across Latitude, Elevation and Disturbance Gradients: A Review of Forest Studies from Puerto Rico during the Past 25 Years

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Abstract: Progress in understanding changes in soil biology in response to latitude, elevation and disturbance gradients has generally lagged behind studies of above-ground plants and animals owing to methodological constraints and high diversity and complexity of interactions in below-ground food webs. New methods have opened research opportunities in below-ground systems, leading to a rapid increase in studies of below-ground organisms and processes. Here, we summarize results of forest soil biology research over the past 25 years in Puerto Rico as part of a 75th Anniversary Symposium on research of the USDA Forest Service International Institute of Tropical Forestry. These results are presented in the context of changes in soil and forest floor biota across latitudinal, elevation and disturbance gradients. Invertebrate detritivores in these tropical forests exerted a stronger influence on leaf decomposition than in cold temperate forests using a common substrate. Small changes in arthropods brought about using different litterbag mesh sizes induced larger changes in leaf litter mass loss and nutrient mineralization. Fungi and bacteria in litter and soil of wet forests were surprisingly sensitive to drying, leading to changes in nutrient cycling. Tropical fungi also showed sensitivity to environmental fluctuations and gradients as fungal phylotype composition in soil had a high turnover along an elevation gradient in Puerto Rico. Globally, tropical soil fungi had smaller geographic ranges than temperate fungi. Invertebrate activity accelerates decomposition of woody debris, especially in lowland dry forest, but invertebrates are also important in early stages of log decomposition in middle elevation wet forests. Large deposits of scoltine bark beetle frass from freshly fallen logs coincide with nutrient immobilization by soil microbial biomass and a relatively low density of tree roots in soil under newly fallen logs. Tree roots shifted their foraging locations seasonally in relation to decaying logs. Native earthworms were sensitive to disturbance and were absent from tree plantations, whereas introduced earthworms were found across elevation and disturbance gradients.

Keywords: tropical forests; invertebrates; microbiota; soil biota; litter; wood; latitude; elevation; disturbance; gradients

1. Introduction

Although below-ground research has lagged behind above-ground studies of plants and animals, especially in tropical forests, the Luquillo Experimental Forest (LEF) in Eastern Puerto Rico has some of the earliest research on effects of disturbance on fungi and ecosystem processes. Research carried out in the 1960s by the US Department of Energy under the Atoms for Peace program, and largely published in a book edited by H.T. Odum and R.F. Pigeon [1] showed that disturbances that open the forest canopy, whether from cutting or gamma irradiation, induce major shifts in fungal communities (see summary in Lodge [2]). The methods used at the time were limited, so the studies of disturbed vs. undisturbed environments by Holler [3] and Holler and Cowley [4] focused on comparisons of morphospecies of fungi that could be grown on agar. Nevertheless, they showed strong responses of litter fungi to disturbance. Those early results have been largely validated more recently using modern techniques that detect all fungi and bacteria, such as identifying phylospecies using Terminal Restriction Length Polymorphism (TRFLP) and sequences of the Internal Transcribed Spacer (ITS)—A DNA region used as a molecular barcode in fungi, and Extracted Microbial Fatty Acid Methyl Ester (FAME) analysis for overall changes in dominance among microbial groups e.g., Cantrell et al. [5,6]. Early work on whole ecosystem respiration [1] has been superseded by soil gas flux measurements using automated samplers for below-ground fluxes e.g., [7–9].

In the tropics, a great deal of attention has been given to above-ground organisms, while few studies deal with the diversity of invertebrates in the soil, leaf litter, or dead wood [10]. There have been some quantitative studies of below-ground invertebrates in tropical forests [11]. Early faunal inventories at El Verde in the Luquillo Experimental Forest [12,13] showed that about half of the faunal biomass was concentrated in the thin upper soil horizon and litter layer. Given the persistence of both anthropogenic and non-anthropogenic disturbances in the tropics, it is important to study the diversity of its fauna and assess how they can affect ecosystem functioning. For example, recent research has focused on the effects of disturbance on arthropods and their connectivity to other biotic and abiotic factors in forested ecosystems that can have significant effects on detrital processes [14–17].

A recent focus of studies in the tropics has been on changes in biotic communities along elevation gradients [18,19]. These studies shed light on the abiotic and biotic factors that control species distributions, biotic assemblages and ecosystem processes. Further, elevation gradient studies provide baseline data for biota that may be imperiled by climate change, especially for species that are restricted to high-elevation cloud forests. Changes in ecological space along elevation gradients can be used as a proxy for environmental changes across latitudinal gradients [18,19]. While species distributions may respond similarly to changes in ecological space along both elevation and latitudinal gradients, they are also influenced by barriers to dispersal and colonization (i.e., filters) at the longer distances associated with latitudinal gradients.

The aim of this paper is to review the salient results of research on soil and litter biota in forests over the last 25 years in Puerto Rico. This manuscript is part of a Special Issue comprised of presentations at the 75th anniversary of the establishment of the International Institute of Tropical Forestry in Puerto Rico (United States Department of Agriculture, Forest Service).

2. Summary of Results over the Past 25 Years

2.1. Latitudinal Gradients

The status of information on soil animal diversity in the tropics is limited, particularly when compared to other ecosystems such as temperate forests, grasslands and deserts [11]. In Puerto Rico (as in many other tropical regions), when present, earthworms compose the highest biomass among the soil macrofauna [1]; and thus play important roles in regulating soil processes [20]. The density of macroarthropods (such as myriapodans and crustaceans) is higher at LEF than in tropical sites elsewhere; ants are also an important component of the litter invertebrate community with densities ranging from 500 to 1200 m^{-2} [13,21]. In the LEF, millipedes appear to be the predominant taxa in the tabonuco forest litter at mid-elevations in terms of standing stocks (0.6 $g \cdot m^{-2}$; Pfeiffer, [13]). Yet, the contribution of soil fauna activities to ecosystem processes varies widely along latitudinal gradients because it depends on the confounding effects of the size, abundance, diversity, and functionality e.g., [22–26].

2.1.1. Arthropods Are More Diverse and Accelerate Leaf Litter Mass Loss More in Wet Tropical Forest than in Cold Temperate Forest

Soil fauna can influence decomposition and mineralization processes either directly by modifying litter and soil environments or indirectly via interactions with the microbial community [27–30]. In a study comparing leaf decomposition across a latitudinal gradient between wet tropical forest in Puerto Rico and subalpine forest in Colorado, soil fauna appeared to have greater direct effects via grazing on the microbial community whereas in the tropical forest, soil fauna appeared to have primarily indirect effects via litter comminution [25–27]. Comminution fragments litter and opens fresh surfaces to microbial decomposers. González and Seastedt [25] compared leaf decomposition rates and arthropod higher-order assemblage diversity (expressed as the number of orders) in wet and dry tropical forests of Puerto Rico and temperate subalpine forest in Colorado and found highest diversity and decomposition rates in wet tropical forest. Similarly, Heneghan et al. [23,31] compared decomposition of a common substrate (*Quercus* leaves) among wet neotropical forests of Puerto Rico and Costa Rica and warm temperate forest in North Carolina, and found highest decomposition rates among neotropical forests despite having similar or even lower species diversity. On the other hand, data of Crossley in Coleman et al. [32] showed high magnitude (45%–71%) soil fauna effects in warm temperate forest in western North Carolina, USA. Similarly, soil fauna can account for up to 66% of the total decomposition of tough *Cecropia schreberiana* leaves with high lignocellulose content in the tropical wet forest in Puerto Rico [25], and macroarthropods involved in comminution of litter, such as millipedes, can have the strongest effect on leaf litter mass loss. For example, González et al. [33] found that millipedes can affect leaf litter decomposition both directly and indirectly, but the extent of their effect depends on their density and the quality of the substrate (leaf lignin content). Also, Ruan et al. [34] found that millipede density explained 40% of the variation in leaf decomposition rates, whereas microbial biomass explained only 19% of the variance. Leaf litter comminution by termites is common in the paleotropics where fungal gardening termites occur, but not in neotropical forests where this termite feeding guild is absent. Termites that consume leaf litter are either uncommon or poorly documented in neotropical forests, though there is a specialized grass-feeding termite in the grasslands of the Great Savanna of Venezuela. There are no termite species that consume leaf litter in Puerto Rico.

