

Comparing Litterfall and Standing Vegetation: Assessing the Footprint of Litterfall Traps

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1. Introduction

Litterfall traps could preferentially represent certain kinds of leaf litter. Several factors may cause bias while sampling litterfall leading to over- or under-representation of the species present in the surrounding vegetation. For example, species standing precisely above litterfall traps, having big and wide crowns, and/or with high leaf fall rate may be over-represented in litterfall samples. Additionally, species standing upslope or in the windward side of litterfall traps may be more likely to be collected in litterfall traps (Staelens et al., 2003). Conversely, species with big and/or heavy leaves or fronds such as palms or species from the *Cecropia* and *Heliconia* genera may be under-represented in litterfall traps (Clark et al., 2001). However, the few studies dealing with patterns of litterfall dispersal and collection have found contradictory results. For example, in Australian rainforests Lowman (1988) found that collected litterfall was not necessarily biased toward leaves coming from trees located precisely above traps. Similarly, in a dry forest in Costa Rica, Burnham (1997) found a low spatial correspondence between location of source stems and litterfall samples. In contrast, for a temperate mixed forest in northeastern Japan, Hirabuki (1991) found that estimated patterns of litterfall spatial distribution corresponded to the distribution of stems in the studied plot. In this chapter we report results from a study that takes advantage of an ongoing experiment in the Luquillo Experimental Forest, Puerto Rico, to examine the correspondence between litterfall samples and standing vegetation. Such correspondence was analyzed at three different spatial scales defined by the sampling units already in place: forest stand (10^6 m²), sampling blocks (4×10^4 m²), and plots (4×10^2 m²). Our first objective was to examine which factors, in addition to relative abundance of species in the vegetation, could affect the relative abundance of species in litterfall samples. Specifically, we evaluated the effect of tree size (measured as height and crown area), leaf size (measured as leaf area), and distance to litter traps using a stepwise regression procedure. We hypothesized that bigger trees (i.e., having high height and crown area) would produce more leaf litter and therefore would tend to occur more abundantly in litterfall samples; while trees with relatively big leaves would be in general under-estimated in litterfall samples because traps would fail to catch those leaves. Finally, if traps were capturing leaves from trees standing precisely above, then trees being closer to litter traps would tend to present higher relative abundances in litterfall samples. Additionally, we analyzed the similarity between litterfall and particular sub-sets of the whole vegetation community. Sub-sets were defined by tree height, crown area, and distance to traps, such that if litter traps were preferentially

collecting leaves from any particular sub-set of the vegetation (e.g., bias toward either canopy or understory trees, wide-crowned trees, or trees located closer to traps), those sub-sets should bear a higher compositional similarity with the litterfall samples than the whole vegetation community.

The particular experimental set up used in this study (cf., Fig. 1), allowed us also to ask if litter traps located in the center of vegetation plots (i.e., surrounding plots. See Fig. 1) provided more representative samples of the surrounding vegetation than traps located adjacent to vegetation plots (i.e., adjacent plots. See Fig. 1). To address this second objective, we compared the composition and relative abundance of species collected in litter traps with the same parameters of the vegetation from the surrounding and adjacent plots (Fig. 1), using similarity indexes and parametric and non-parametric correlations. We hypothesized that if litter traps were collecting litterfall coming from all directions with the same likelihood, a higher similarity between litterfall samples and vegetation would be found for surrounding than for adjacent plots, both for the scale of the forest as for the scale of individual plots and for particular species.