Wood is the main constituent of tropical forest detritus [35]. Boreal, 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 [36,37]. Thus, González et al. [34] set up a wood decomposition experiment to quantify the decay of aspen stakes (*Populus tremuloides*) in dry and moist boreal, temperate and tropical (Puerto Rico) forest types. They concluded that moisture content is an important control of wood decomposition over broad climate gradients, and that such relationship can be non-linear. Furthermore, they also found that the presence termites significantly altered the decay rates of wood in ways that cannot be predicted solely with climatic factors. These data suggest that biotic controls, rather than abiotic constraints, can better predict wood decay in tropical regions [36].

2.1.2. Tropical Soil Fungi Are Generally More Diverse and Have Smaller Geographic Ranges than Temperate Fungi, and Fungal Diversity Is Related to Rates of Leaf Decomposition

Comparisons of fungal diversity between tropical and temperate forests have previously been generated using a few well-studied plots across latitudinal gradients and then making projections based on fungi to plant species richness ratios [38,39]. For example, Mueller et al. [38] used inventories and name databases to validate macrofungal (those with fruiting bodies visible without magnification) to plant species ratios and arrived at a ratio of 2:1 for temperate regions and 5:1 for tropical regions. Since tropical regions have much higher plant diversity than temperate regions, this led to much higher estimates of macrofungal diversity in the tropics. Further, Mueller et al. [38] indicated that tropical macrofungi had higher rates of regional endemism than temperate fungi. Lodge et al. [40]

also found that in two families of mushrooms, 41% of Hygrophoraceae and 54% of Entolomataceae species were endemic to the Greater Antilles or the Caribbean islands. Animals, including detrital invertebrates, have long been known to have smaller geographic ranges in the tropics than at higher latitudes—A pattern now referred to as part of Rapoport's Rule [41]. Several publications correctly noted the relationship between larger body sizes among detrital invertebrates and more discontinuous and narrower distributions, but they incorrectly assumed that microorganisms including fungi fit into the small body size end of this scheme and had predominantly wide, ubiquitous distributions [42–44]. A more recent global analysis by Tedersoo et al. [45] of all soil fungal diversity based on DNA barcode sampling of natural communities in soils including El Verde in the Luquillo Experimental Forest of Puerto Rico supports the patterns of latitudinal gradients in fungal diversity observed by Mueller et al. [38], and also high abundance of regional endemism found by Mueller et al. [38] and Lodge et al. [40]. Except for ectomycorrhizal fungi that are obligate symbionts of mostly temperate and boreal trees, Tedersoo et al. [45] found that soil fungal diversity was generally greater at low than at high latitude. Furthermore, Tedersoo et al.'s [45] results are consistent with those of Mueller et al. [38] and Rapoport's Rule in showing that geographic ranges of tropical fungi are smaller than those of high latitude fungi. Tedersoo et al.'s [45] study greatly underestimates forest floor fungal diversity in tropical forests, however, as they removed loose leaf litter and duff from the soil before collecting samples of humus and soil. Polishook et al. [46] studied microfungi (not visible without magnification) in decomposing leaves of two tree species that occurred together on the forest floor at El Verde in Puerto Rico and showed they had strong differential abundances. These host 'preferences' were strongest among the dominant microfungi of each leaf species [46]. The segregation of decomposer microfungi among leaf species helps explain the high species richness of microfungi in decomposing litter of wet tropical forests [46]. Further, Polishook et al. [46] showed that while some species are ubiquitous, a large proportion are regionally or locally endemic. Santana et al. [47] later showed that the dominant microfungi on leaves of five tree species decomposed their source leaves faster than dominant microfungi from the other four leaf species. This result indicates that the high species richness of microfungal leaf decomposers is related to rates of decomposition because different leaves have different fungal dominants that are more efficient at decomposing their preferred hosts. The Santana et al. [47] study published in 2005 was among the first to show that diversity of primary decomposers was related to ecosystem function, and that there is more complementarity and less redundancy in below-ground ecosystems than previously thought. A subsequent review by Eisenhauer [48], supports the theoretical basis for diversity effects on ecosystem function through complementarity in below-ground systems, whereas Bardgett and van der Putten [49] have argued that species richness only has effects in very simple systems because there is much redundancy. Most recently, analyses of European grasslands by Soliveres et al. [50] showed that multitrophic diversity strongly predicted ecosystem functions, and that diversity of microbial decomposers has a particularly strong effect.

2.2. Elevation Gradients

Changes in biotic assemblages along elevation gradients can reveal sensitivities in particular groups of organisms to environmental variation that is correlated with elevation [18,19], or dependencies on other organisms that respond strongly to climate [51]. High turnover in microbial species assemblages along an elevation gradient in eastern Puerto Rico [5] resembles patterns found on mountains in Malaysia, Mexico and Peru where high turnover of plant and fungal assemblages along elevation gradients are also found [52–55]. The study of phylogenetic origins of endemic species of plants, animals and fungi on a young mountain in Malaysia by Merckx et al. [52] showed strong niche conservatism that results in high species turnover along the elevation gradient [55,56]. A subsequent analysis by Geml et al. [57] from the same mountain showed that the peak in species richness of ectomycorrhizal fungi at lower-middle elevation was primarily tied to narrow environmental niches and not the result of broad-range species overlapping in the middle of the gradient (known as the mid-domain effect). Sensitivities of tropical montane organisms to changes in environmental factors is important in the context of climate change [18,19,51,58], but not all changes in biota are direct responses to environment [51]. For example, restriction to neotropical cloud forests of certain Ascomycete species in the genus *Xylaria* was related to their specificity to endemic cloud forest plants rather than to the environment per se [51].

2.2.1. Invertebrate Diversity and Abundance along an Elevation Gradient in Puerto Rico

The Luquillo Mountains represent an ideal setting to study dramatic changes in climatic characteristics over a short distance inland (25 km), as an elevation gradient spanning about 1000 m and differences in temperature and precipitation of about 5 °C and 2600 mm respectively, can be found going from the coast to the top of the mountain. Even though the pattern of tree species abundance along this elevation gradient shows species with narrow as well as wide ranges [59], four forest types have been recognized within LEF [60]. In an effort to relate species richness and abundance of litter-based invertebrate communities to forest productivity along elevational/ecological gradients, Richardson et al. [21] controlled for forest types by comparing mixed forest stands with adjacent areas under palm vegetation at different elevations within the Luquillo Mountains. In forest floor litter communities, using palm litter as a control for forest type, they found that although overall net primary productivity (NPP) declined with increasing elevation and rainfall, animal abundance, biomass, and species richness were remarkably similar along the gradient. In non-palm litter, all community parameters declined with increasing elevation, along with NPP and litter nutrient concentrations [61]. Therefore, they found differences observed in animal abundance and species richness, and the uniformity of communities along the increasing elevational gradient were better explained by the contribution of forest composition to the chemical and physical nature of litter and forest heterogeneity, rather than to direct effects of temperature and rainfall differences [19]. Likewise, Willig et al. [62] have shown that abundances of most species of terrestrial gastropod decrease with increasing elevation, as do metrics of taxonomic biodiversity (i.e., species richness, species rarity, species diversity). González et al. [63] found that the number of earthworm species significantly increases as elevation and annual rainfall increase and temperature decreases. The highest numbers of native earthworm species were found in the elfin and palo colorado forests (10 and five species, respectively). Introduced earthworms were also widespread. *Pontoscolex corethrurus* (pantropical introduced worm) was found in all but the dry, *Pterocarpus* and mangrove forests. The exotic *Ocnerodrilus occidentalis* was found in all but the palo colorado, *Pterocarpus* and mangrove forests. The lowland moist forest had the highest presence of exotic worms. Richardson et al. [64] studied the effects of nutrient availability and other elevational changes on bromeliad populations and their invertebrate comminuters. They found that animal abundance in bromeliads peaked at intermediate elevations.

Woody debris is an important component of the carbon pool and a potential carbon sink in terrestrial ecosystems globally [65–67]. Yet, most surveys of amounts and properties of woody debris have been performed within temperate systems as well as the mainland tropics where these collections are often limited to a few forest types encompassing large land areas [68,69]. In Puerto Rico, González and Luce [35] characterized coarse woody debris (CWD) and fine woody debris at 24 sites (encompassing eight distinct forest types) along an elevation gradient in northeastern Puerto Rico. They found that the contribution of different groups of decomposers to the decay of CWD varies among different forest types located along elevation and environmental gradients [35]. For example, they found in the elfin forest (on peaks in the LEF), the decay class of CWD was most strongly correlated with white rot fungi. Termites were most abundant in dry forests at low elevation. Fungal white-rot was positively correlated with mean annual precipitation and was most abundant at high elevation whereas brown-rot was most abundant at middle elevations [35].

2.2.2. Microbial Diversity, Abundance and Turnover along an Elevation Gradient in Puerto Rico

Microbial biomass and diversity are often correlated [70,71]. Zalamea and González [71] found a decline in total microbial biomass with increasing elevation and moisture from dry coastal forest to mid-elevation wet forest in the Luquillo Mountains of Eastern Puerto Rico using a substrate induced respiration method. Similarly, Cantrell et al. [5] found an overall decline in microbial fatty acid diversity from dry coastal forest to montane rain forest along the same gradient using FAME and TRFLP analyses. The peak in soil fungal abundance and fungal to bacteria ratios occurred in mid-elevation wet forest [5]. Correspondingly, abundance of decomposer basidiomycete (macrofungi that cause white rot) mycelia in leaf litter (% forest floor cover) also declined with elevation from wet mid-elevation forest to montane rain forest at the peak of the Luquillo Mountains [5,72]. White-rot in wood, however, increased with elevation and annual precipitation, whereas brown-rot (caused by different species of basidiomycete macrofungi) was most abundant in the middle of the elevation gradient [35]. Diversity and abundance of Mycetozoa ('slime molds') decreased with increasing elevation in the Luquillo Mountains [5,73–76]. In contrast, bacteria abundance, especially among G- bacteria, was greatest at the two ends of the elevation gradient and lowest in mid-elevation wet forest [5]. The highest diversity of sulfidogenic bacteria and Chrenarchaeota was in the frequently waterlogged soils at high elevation where rainfall is highest [5]. Waterlogging reduces soil oxygen and redox potential, which also favors growth and activity of methaogenic bacteria, so methane production was found to increase with elevation in the Luquillo Mountains [7,8].

Similar to patterns found elsewhere in tropical forest elevation gradients, the turnover of fungal assemblages along the elevation gradient in the Luquillo Mountains of Puerto Rico was strong with little overlap between adjacent forest types using TRFLP analyses [5]. Similar patterns have been observed along elevation gradients in Borneo, Mexico and Peru [52,53,70]. The turnover of protists (bacteria and Chrenarecheaota) between adjacent forest types was not as strong as the turnover in soil fungi, but the two highest elevation forests had species unique to this zone [5]. Changing the location of organisms along an elevation gradient is often used as a proxy for detecting responses to climate change. Differences in soil microbiota were thought to have contributed to increased carbon loss when soil cores were translocated from both low to high and high to low elevation relative to cores translocated within the same habitat [77].

2.3. Disturbance Gradients

Tropical forests are exposed to an array of disturbance types that vary in intensity, frequency and duration [78,79]. These include events such as tropical cyclones, landslides and droughts [78–80] and anthropogenic disturbances such as timber and charcoal extraction and conversion of forest to plantations, agricultural crops and pastures. The responses of soil biota to these disturbances depends on characteristics of the phylogenetic group or species, the nature and severity of the disturbance, and interactions with other organisms in the below-ground food web.

2.3.1. Invertebrate Responses to Disturbance Gradients

The responses of invertebrates to disturbance in tropical forests vary among phylogenetic groups from phyla to species. For example, native earthworms were abundant in natural second growth forest in Puerto Rico, but absent from adjacent tree plantations, indicating that they are sensitive to disturbance [81]. Further, earthworm dry weight and abundance were twice as high in native second growth forest than in more disturbed tree plantations [81]. Once an introduced species has been established in a new place, the site and species characteristics seem to be key factors determining its spread [82]. In contrast to introduced species, native earthworms are not as tolerant to a shift to dryer grassland microclimate conditions, and are mostly restricted to natural ecosystems [81,83,84]. For example, the introduced *P. corethrurus* can reach an abundance of 1000 individuals per square meter (25 cm deep) in disturbed agricultural pastures [83]. The rapid population growth of this worm may increase competition pressure on food resources on the local earthworm community [85], further leading to changes in N dynamics at the site. It has been shown that *P. corethrurus* enhance nitrogen availability and mineralization in pasture soils [86]. However, Huang et al. [85] showed soil N mineralization by individual *Estherella* spp. and *O. borincana* (native worms) was reduced in the mixed-species treatments containing *P. corethrurus*. Huang et al. [85] proposed that biotic factors, such as competitive exclusion of native earthworms by introduced earthworms, may have considerable effects on retarding their re-colonization and/or causing the disappearance of native earthworm population in disturbed areas. It has been suggested that habitat disturbance, such as fertilizer amendments or vegetation conversion, increase resource availability to anthropochorous earthworms, thus enhancing their ability to invade disturbed sites [87,88]. However, results from the subtropical wet forest (tabonuco) in Puerto Rico support the contention that worm density and biomass can be decreased by fertilization via changes in soil acidity [89]. Barberena-Arias and Aide [90] and Osorio-Pérez et al. [91] studied litter insect diversity and trophic composition during plant secondary succession in Puerto Rico. They found that arthropod species composition was significantly different between early and intermediate/late forests where early successional habitats had few unique species, and intermediate/late habitats had more species specific to woody habitats—suggesting the recovery of arthropod diversity during plant secondary succession is dependent not only on the increase of wood and concomitant resources but also on the recovery of plant diversity [92].

Canopy opening in a simulated hurricane treatment induced shifts in dominance in the litter from macroarthropods such as isopods and millipedes, which are light-averse, to microarthropods, particularly mites [14,24]. Further, González et al. [15] found a negative correlation between the Margalef index of diversity of the litter arthropods and the percent of mass remaining of mixed species of litter, suggesting functional complexity is an important determinant of decay in the LEF. Snail species responded idiosyncratically to the effects of canopy opening and debris deposition. Abundances of all gastropods (combined) as well as abundances of each of three species responded to canopy opening, while abundances of two other species in the same genera responded to debris deposition but not canopy opening [93,94]. Similarly, Torres and González [95] studied the decomposition of *Cyrilla racemiflora* logs over a 13-year period in tropical dry and wet forests in Puerto Rico and found that termites were more abundant in the logs from the tropical dry forest than from the tropical wet forest. High moisture content and low animal diversity seemed to retard wood decay in wet forest, while high diversity of species and functional groups of wood-inhabiting organisms appeared to increase wood decay rates in tropical dry forest.