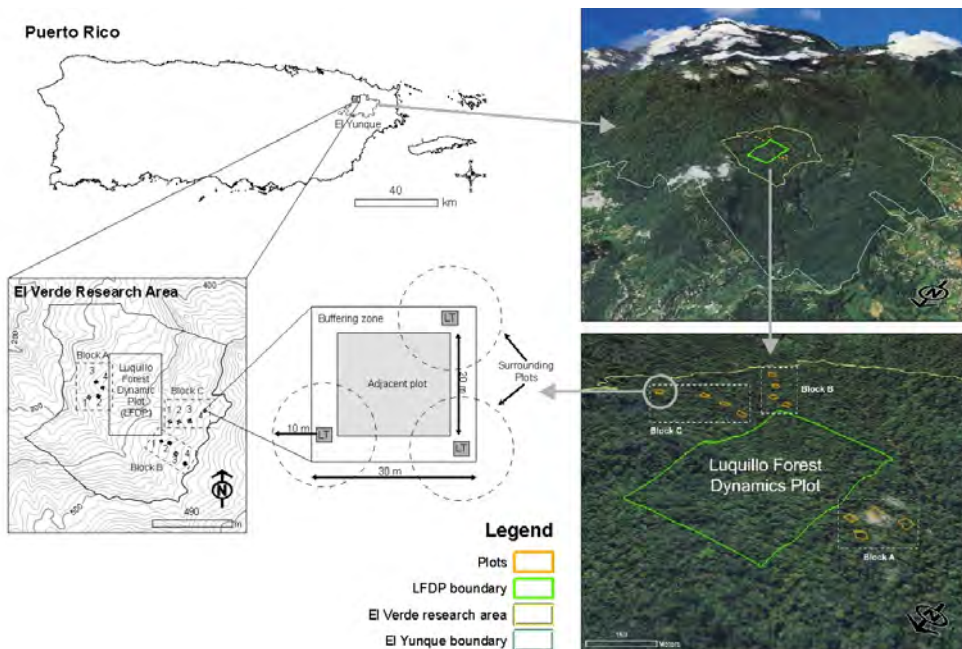


Fig. 1. Location of blocks, adjacent plots (square plots, numbered 1-4 within each block), surrounding plots (circular plots), and litter traps (LT) in El Verde research area within the Luquillo Experimental Forest. Inferred area covered by each block is 40,000 m² (broken lines). The complete study area covers around 10⁶ m². The 16-ha Luquillo Forest Dynamic Plot (LFDP) is shown as reference; for more information about the LFDP please see Thompson et al. (2002)

Finally, our third objective was to gain insights for the scaling of litterfall data from the level of sampling plots up to the level of the forest stand. We addressed this by comparing the

similarity between vegetation and litterfall across the three different scales mentioned before (i.e., plots, blocks and the forest stand; cf. Fig. 1) using similarity indexes, correlations, multivariate ordinations, and Mantel tests. An important aspect when examining the correspondence between litterfall and vegetation across different spatial scales is related to whether litter traps are capturing leaves from a wide range or only from the near vicinity around traps. On one hand, considering the potential far-ranged and random patterns of leaf dispersal (Jonard et al., 2006), a high compositional similarity between litterfall and vegetation at the scale of the forest type together with a low similarity at the smaller scales of sampling units might be expected. On the other hand, if litter traps are collecting leaf litter mainly from the vegetation in the near vicinity (for example, 10 m around traps), a high similarity between litterfall and vegetation at the scale of sampling units should be encountered as well. Particularly, the following outcomes could be expected: 1) high correlation between litterfall and vegetation dissimilarity matrices calculated for the smallest sampling units (i.e., plots), namely, pairs of plots with high dissimilarity in their vegetation should be also highly dissimilar in their litterfall; 2) litterfall and vegetation samples from the same plots should cluster together in an ordination space accurately representing compositional distances among sampling units; and 3) strong correlation between similarity among pairs of litterfall samples and the physical distance separating those samples (i.e., distance among plots), namely, the more distant the plots were located, the higher the dissimilarity between them would be.

Litterfall collection using litter traps has become a ubiquitous method in terrestrial ecology. Thus it is important to understand the relevant variables behind the method and the implications of its limitations. We believe our findings will prove instrumental for the improvement of methods in terrestrial and forest ecology especially in the tropics where the high species diversity and structural complexity of forests impose tough challenges to the study of forest structure and dynamics.