2.3.2. Microbial Responses to Disturbances

The responses of microbes to disturbance and environmental stress depends on the sensitivity of the organisms and the nature and severity of the disturbance. According to Stephenson et al., Dictyostelid (cellular), protestelid (amoeboid) and myxomycete (plasmodial) slime molds were most abundant in disturbed habitats in mid-elevation wet forest of Puerto Rico [76]. These disturbed sites correspond to the highest functional diversity of the slime mold's prey (primarily bacteria and yeasts) [96]. In contrast, fungi of wet forest in Puerto Rico were found to be surprisingly sensitive to disturbance, especially those associated with a drier environment. Lodge [97] found that fungal biomass in the litter layer sometimes tripled or decreased by half depending on the number of days in the preceding week in which throughfall reached the forest floor. Similarly, reduced litter moisture in plots where the canopy had been removed relative to untrimmed forest was associated with reductions in basidiomycete fungi. Lodge et al. [98,99] found large reductions in ground cover by basidiomycete leaf decomposer mycelial mats in the drier litter of trimmed plots, and abundances of basidiomycete fungal connections between litter layers were also reduced. Soil fungal biomass also varied with soil moisture [97]. Lodge and Ingham [100] found that soil fungal hyphal diameter distributions had almost no overlap between the wetter and drier seasons, indicating a radical change in fungal community dominance between seasons despite the mid-elevation forest where the samples were taken being classified as 'non-seasonal' in the Holdridge Life Zone system. Li and González [44] found significant decreases in total and active fungal and bacterial biomass in the drier season compared to the wetter season working at the same site as Lodge and Ingham [100]. Soil bacteria as well as fungi were found to be highly sensitive to low moisture using a throughfall exclosure experiment, particularly at a low-moisture threshold [101,102]. While canopy trimming in the hurricane simulation experiment decreased litter moisture, soil moisture increased due to reduction of evapotranspiration [14,17,103]. It is therefore not surprising that Cantrell et al. [6] found no effects of canopy trimming and debris deposition treatments in soil microbial communities using FAME and TRFLP analyses, but did find differences attributable to drought in the control plots between years.

2.3.3. Biotic Changes and Interactions in the Detrital Food Web Affect Nutrient and Carbon Cycling

While invertebrates generally have a dominant role in decomposition of organic matter in tropical forests, they also interact with microbial decomposers. For example, freshwater shrimp consumed leaf litter differentially depending on preconditioning by different types of terrestrial fungi. Using paired presentations of leaf discs cut from different parts of the same leaves that had been decomposed by basidiomycete macrofungi versus microfungi, freshwater shrimp selected tough leaves with basidiomycete fungi over microfungi, but had no preferences between rot types in soft leaves [104]. Biotic interactions between plants and detrital communities have also been seen in cross-site leaf decomposition studies. Home-field advantage has been observed where detrital processing and mass loss was faster in the forest type of origin than when translocated to other forest types in the same region or across latitudinal gradients [25,105,106]. Basidiomycete fungi soften decomposing leaves by degrading lignocellulose, so are more important for preconditioning of tough leaves to make them palatable to invertebrates. In a hurricane simulation experiment, a shift in dominance in fungal decomposers from basidiomycete macrofungi to microfungi was associated with increases in fungivore specialist groups (mites, collembola and psocoptera) [14,17,24]. Furthermore, reductions in macroarthropod comminuters of litter and basidiomycete decomposer fungi that degrade lignin together were likely responsible for reduction in rates of leaf decomposition in plots where the canopy was opened [14,17,24,98]. Reduction of basidiomycete fungi was associated with reduced accumulation of phosphorus via translocation by fungal root-like structures, which could have contributed to slowing of leaf decomposition in plots where the canopy was opened [98]. In undisturbed wet forest under closed canopy, drying cycles that kill basidiomycete fungal hyphae followed by rewetting can lead to a pulse of phosphorus released from the litter to soil [107,108]. Such pulsed releases of phosphorus may favor plant root uptake at times when competing soil microbial biomass has been reduced by lower soil moisture [104,105]. Exclusion of macroarthropods from leaf litter via mesh bags confirmed their strong contribution to decomposition rates [14,15]. González et al. [25] showed that soil fauna activity depressed salicylate oxidizers in litter. Methyl salicylate elicits plant defenses and is part of the defense signaling pathway. In the soil, Huang et al. [85] used ^{13}C-labeled litter and showed the exotic earthworm *P. corethrurus* facilitated soil respiration by stimulating microbial activity; however, this effect was suppressed possibly due to the changes in the microbial activities or community when coexisting with the native worm *O. borincana*. Macroarthropod activity in decomposing wood may have especially strong effects on both wood decomposition [35,95] and nutrient cycling in the soil beneath the logs [99,109–111]. Zimmerman et al. [109] found that soil microbial biomass increased beginning 5–7 months after hurricane Hugo, corresponding to the disappearance of soil nitrate via nutrient immobilization and slowing of canopy closure in plots where woody debris was left on the forest floor, whereas soil microbial biomass was lower, soil nitrate levels were higher, and canopy closure was more rapid in plots from which debris was removed. The timing of soil microbial and plant competition for nitrogen (and possibly other limiting nutrients) coincided with deposition of large scolytine (Curculionidae, Subfamily Scolytinae) bark beetle frass piles beneath fallen logs. Lodge et al. [112] found that roots in the upper 10 cm of soil were more abundant away from trunks felled by hurricane Georges seven months earlier, and that carbon to nitrogen ratios in scolytine bark beetle frass were high enough to stimulate microbial nutrient immobilization. Several studies in wet mid-elevation forests in Puerto Rico have shown that tree roots change their foraging patterns depending on relative availability of resources. Zalamea et al. [111] found that soil under decaying wood had fewer roots and lower nitrate and magnesium concentrations than paired samples collected 50 cm away from the logs. Lodge et al. [112] found that root abundance under versus away from logs changed seasonally, likely due to shifts in relative nutrient availability.

3. Summary of Key Findings

Many of the studies summarized here were among the first to examine latitudinal differences in biotic control of litter decomposition, elevation gradients in litter and soil biota in tropical forests, and effects of disturbance on below-ground organisms and the processes they mediate. Studies elsewhere in the tropics or part of the same studies presented here have confirmed the general patterns reported from Puerto Rico.

Salient results from research on soil biota from Puerto Rico along gradients are:

Latitude

- Soil fauna are more diverse and accelerate leaf decomposition more in wet tropical forests than in cold temperate forests, but not warm temperate forest.
- Reciprocal translocation experiments across latitudinal gradients sometimes show that leaf litter decomposes faster at the home-site owing to biotic influences, overriding climatic effects.
- Soil fauna have stronger effects on leaf decomposition than microbes in wet neotropical forests.
- Macroarthropods indirectly affect tropical leaf decomposition via comminution whereas microarthropods have stronger direct effects in temperate forests via fungivory.
- Microfungal diversity is related to rates of leaf decomposition.
- Tropical soil fungi are more diverse and have smaller geographic ranges than temperate fungi.

Elevation

- In the Luquillo Mountains, the number of native and total earthworm species significantly increased as elevation and annual rainfall increased and air temperature decreased.
- Abundance of litter invertebrates and NPP declined with increasing elevation, but species richness and animal biomass peaked at mid-elevation, as in other tropical elevation studies.
- Termites have stronger effects on wood decomposition in tropical low elevation dry forests than in higher elevation wet forests.
- Fungal assemblages turn over more rapidly than protists along tropical elevation gradients.
- Fungi and Mycetozoa decline with elevation or reach a peak at mid-elevation whereas bacteria and Chrenarchaeota are most abundant and diverse at the extreme ends of the gradient.

Disturbance

- Native earthworms of tropical forest are sensitive to disturbance.
- Bark beetle frass from freshly fallen wood apparently stimulates microbial immobilization of nitrogen in the underlying soil, causing roots to initially proliferate away from logs.
- Root abundance changes spatially between seasons based on ephemeral resource hotspots.
- Litter and soil fungi from wet tropical forests are more sensitive to dry cycles and drought than to other types of disturbance.
- Soil microbial communities of wet tropical forest are highly sensitive to drought.
- Small changes and interactions in the detrital food web affect nutrient and carbon cycling.

4. Conclusions

Invertebrates and microbes in litter and soil of tropical forests in Puerto Rico independently and together influence rates of decomposition and availability of nutrients to tree roots. Research from the

Luquillo Mountains of Puerto Rico was among the first to show that litter and soil microbes of wet tropical forests were especially sensitive to drying. Narrow ecological tolerances are consistent with the high turnover of microbial communities along the elevation gradient in the Luquillo Mountains and elsewhere in the tropics, and also the strong response to reciprocal soil transplants across the elevation gradient. Macroinvertebrates have stronger effects than microbes on decomposition of both litter and wood in neotropical forests. Yet, understanding how environmental variation affects the dynamics of different soil microbial and faunal assemblages, and how variation in the composition of such assemblages controls decomposition processes and nutrient cycling is critical for long-term sustainability and management of ecosystems that are subject to global change. Additional future work in the Luquillo Mountains and other tropical forests might focus on (1) the potential deleterious effects of the abundant surface earthworm casting on soil erosion and aeration, and seed germination in pasture lands; (2) whether multi-trophic richness and abundance support ecosystem functioning (i.e., Soliveres et al. [50]); (3) biotic effects of decomposer microorganisms and detritivores in the uppermost soil horizons, where fine roots are concentrated; (4) whether carbon sequestered at greater soil depths contributes to soil fertility and forest productivity; and (5) the potential effects of introduced predators (such as planaria) on earthworms.

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References

1. Odum, H.T.; Pigeon, R.F. *A tropical Rain Forest: A Study of Irradiation and Ecology at El Verde, Puerto Rico*; Odum, H.T., Pigeon, R.F., Eds.; Division of Technical Information, United States Atomic Energy Commission: Washington, DC, USA, 1970.
2. Lodge, D.J. Microorganisms. In *The Food Web of a Tropical Forest*; Regan, D.P., Waide, R.B., Eds.; University of Chicago Press: Chicago, IL, USA, 1996; pp. 53–108.
3. Holler, J.R. 1966. Microfungi of Soil, Roots and Litter of a Puerto Rican Lower Montane Rain Forest. Ph.D. Thesis, University of South Carolina, Columbia, SC, USA, 1966.
4. Holler, J.R.; Cowley, G.T. Response of soil, root and litter microfungal populations to radiation. In *A Tropical Rain Forest: A Study of Irradiation and Ecology at El Verde, Puerto Rico*; Odum, H.T., Pigeon, R.F., Eds.; United States Atomic Energy Commission: Washington, DC, USA, 1970; pp. F35–F39.
5. Cantrell, S.A.; Lodge, D.J.; Cruz, C.A.; García, L.M.; Pérez-Jiménez, J.R.; Molina, M. Differential abundance of microbial functional groups along the elevation gradient from the coast to the Luquillo Mountains. *Ecol. Bull.* **2013**, *54*, 87–100.
6. Cantrell, S.A.; Molina, M.; Jean Lodge, D.; Rivera-Figueroa, F.J.; Ortiz-Hernández, M.L.; Marchetti, A.A.; Cyterski, M.J.; Pérez-Jiménez, J.R. Effects of a simulated hurricane disturbance on forest floor microbial communities. *For. Ecol. Manag.* **2014**, *332*, 22–31. [CrossRef]
7. Silver, W.L.; Lugo, A.E.; Keller, M. Soil oxygen availability and biogeochemistry along rainfall and topographic gradients in upland wet tropical forest soils. *Biogeochemistry* **1999**, *44*, 301–328. [CrossRef]
8. Silver, W.L.; Liptzin, D.; Almaraz, M. Soil redox dynamics and biogeochemistry along a tropical elevation gradient. *Ecol. Bull.* **2013**, *54*, 195–209.

9. Wood, T.E.; Detto, M.; Silver, W.L. Sensitivity of Soil Respiration to Variability in Soil Moisture and Temperature in a Humid Tropical Forest. *PLoS ONE* **2013**, *8*, e80965. [CrossRef] [PubMed]
10. Wall, D.H.; González, G.; Simmons, B. Seasonally dry forest soil biodiversity and functioning. In *Seasonally Dry Tropical Forests, Ecology and Conservation*; Dirzo, R., Young, H.S., Mooney, H.A., Ceballos, G., Eds.; Island Press: Washington, DC, USA, 2011; pp. 61–70.
11. González, G.; Barberena-Arias, M.F. Ecology of soil arthropod fauna in tropical forests: A review of studies from Puerto Rico. *J. Ag. UPR.* **2017**, in press.
12. Odum, H.T.; Abbott, W.; Selander, R.K.; Golley, F.B.; Wilson, R.F. Estimates of chlorophyll and biomass of the Tabonuco forest of Puerto Rico. In *A Tropical Rain Forest: A Study of Irradiation and Ecology at El Verde, Puerto Rico.*; Odum, H.T., Pigeon, R.F., Eds.; Division of Technical Information, United States Atomic Energy Commission: Washington, DC, USA, 1970; pp. I3–I19.
13. Pfeiffer, W.J. Litter invertebrates. In *The Food Web of a Tropical Forest*; Regan, D.P., Waide, R.B., Eds.; University of Chicago Press: Chicago, IL, USA, 1996; pp. 137–181.
14. Richardson, B.A.; Richardson, M.J.; González, G.; Shiels, A.B.; Srivastava, D.S. A Canopy Trimming Experiment in Puerto Rico: The Response of Litter Invertebrate Communities to Canopy Loss and Debris Deposition in a Tropical Forest Subject to Hurricanes. *Ecosystems* **2010**, *13*, 286–301. [CrossRef]
15. González, G.; Lodge, D.J.; Richardson, B.A.; Richardson, M.J. 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. *For. Ecol. Manag.* **2014**, *332*, 32–46. [CrossRef]
16. Shiels, A.B.; González, G.; Willig, M.R. Responses to canopy loss and debris deposition in a tropical forest ecosystem: Synthesis from an experimental manipulation simulating effects of hurricane disturbance. *For. Ecol. Manag.* **2014**, *332*, 124–133. [CrossRef]
17. Shiels, A.B.; González, G.; Lodge, D.J.; Willig, M.R.; Zimmerman, J.K. Cascading Effects of Canopy Opening and Debris Deposition from a Large-Scale Hurricane Experiment in a Tropical Rain Forest. *Bioscience* **2015**, *65*, 871–881. [CrossRef]
18. González, G.; Willig, M.; Waide, R. Ecological gradient analyses in a tropical landscape: Multiples perspectives and emerging themes. *Ecol. Bull.* **2013**, *54*, 13–20.
19. González, G.; Waide, R.B.; Willig, M.R. Advancements in the understanding of spatiotemporal gradients in tropical landscapes: A Luquillo focus and global perspective. *Ecol. Bull.* **2013**, *54*, 245–250.
20. Fragoso, C.; Lavelle, P. Earthworm communities in tropical rain forests. *Soil Biol. Biochem.* **1992**, *24*, 1397–1408. [CrossRef]
21. Richardson, B.A.; Richardson, M.J.; Soto-Adames, F.N. Separating the effects of forest type and elevation on the diversity of litter invertebrate communities in a humid tropical forest in Puerto Rico. *J. Anim. Ecol.* **2005**, *74*, 926–936. [CrossRef]
22. Hansen, R.A. Red oak litter promotes a microarthropod functional group that accelerates its decomposition. *Plant Soil* **1999**, *209*, 37–45. [CrossRef]
23. Heneghan, L.; Coleman, D.C.; Zou, X.; Crossley, D.A.; Haines, B.L. Soil microarthropod contributions to decomposition dynamics: Tropical-temperate comparisons of a single substrate. *Ecology* **1999**, *80*, 1873–1882.
24. Irmler, U. Changes in the fauna and its contribution to mass loss and N release during leaf litter decomposition in two deciduous forests. *Pedobiologia (Jena)* **2000**, *44*, 105–118. [CrossRef]
25. Gonzalez, G.; Seastedt, T. Soil fauna and plant litter decomposition in tropical and subalpine forests. *Ecology* **2001**, *82*, 955–964. [CrossRef]
26. Gonzalez, G. Soil Organisms and LitterDecomposition. In *Modern Trends in Applied Terrestrial Ecology*; Ambasht, R.S., Ambasht, N.K., Eds.; Kluwer Academic/Plenum Publishers: Berlin, Germany, 2002; pp. 315–329.
27. González, G.; Ley, R.E.; Schmidt, S.K.; Zou, X.; Seastedt, T.R. Soil ecological interactions: Comparisons between tropical and subalpine forests. *Oecologia* **2001**, *128*, 549–556. [CrossRef]
28. Seastedt, T.R. The role of microarthropods in decomposition and mineralization processes. *Annu. Rev. Entomol.* **1984**, *29*, 25–46. [CrossRef]
29. Brown, G.G. How do earthworms affect microfloral and faunal community diversity? *Plant Soil* **1995**, *170*, 209–231. [CrossRef]
30. Lavelle, P.; Bignell, D.; Lepage, M.; Wolters, W.; Roger, P.; Ineson, P.; Heal, O.W.; Dhillion, S. Soil function in a changing world: The role of invertebrate ecosystem engineers. *Eur. J. Soil Biol.* **1997**, *33*, 159–193.