2. Methods

2.1 Study site

The study was carried out in a subtropical wet forest in northeastern Puerto Rico (18°20'N, 65°49'W) in the Luquillo Experimental Forest. Mean monthly temperature is 23.03 °C and mean annual rainfall is 3592.3 mm (Zalamea & González, 2008). Soils are a complex of well- and poorly-drained ultisols and oxisols (Ruan et al., 2004). The forest type studied is dominated by *Dacryodes excelsa* Vahl., *Buchenavia tetraphila* (Vahl.) Eichl., *Homalium racemosum* Jacq., *Guarea guidonia* (L.) Sleumer, *Sloanea berteriana* Choisy, and *Prestoea montana* (Graham) Nicholson (Thompson et al., 2002). Mean canopy height is 21 m with some emergent trees reaching up to 30 m (Brokaw & Grear, 1991).

2.2 Sampling design

We followed the experimental design of a larger ongoing study in the Luquillo Long-Term Ecological Research program (LUQ- LTER) in Puerto Rico (See Richardson et al., 2010 for a description of the Canopy Trimming Experiment, CTE). Experimental layout of this experiment consists of three blocks (labeled A, B, and C) representing an area of around 4×10^4 m² each (Fig. 1). Block A is located between 340-360 m on a slight SW-facing slope;

block B is located between 450-485 m on a slight W-SW facing slope, while block C is at 435-480 m on a slight W-facing slope. Each block contains four 20 x 20 m square plots distanced at least 30 m from each other. In the buffering zone (cf. Fig. 1), three litter traps of 3 m² (1.73 m side length) were randomly installed adjacent to each square plot (around 1.6 m from plots border) at 1.3 m from ground level. Over this initial experimental set up, we installed 10 m radius circular plots around each litter trap (Fig. 1). Hereafter, we will refer to square plots as “adjacent” plots and to circular as “surrounding” plots to emphasize the respectively “lateral” and “central” position of litter traps relative to the two kinds of plots. Given the spatial distribution of blocks (cf. Fig.1), we assumed that data resulting from pooling all plots and blocks was a representative sample of the forest stand and corresponded to an area of 10⁶ m².

2.3 Litterfall collection and vegetation inventories

Litter was collected every two weeks from November 2002 to November 2003. These samples served as base line data for planning a decomposition experiment as part of the CTE. The CTE was designed to experimentally disentangle the effects of canopy opening vs. debris deposition resulting from hurricane disturbance on organismal and ecosystem responses in a subtropical wet forest. Leaves were picked up from other litterfall components (such as reproductive parts, wood, and miscellaneous) and sorted out to species following Acevedo-Rodríguez (2003), and Little et al. (1974). Species belonging to the same genera and having similar leaf morphology were pooled for data analysis. That was the case for *Miconia tetrandra* and *M. prasina* (pooled as *Miconia* spp.) and *Myrcia fallax*, and *M. leptoclada* (pooled as *Myrcia* spp.). Samples from all three traps around each square plot were pooled together, air-dried and weighed. Thus, the minimal sampling unit for litterfall was the plot. Species relative abundances in litterfall were calculated as % of annual litterfall per plot. Data for plots were then pooled to calculate % contribution of each species to total annual litterfall for each block and for the whole forest (i.e., after pooling all blocks).

Vegetation data for the adjacent plots was obtained from the Luquillo LTER web site (<http://luq.lternet.edu>, lterdb144) and corresponds to a vegetation survey carried out in April 2003 -as part of the CTE- in which all stems greater than 1 cm diameter at 1.3 m height (DBH) were tagged, identified to species and measured for DBH and height (see details about methods in <http://luq.lternet.edu>). In the surrounding plots, we carried out a vegetation inventory for all stems greater than 1 cm of DBH, for which we recorded: tree species, DBH, height, crown relative position (as canopy, sub-canopy, and understory), crown area, and distance of stem center to litter trap. Relative abundances were calculated as importance values: $IV = (\text{Relative density} + \text{Relative dominance})/2$, where relative density is the % of total individuals per species per plot and relative dominance is the % of the total basal area per species per plot. We chose IV instead of just basal area to avoid big but non-numerous species to appear over-represented in the dataset (which in fact was the case for species such as *Ormosia krugii*). All the measured individuals in the surrounding plots were classified into three height, crown area, and distance classes. Distance and crown area classes were chosen arbitrarily to ensure that each class included roughly the same number of stems. Height classes, however, were chosen on the basis of the vertical structure of the forest (as described in Brokaw & Grear, 1991) and therefore the number of stems included in each class was not even. Height classes were: >10 m (447 stems), 10-5 m (979 stems), ≤5 m (529 stems), roughly corresponding to the crown relative position categories