31. Heneghan, L.; Coleman, D.; Zou, X.; Crossley, D.; Haines, B. Soil microarthropod community structure and litter decomposition dynamics: A study of tropical and temperate sites. *Appl. Soil Ecol.* **1998**, *9*, 33–38. [CrossRef]
32. Coleman, D.; Crossley, D.A., Jr.; Hendrix, P.F. *Fundamentals of Soil Ecology*, 2nd ed.; Elsevier Academic Press: New York, NY, USA, 2004.
33. González, G.; Murphy, C.M.; Belén, J. Direct and indirect effects of millipedes on the decay of litter of varying lignin Content. *Trop. For.* **2012**, *2*, 37–50.
34. Ruan, H.; Li, Y.; Zou, X. Soil communities and plant litter decomposition as influenced by forest debris: Variation across tropical riparian and upland sites. *Pedobiologia (Jena)* **2005**, *49*, 529–538. [CrossRef]
35. Zalamea-Bustillo, M. 2005. Soil biota, nutrients, and organic matter dynamics under decomposing wood. Master's Thesis, University of Puerto Rico, Puerto Rico, UT, USA, 2005.
36. González, G.; Gould, W.A.; Hudak, A.T.; Hollingsworth, T.N. Decay of aspen (*Populus tremuloides* Michx.) wood in moist and dry boreal, temperate, and tropical forest fragments. *AMBIO* **2008**, *37*, 588–597. [CrossRef] [PubMed]
37. González, G.; Luce, M.M. Woody debris characterization along an elevation gradient in northeastern Puerto Rico. *Ecol. Bull.* **2013**, *54*, 181–193.
38. Mueller, G.M.; Schmit, J.P.; Leacock, P.R.; Buyck, B.; Cifuentes, J.; Desjardin, D.E.; Halling, R.E.; Hjortstam, K.; Iturriaga, T.; Larsson, K.H.; et al. Global diversity and distribution of macrofungi. *Biodivers. Conserv.* **2007**, *16*, 37–48. [CrossRef]
39. Hawksworth, D.L. The magnitude of fungal diversity: The 1.5 million species estimate revisited. *Mycol. Res.* **2001**, *105*, 1422–1432. [CrossRef]
40. Lodge, D.; Baroni, T.; Cantrell, S. Basidiomycetes of the Greater Antilles Project. *Mycologist* **2002**, *15*, 107–112.
41. Rapoport, E. *Aereogeography: Geographical Strategies of Species*; Pergamon Press: Oxford, UK, 1982.
42. Anderson, J. The organization of soil animal communities. In *Organisms as Components of Ecosystems. Proceedings of the VI International Zoology Colloquim of the International Society of Soil Science (SSSA)*; Lohm, U., Persson, T., Eds.; Swedish Natural Science Research Council: Stockholm, Sweden, 1977; pp. 15–23.
43. Swift, M.J.; Heal, O.W.; Anderson, J.W. *Decomposition in Terrestrial Ecosystems*; Blackwell: Oxford, UK, 1979.
44. Li, Y.; González, G. Soil Fungi and Macrofauna in the Neotropics. In *Post-Agricultural Succession in the Neotropics*; Myster, R.W., Ed.; Springer: Berlin, Germany, 2008; pp. 93–114.
45. Tedersoo, L.; Bahram, M.; Polme, S.; Koljalg, U.; Yorou, N.S.; Wijesundera, R.; Ruiz, L.V.; Vasco-Palacios, A.M.; Thu, P.Q.; Suija, A.; et al. Global diversity and geography of soil fungi. *Science* **2014**, *346*, 1256688. [CrossRef] [PubMed]
46. Polishook, J.D.; Bills, G.F.; Lodge, D.J. Microfungi from decaying leaves of two rain forest trees in Puerto Rico. *J. Ind. Microbiol. Biotechnol.* **1996**, *17*, 284–294. [CrossRef]
47. Santana, M.E.; Lodge, D.J.; Lebow, P. Relationship of host recurrence in fungi to rates of tropical leaf decomposition. *Pedobiologia* **2005**, *49*, 549–564. [CrossRef]
48. Eisenhauer, N. Aboveground—Belowground interactions as a source of complementarity effects in biodiversity experiments. *Plant Soil* **2012**, *351*, 1–22. [CrossRef]
49. Bardgett, R.D.; van der Putten, W.H. Belowground biodiversity and ecosystem functioning. *Nature* **2014**, *515*, 505–511. [CrossRef] [PubMed]
50. Soliveres, S.; van der Plas, F.; Manning, P.; Prati, D.; Gossner, M.M.; Renner, S.C.; Alt, F.; Arndt, H.; Baumgartner, V.; Binkenstein, J.; et al. Biodiversity at multiple levels is needed for ecosystem multifunctionality. *Nature* **2017**, *536*, 456–459. [CrossRef] [PubMed]
51. Lodge, D.; Læssøe, T.; Aime, M.; Henkel, T. Montane and cloud forest specialists among neotropical Xylaria species. *N. Am. Fungi* **2008**, *3*, 193–213. [CrossRef]
52. Merckx, V.S.F.T.; Hendriks, K.P.; Beentjes, K.K.; Mennes, C.B.; Becking, L.E.; Peijnenburg, K.T.C.A.; Afendy, A.; Arumugam, N.; de Boer, H.; Biun, A.; et al. Evolution of endemism on a young tropical mountain. *Nature* **2015**, *524*, 347–350. [CrossRef] [PubMed]
53. Geml, J.; Pastor, N.; Fernandez, L.; Pacheco, S.; Semenova, T.A.; Becerra, A.G.; Wicaksono, C.Y.; Nouhra, E.R. Large-scale fungal diversity assessment in the Andean Yungas forests reveals strong community turnover among forest types along an altitudinal gradient. *Mol. Ecol.* **2014**, *23*, 2452–2472. [CrossRef] [PubMed]
54. Gomez-Hernandez, M.; Williams-Linera, G.; Lodge, D.J. Phylogenetic diversity of macromycetes and woody plants along an elevational gradient in Eastern Mexico. *Biotropica* **2016**, *48*, 577–585. [CrossRef]