mentioned before (canopy, sub-canopy, and understory) which were obtained by visual examination of each tree in relation to neighboring trees. Crown area classes were: 0-1 m² (626 stems), 1-6.25 m² (788 stems), and >6.25 m² (541 stems). Distance classes were: 0-5.5 m (623 stems), 5.5-8 m (675 stems), and 8-10 m (657 stems).

2.4 Data analysis

A stepwise linear regression (SPSS 2002, version 11.5, Chicago, Illinois, USA) was carried out to determine the effect of: tree height, crown area, leaf size, and distance to litter trap, as the independent variables, over the % of annual litterfall per species, as the dependent variable. Values of height, crown area, and distance to trap per species were calculated as the corresponding importance values for each height, crown area and distance class. Leaf area (cm²) for each species was calculated from digital images of herbaria and fresh specimens available in the following Internet sites: New York Botanical Garden Virtual Herbarium (<http://sciweb.nybg.org/Science2/VirtualHerbarium.asp>), Missouri Botanical Garden (<http://mobot.mobot.org/W3T/Search/classicvast.html>), Herbarium Berolinense (<http://ww2.bgbm.org/herbarium/>, Barcode B 10 0247501, ImageId 253751, accessed 28-May-08), La Selva Digital Flora (<http://sura.ots.ac.cr/local/florula3/en/index.htm>), and Biodiversity Information System for the Andes to Amazon Biodiversity Program -Atrium (<http://atrium.andesamazon.org>). Images were analyzed with Scion Image Software for Windows (Scion Corporation 2000-2001, version Alpha 4.0.3.2, Maryland, USA) by taking the area of 5 leaves from each herbaria specimen and calculating the average. Scale was set for each individual image before calculating leaf area. For some species images were not available. In those cases images from related species within the same genera and having similar leaf morphology were taken instead. Only species with >3 stems and IV > 0.1 were included in the regression analysis (44 out of the total pool of 91 species). Regression analysis was carried out in SPSS for Windows (SPSS 2002, version 11.5, Chicago, Illinois, USA) using arcsine-transformed data and standardized values (z-scores) in order to minimize the effect of collinearity among the independent variables included over the regression model (Rawlings et al., 1998, p. 370).

To determine how representative of the surrounding and adjacent vegetation were litterfall samples caught by central and lateral traps respectively, we used Spearman non-parametric correlation between the importance value of individual species and its correspondent % annual litterfall per plot (SPSS 2002, version 11.5, Chicago, Illinois, USA). Species with IV < 0.1, number of stems < 3, or frequency < 3 plots (either in litterfall, surrounding or adjacent plots) were excluded from this analysis. Out of 91 species in the combined data set of litterfall and vegetation plots, correlations were carried out for 41 species. Spearman's rank correlation was preferred over the parametric Pearson correlation because we were interested in accounting also for absences (i.e., zeros in the data set representing cases in which a given species occurred in the vegetation of a given plots but not in the litterfall or vice versa) and the Pearson correlation is known to be distorted by the presence of many zero values (Waite, 2000).

Differences in composition and relative abundance of species between vegetation and litterfall across spatial scales were explored by the Bray-Curtis index of dissimilarity, which is equivalent to the Sorensen index of similarity when subtracted from 1 (Waite, 2000). Similarities were calculated for the forest, blocks and plots scales by pooling data from plots

into blocks and finally all blocks to get the complete forest type. Matrices for Mantel tests and multivariate ordinations were based on dissimilarities, while resemblances between litterfall and vegetation at different scales are hereafter presented as % of similarity for more clarity. Additionally, as another measure of similarity at the forest level we calculated the Pearson parametric correlation coefficient between % annual litterfall per species and the total abundance of each species in the forest (i.e., after pooling up data from all plots) for vegetation data obtained from the surrounding and adjacent plots separately. Data was arcsine-transformed before carrying out the correlations as recommended for relative values such as percentages (Waite, 2000).

Comparisons of litterfall and vegetation at the scale of blocks and plots were done using two methods: Mantel test and ordination analyses. Mantel test assesses correlation between two distance matrices (Lefkovich, 1984). This method has been widely used in landscape ecology and population genetics where geographical distances are compared to genetic or ecological distances (e.g., Manel et al., 2003; Stehlik et al., 2001). In this case we compared: 1) the physical separation among plots (in meters) with the compositional dissimilarity among litterfall samples, and 2) the dissimilarity matrices for litterfall and vegetation (i.e., dissimilarity matrix of vegetation against vegetation vs. matrix for litter against litter in all plots). Physical distance matrix for plots was generated using a Geographic Distance Matrix Generator (Ersts P.J., version 1.2.2, American Museum of Natural History, Center for Biodiversity and Conservation. URL: http://biodiversityinformatics.amnh.org/open_source/gdmg. Accessed on 2008-4-3), based on State Plane Coordinates for Puerto Rico, which were obtained from the Luquillo LTER home page (<http://luq.lternet.edu/data/>, lterdb 144). Dissimilarity matrices and Mantel tests were done with XLSTAT (Addinsoft 2008, version 3.01, New York, USA).

Two ordination analyses were performed: Principal Component Analysis (PCA) and Multi-dimensional Scaling (MDS). PCA was used to explore underlying factors segregating litterfall and vegetation samples. As an explorative tool, PCA is an appropriate method despite no environmental variables were measured (Vervaet et al., 2002). MDS was used to visualize similarities among vegetation and litterfall samples plotted together and to evaluate if litter traps were preferentially collecting leaves from any of the height, crown or distance to trap classes. MDS ordinations were tested with Shepard diagrams using Kruskal's stress type 1 (Kruskal & Wish, 1978) to ensure that distances in the graph were proportional to calculated dissimilarities between plots. Ordination analyses were performed using the PC-ORD 5 software (McCune & Mefford, 2006).

3. Results

The final regression model obtained after the stepwise procedure explained 85% of the variability in the dataset ($r^2 = 0.854$) and included only two variables: tree height (height class >10 m: $r = 0.864$, $P < 0.001$) and crown area (crown area class >6.25 m²: $r = 0.843$, $P < 0.001$), in contrast to 65% of variability accounted when using only the relative abundance of species in vegetation as the independent variable. Distance to traps was only marginally significant (distance class <5 m: $r = 0.626$, $P < 0.055$) meaning that a higher height and a wider crown were more important determining the presence and relative abundance of a species in litterfall samples than a closer location to litter traps. According to the regression model, some species were either over-estimated (e.g., *B. tetraphylla*, *H. rugosa*, and *H.*

racemosum) or under-estimated (*O. krugii* and *P. montana*) in litterfall samples, namely their abundance in litterfall was either higher or lower than expected from their relative abundance, height and crown size (Fig. 2).