55. Wiens, J.J.; Graham, C.H. Niche Conservatism: Integrating Evolution, Ecology, and Conservation Biology. *Annu. Rev. Ecol. Evol. Syst.* **2005**, *36*, 519–539. [CrossRef]
56. Crisp, M.D.; Arroyo, M.T.K.; Cook, L.G.; Gandolfo, M.A.; Jordan, G.J.; McGlone, M.S.; Weston, P.H.; Westoby, M.; Wilf, P.; Linder, H.P. Phylogenetic biome conservatism on a global scale. *Nature* **2009**, *458*, 754–756. [CrossRef] [PubMed]
57. Geml, J.; Morgado, L.N.; Semenova-Nelsen, T.A.; Schilthuizen, M. Changes in richness and community composition of ectomycorrhizal fungi among altitudinal vegetation types on Mount Kinabalu in Borneo. *New Phytol.* **2017**. [CrossRef] [PubMed]
58. Dalling, J.W.; Heineman, K.; González, G.; Ostertag, R. Geographic, environmental and biotic sources of variation in the nutrient relations of tropical montane forests. *J. Trop. Ecol.* **2016**, *32*, 368–383. [CrossRef]
59. Lugo, A.E. Up, down, and across the mountains: A new look at the Luquillo Mountains. *Ecol. Bull.* **2013**, *54*, 9–11.
60. Weaver, P.; Gould, W. Forest vegetation along environmental gradients in northeastern Puerto Rico. *Ecol. Bull.* **2013**, *54*, 43–65.
61. Richardson, B.A.; Richardson, M.J. Litter-based invertebrate communities in forest floor and bromeliad microcosms along an elevational gradient in Puerto Rico. *Ecol. Bull.* **2013**, *54*, 101–115.
62. Willig, M.; Presley, S.; Bloch, C.P.; Alvarez, J. Population, community, and metacommunity dynamics of terrestrial gastropods in the Luquillo Mountains: A gradient perspective. *Ecol. Bull.* **2013**, *54*, 117–140.
63. González, G.; García, E.; Cruz, V.; Borges, S.; Zalamea, M.; Rivera, M.M. Earthworm communities along an elevation gradient in Northeastern Puerto Rico. *Eur. J. Soil Biol.* **2007**, *43*, S24–S32. [CrossRef]
64. Richardson, B.A.; Richardson, M.J.; Scatena, F.N.; Mcdowell, W.H.; Richardson, B.A.; Richardson, M.J.; Scatena, F.N. Effects of nutrient availability and other elevational changes on bromeliad populations and their Effects of nutrient availability and other elevational changes on bromeliad populations and their invertebrate communities in a humid tropical forest in Puer. *J. Trop. Ecol.* **2000**, *16*, 167–188. [CrossRef]
65. Harmon, M.E.; Hua, C. Coarse Woody Debris Dynamics in Two Old-Growth Ecosystems. *Bioscience* **1991**, *41*, 604–610. [CrossRef]
66. Torres, J.A. Wood Decomposition of *Cyrilla racemiflora* in a Tropical Montane Forest. *Biotropica* **1994**, *26*, 124. [CrossRef]
67. Creed, I.F.; Morrison, D.L.; Nicholas, N.S. Is coarse woody debris a net sink or source ofnitrogen in the red spruce—Fraser fir forest ofthe southern Appalachians, U.S.A.? *Can. J. For. Res.* **2004**, *34*, 716–727. [CrossRef]
68. Delaney, M.; Brown, S.; Lugo, A.E.; Torres-Lezama, A.; Quintero, N.B. The Quantity and Turnover of Dead Wood in Permanent Forest Plots in Six Life Zones of Venezuela1. *Biotropica* **1998**, *30*, 2–11. [CrossRef]
69. Nascimento, H.E.M.; Laurance, W.F. Total aboveground biomass in central Amazonian rainforests: A landscape-scale study. *For. Ecol. Manag.* **2002**, *168*, 311–321. [CrossRef]
70. Gómez-Hernández, M.; Williams-Linera, G.; Guevara, R.; Lodge, D.J. Patterns of macromycete community assemblage along an elevation gradient: Options for fungal gradient and metacommunity analyse. *Biodivers. Conserv.* **2012**, *21*, 2247–2268. [CrossRef]
71. Zalamea, M.; González, G. Substrate-Induced Respiration in Puerto Rican Soils: Minimum glucose amendment. *Acta Científica* **2007**, *21*, 11–17.
72. Lodge, D.J.; McDowell, W.H.; Macy, J.; Ward, S.K.; Leisso, R.; Claudio Campos, K.; Kuhnert, K. Distribution and role of mat-forming saprobic basidiomycetes in a tropical forest. In *Ecology of Saprobic Basidiomycetes*; Boddy, L., Frankland, J.C., Eds.; Academic Press, Elsevier LTD: Amsterdam, The Netherland, 2008; pp. 197–209.
73. Moore, D.L.; Spiegel, F.W. Microhabitat Distribution of Protostelids in Tropical Forests of the Caribbean National Forest, Puerto Rico. *Mycologia* **2000**, *92*, 616. [CrossRef]
74. Novozhilov, Y.K.; Schnittler, M.; Rollins, A.W.; Stephenson, S. L. Myxomycetes from different forest types in Puerto Rico. *Mycotaxon* **2001**, *77*, 285–299.
75. Schnittler, M.; Stephenson, S.L. Inflorescences of Neotropical herbs as a newly discovered microhabitat for myxomycetes. *Mycologia* **2002**, *94*, 6–20. [CrossRef] [PubMed]
76. Stephenson, S.L.; Landolt, J.C.; Moore, D.L. Protostelids, dictyostelids, and myxomycetes in the litter microhabitat of the Luquillo Experimental Forest, Puerto Rico. *Mycol. Res.* **1999**, *103*, 209–214. [CrossRef]
77. Chen, D.; Yu, M.; González, G.; Zou, X.; Gao, Q. Climate Impacts on Soil Carbon Processes along an Elevation Gradient in the Tropical Luquillo Experimental Forest. *Forests* **2017**, *8*, 90. [CrossRef]