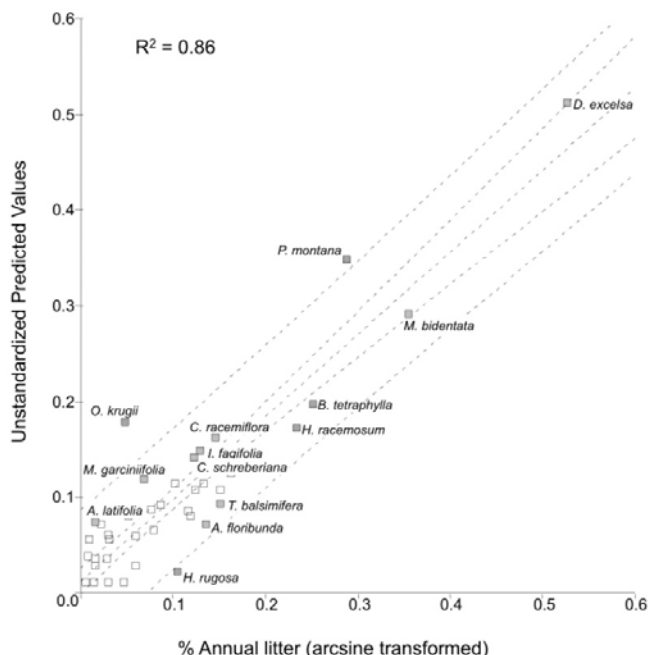


Fig. 2. Stepwise regression model for % annual litterfall (as the dependent variable) and importance values of vegetation for height class >10 m and crown area class >25 m² (as the independent variables). Unstandardized predicted values were obtained using SPSS 2002, version 11.5, Chicago, Illinois, USA. Refer to Table 1 for complete species names.

Although there was not any significant correlation between regression standardized residues (i.e., observed - predicted values, as a measure of over- or under- estimation) and leaf size, trees with small leaves tended to be over-estimated, while the two species that were under-estimated both have relatively big leaves (Fig. 3).

Comparisons of vegetation sub-sets and litterfall also suggested that distance to traps was not an important factor determining how representative of the vegetation were the litterfall samples, because sub-sets defined by distance to traps did not differ from the dissimilarity value calculated for the whole community (Fig. 4). In contrast, ordinations and similarity matrices for height, relative crown position, crown area, and distance to trap classes showed that vegetation sub-sets made up of the tallest trees (>10 m), occupying the canopy stratum, and having the biggest crowns (>6.25 m²) presented the lowest dissimilarity between litterfall and vegetation (Fig. 4).

Similarity between litterfall and vegetation was 68% for surrounding and adjacent plots indicating that both types of plots provided equally representative samples of leaf litterfall

at the scale of the forest. This result was corroborated by a high and positive correlation coefficient between vegetation relative abundance in both types of plots and % annual litterfall for the forest stand (r_{Pearson} were 0.8 and 0.7 for surrounding and adjacent plots respectively; $P < 0.0001$ in both cases). In contrast, correlations between % annual litterfall and relative abundance of vegetation species at the scale of plots showed that central traps provided better representative samples of leaf litter than lateral traps (Table 1). Percentage of annual litterfall for 20 out of the 41 species analyzed was positively correlated with relative abundance of vegetation species in surrounding plots, while only 6 species were correlated with vegetation in adjacent plots. For some species (*Cyathea arborea*, *Cyrtilla racemiflora*, *Hirtella rugosa*, *Laetia procera*, *Manilkara bidentata*, *Matayba domingensis*, *Micropholis garciniifolia*, *Sapium laurocerasus*, *Tabebuia heterophylla*, and *Tetragastris balsamifera*) correlation coefficients were very high –especially between litterfall and vegetation in the surrounding plots. This might imply that leaf litter from these species has a relatively low range of horizontal mobility. However, correlation strength (measured as the Spearman coefficient magnitude) was not correlated with the species relative abundance, average height, average crown area, or leaf size.

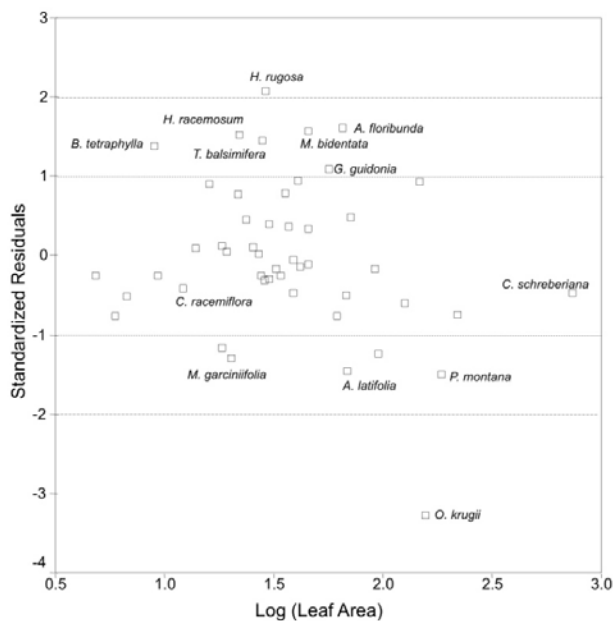


Fig. 3. Standardized regression residues as a function of log of leaf size. Analysis performed using SPSS 2002, version 11.5, Chicago, Illinois, USA. One and two standard deviations from the zero mean are indicated with dotted lines. Note that species with relatively big leaves such as *P. montana* and *O. krugii* are located in the lower right area of the graph, while species with relatively small leaves such as *H. rugosa* and *B. tetraphylla* are located in the upper left area.

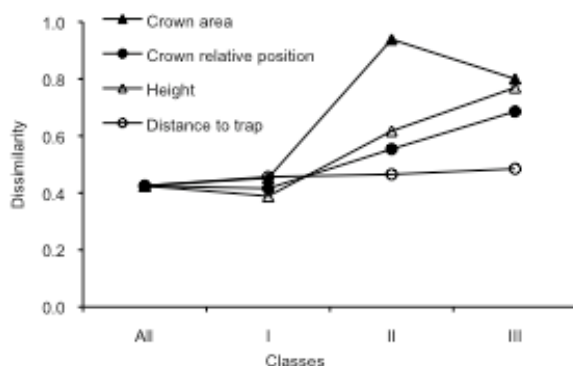


Fig. 4. Average dissimilarity between vegetation and litterfall from the same plot for the complete vegetation community and each of the three sub-sets corresponding to height (class I: >10m, II: 5-10 m, III: <5 m), crown relative position (I: canopy, II: sub-canopy, III: understory), crown area (I: >6.25 m², II: 1-6.25 m², III: <1 m²), and distance to traps (I: 0-5.5 m, II: 5.5-8 m, III: 8-10 m) classes. Differences between the dissimilarity for the whole community (all classes) and the sub-communities were significant for all factors except for distance to traps.

Species	r_{Spearman} (P -value)			
	Litterfall vs. Surrounding vegetation		Litterfall vs. Adjacent vegetation	
<i>Alchornea latifolia</i>	0.391	(0.206)	0.389	(0.209)
<i>Alchorneopsis floribunda</i>	0.47	(0.123)	-0.213	(0.507)
<i>Ardisia glauciflora</i>	Not present in litterfall			
<i>Buchenavia tetraphylla</i>	0.599	(0.043)*	0.481	(0.114)
<i>Byrsonima spicata</i>	0.612	(0.035)*	0.393	(0.206)
<i>Byrsonima wadsworthii</i>	0.631	(0.028)*	0.631	(0.028)*
<i>Casearia arborea</i>	0.656	(0.020)*	-0.194	(0.546)
<i>Casearia sylvestris</i>	0.372	(0.234)	0.549	(0.065)
<i>Cecropia schreberiana</i>	0.688	(0.013)*	0.135	(0.676)
<i>Coccoloba swartzii</i>	0.264	(0.407)	-0.134	(0.677)
<i>Cordia borinquensis</i>	0.324	(0.304)	0.345	(0.272)
<i>Cordia sulcata</i>	0.054	(0.865)	0.322	(0.302)
<i>Croton poecilanthus</i>	0.492	(0.054)	-0.06	(0.828)
<i>Cyathea arborea</i>	1	(<0.001)***	Not present in plots	
<i>Cyrilla racemiflora</i>	0.825	(<0.001)***	0.778	(0.001)***
<i>Dacryodes excelsa</i>	0.21	(0.506)	0.524	(0.082)
<i>Drypetes glauca</i>	0.709	(0.003)**	0.372	(0.155)
<i>Eugenia stahlii</i>	0.448	(0.082)	-0.201	(0.455)
<i>Faramea occidentalis</i>	Not present in litterfall			
<i>Garcinia portoricensis</i>	-0.134	(0.677)	-0.243	(0.446)