78. Scatena, F.N.; Blanco, J.F.; Beard, K.H.; Waide, R.B.; Lugo, A.E.; Brokaw, N.V.L.; Silver, W.L.; Haines, B.L.; Zimmerman, J.K. Disturbance regime. In *A Caribbean Forest Tapestry: The Multidimensional Nature of Disturbance and Response*; Brokaw, N.V.L., Crowl, A.T., Lugo, A.E., McDowell, W.H., Waide, R.B., Willig, M., Eds.; Oxford University Press: Oxford, UK, 2012; pp. 42–71.
79. Waide, R.B.; Willig, M.R. Conceptual overview: disturbance, gradients, and response. In *A Caribbean Forest Tapestry: The Multidimensional Nature of Disturbance and Response*; Brokaw, N.V.L., Crowl, A.T., Lugo, A.E., McDowell, W.H., Waide, R.B., Willig, M., Eds.; Oxford University Press: Oxford, UK, 2012; pp. 42–71.
80. Lundquist, J.E.; Camp, A.E.; Tyrrell, M.L.; Seybold, S.J.; Cannon, P.; Lodge, D.J. *Earth, Wind, and Fire: Abiotic Factors and the Impacts of Global Environmental Change on Forest Health*; Cambridge University Press: Cambridge, UK, 2011.
81. González, G.; Zou, X.; Borges, S. Earthworm abundance and species composition in abandoned tropical crop lands comparisons of tree plantations and secondary forests. *Pedobiologia* **1996**, *40*, 385–391.
82. González, G.; Huang, C.Y.; Zou, X.; Rodríguez, C. Earthworm invasions in the tropics. *Biol. Invasions* **2006**, *8*, 1247–1256. [CrossRef]
83. Zou, X.; González, G. Changes in earthworm density and community structure during secondary succession in abandoned tropical pastures. *Soil Biol. Biochem.* **1997**, *29*, 627–629. [CrossRef]
84. Leon, Y.S.-D.; Zou, X.; Borges, S.; Ruan, H. Recovery of Native Earthworms in Abandoned Tropical Pastures. *Conserv. Biol.* **2003**, *17*, 999–1006. [CrossRef]
85. Huang, C.Y.; González, G.; Hendrix, P. Resource Utilization by Native and Invasive Earthworms and Their Effects on Soil Carbon and Nitrogen Dynamics in Puerto Rican Soils. *Forests* **2016**, *7*, 277. [CrossRef]
86. González, G.; Zou, X. Earthworm influence on N availability and the growth of Cecropia schreberiana in tropical pasture and forest soils. *Pedobiologia* **1999**, *43*, 824–829.
87. Fragoso, C.; Lavelle, P.; Blanchart, E.; Senapati, B.K.; Jimenez, J.J.; Angeles Martinez, M.; de los Decaëns, T.; Tondoh, J. Earthworm communities of tropical agroecosystems: Origin, structure and influence of management practices. In *Earthworm Management in Tropical Agroecosystems*; CABI: Wallingford, UK, 1999; pp. 27–55.
88. Winsome, T.; Epstein, L.; Hendrix, P.F.; Horwath, W.R. Habitat quality and interspecific competition between native and exotic earthworm species in a California grassland. *Appl. Soil Ecol.* **2006**, *32*, 38–53. [CrossRef]
89. González, G.; Li, Y.; Zou, X. Effects of post-hurricane fertilization and debris removal on earthworm abundance and biomass in subtropical forests in Puerto Rico. In *Minhocas na America Latina: Biodiversidade e Ecologia*; Brown, G.G., Fragoso, C., Eds.; EMBRAPA: London, UK, 2007; pp. 99–108.
90. Barberena-Arias, M.F.; Aide, T.M. Species diversity and trophic composition of litter insects during plant secondary succession. *Caribb. J. Sci.* **2003**, *39*, 161–169.
91. Osorio-Pérez, K.; Barberena-Arias, M.F.; Aide, T.M. Changes in Ant Species Richness and Composition During Plant Secondary Succession in Puerto Rico. *Caribb. J. Sci.* **2007**, *43*, 244–253. [CrossRef]
92. Barberena-Arias, M.F.; Aide, T.M. Variation in species and trophic composition of insect communities in Puerto Rico. *Biotropica* **2002**, *34*, 357–367. [CrossRef]
93. Secrest, M.F. 1995. The Impacts of Hurricane Hugo on Two Common Tree Snails in the Luquillo Experimental Forest of Puerto Rico. Master's Thesis, Texas Tech University, Lubbock, TX, USA, 1995.
94. Willig, M.R.; Bloch, C.P.; Presley, S.J. Experimental decoupling of canopy opening and debris addition on tropical gastropod populations and communities. *For. Ecol. Manag.* **2014**, *332*, 103–117. [CrossRef]
95. Torres, J.A.; Gonzalez, G. Wood Decomposition of *Cyrilla racemiflora* (Cyrillaceae) in Puerto Rican Dry and Wet Forests: A 13-year Case Study1. *Biotropica* **2005**, *37*, 452–456. [CrossRef]
96. Willig, M.R.; Willig, M.R.; Moorhead, D.L.; Moorhead, D.L.; Cox, S.B.; Cox, S.B.; Zak, J.C. Functional diversity of soil bacterial communities in the tabonuco forest: Interaction of anthropogenic and natural disturbance. *Biotropica* **1996**, *28*, 471–483. [CrossRef]
97. Lodge, D.J. Nutrient cycling by fungi in wet tropical forests. In *Aspects of Tropical Mycology*; Isaac, S., Frankland, J.C., Watling, R., Whalley, A.J.S., Eds.; Cambridge University Press: Cambridge, UK, 1993; pp. 37–57.
98. Lodge, D.J.; Cantrell, S.A.; González, G. Effects of canopy opening and debris deposition on fungal connectivity, phosphorus movement between litter cohorts and mass loss. *For. Ecol. Manag.* **2014**, *332*, 11–21. [CrossRef]

99. Lodge, D.J.; Cantrell, S.A.; González, G.; Stankavich, S.; Shaffer, A.; Stock, M.; Colón Hernández, V.N. Simulated Hurricane Treatment Reduces Basidiomycete Litter Mat Cover in Subtropical Wet Forest. Available online: http://2015.botanyconference.org/engine/search/ind2015 (accessed on 20 October 2015).
100. Lodge, D.J.; Ingham, E.R. A comparison of agar film techniques for estimating fungal biovolumes in litter and soil. *Agric. Ecosyst. Environ.* **1991**, *34*, 131–144. [CrossRef]
101. Bouskill, N.J.; Lim, H.C.; Borglin, S.; Salve, R.; Wood, T.E.; Silver, W.L.; Brodie, E.L. Pre-exposure to drought increases the resistance of tropical forest soil bacterial communities to extended drought. *ISME J.* **2013**, *7*, 384–394. [CrossRef] [PubMed]
102. Bouskill, N.J.; Wood, T.E.; Baran, R.; Ye, Z.; Bowen, B.P.; Lim, H.C.; Zhou, J.; van Nostrand, J.D.; Nico, P.; Northen, T.R.; et al. Belowground response to drought in a tropical forest soil. I. Changes in microbial functional potential and metabolism. *Front. Microbiol.* **2016**, *7*, 1–11. [CrossRef] [PubMed]
103. Shiels, A.B.; González, G. Understanding the key mechanisms of tropical forest responses to canopy loss and biomass deposition from experimental hurricane effects. *For. Ecol. Manag.* **2014**, *332*, 1–10. [CrossRef]
104. De Jesús, M.; Lodge, D.; Crowl, T. Palatability of leaf litter conditioned by white-rot vs. non-white-rot fungi to leaf shredders in a freshwater stream. In Proceedings of the North American Benthalogical Society (NABS) 56th Annual Meeting, Salt Lake City, UT, USA, 25–28 May 2008; p. P3233.
105. González, G.; Seastedt, T.R.; Donato, Z. Earthworms, arthropods and plant litter decomposition in aspen (Populus tremuloides) and lodgepole pine (Pinus contorta) forests in Colorado, USA. *Pedobiologia* **2003**, *47*, 863–869. [CrossRef]
106. Harmon, M.E.; Silver, W.L.; Fasth, B.; Chen, H.; Burke, I.C.; Parton, W.J.; Hart, S.C.; Currie, W.S. LIDET Long-term patterns of mass loss during the decomposition of leaf and fine root litter: An intersite comparison. *Glob. Chang. Biol.* **2009**, *15*, 1320–1338. [CrossRef]
107. Lodge, D.J.; McDowell, W.H.; McSwiney, C.P. The importance of nutrient pulses in tropical forests. *Trends Ecol. Evol.* **1994**, *9*, 384–387. [CrossRef]
108. Miller, R.M.; Lodge, D.J. Fungal responses to disturbance—Agriculture and forestry. In *The Mycota, Second ed., IV, Environmental and Microbial Relationships*; Esser, K., Kubicek, P., Druzhinina, I.S., Eds.; Springer-Verlag: Berlin, Germany, 2007; pp. 44–67.
109. Zimmerman, J.K.; Pulliam, W.M.; Lodge, D.J.; Quiñones-Orfila, V.; Fetcher, N.; Guzmán-Grajales, S.; Parrotta, J.A.; Asbury, C.E.; Walker, L.R.; Waide, R.B. Nitrogen Immobilization by Decomposing Woody Debris and the Recovery of Tropical Wet Forest from Hurricane Damage. *Oikos* **1995**, *72*, 314–322. [CrossRef]
110. Zalamea, M.; González, G.; Ping, C.L.; Michaelson, G. Soil organic matter dynamics under decaying wood in a subtropical wet forest: effect of tree species and decay stage. *Plant Soil* **2007**, *296*, 173–185. [CrossRef]
111. Zalamea, M.; González, G.; Lodge, D. Physical, Chemical, and Biological Properties of Soil under Decaying Wood in a Tropical Wet Forest in Puerto Rico. *Forests* **2016**, *7*, 168. [CrossRef]
112. Lodge, D.; Winter, D.; González, G.; Clum, N. Effects of Hurricane-Felled Tree Trunks on Soil Carbon, Nitrogen, Microbial Biomass, and Root Length in a Wet Tropical Forest. *Forests* **2016**, *7*, 264. [CrossRef]