<i>Guarea glabra</i>	-0.045	(0.895)	-0.28	(0.379)
<i>Guarea guidonia</i>	0.638	(0.009)*	0.49	(0.055)
<i>Guettarda valenzuelana</i>	0.326	(0.301)	-0.91	(0.779)
<i>Hirtella rugosa</i>	0.73	(0.002)**	0.799	(<0.001)***
<i>Homalium racemosum</i>	0.452	(0.08)	0.34	(0.195)
<i>Inga fagifolia</i>	0.285	(0.281)	-0.381	(0.146)
<i>Laetia procera</i>	0.844	(<0.001)***	0.183	(0.493)
<i>Manilkara bidentata</i>	0.791	(<0.001)***	0.7	(0.003)**
<i>Matayba domingensis</i>	0.854	(<0.001)***	0.776	(0.003)**
<i>Miconia</i> spp (<i>M. prasina</i> and <i>M. tetrandra</i>)	0.707	(0.01)*	-0.029	(0.930)
<i>Micropholis garciniifolia</i>	0.851	(<0.001)***	0.991	(<0.001)***
<i>Myrcia</i> spp (<i>M. fallax</i> , <i>M. splendens</i> , and <i>M. leptoclada</i>)	0.183	(0.569)	-0.118	(0.715)
<i>Ocotea floribunda</i>	-0.201	(0.530)	Not present in plots	
<i>Ocotea leucoxydon</i>	-0.102	(0.756)	-0.03	(0.934)
<i>Ormosia krugii</i>	0.789	(<0.002)**	0.24	(0.453)
<i>Palicourea croceoides</i>	Not present in litterfall			
<i>Prestoea montana</i>	0.403	(0.121)	0.344	(0.190)
<i>Psychotria berteriana</i>	-0.297	(0.349)	-0.087	(0.792)
<i>Sapium laurocerasus</i>	0.839	(<0.001)***	0.35	(0.182)
<i>Schefflera morototoni</i>	0.697	(0.004)**	0.021	(0.936)
<i>Sloanea berteriana</i>	0.059	(0.826)	-0.079	(0.771)
<i>Tabebuia heterophylla</i>	0.874	(<0.001)***	0.403	(0.121)
<i>Tetragastris balsamifera</i>	0.791	(<0.001)***	0.351	(0.181)
<i>Trichilia pallida</i>	0.42	(0.173)	-0.092	(0.780)

Table 1. Spearman's rank correlation (r_{Spearman}) between % annual litterfall and relative abundance of tree species in the surrounding and adjacent vegetation (n = 12 plots each). Degree of significance is indicated besides P-values as: * = $P \leq 0.05$, ** = $P \leq 0.005$, and *** = $P \leq 0.001$.

When the whole vegetation community was compared with litterfall across scales, there was a general trend of decreasing similarity from the scale of the forest to the scale of plots. When litterfall and vegetation from the same block were compared (i.e., A vs. A, B vs. B, and C vs. C), we found an average similarity of 72% (ranging from 63 to 82%); while among different blocks (i.e., A vs. B, A vs. C, and B vs. C) we found an average similarity of 56% (ranging from 42 to 68%). Litterfall and vegetation from the same plot had an average similarity of 58% (ranging from 34 to 70%). While, average similarity between litterfall and vegetation from different plots but within the same block was 45% (varying between 28 and 75%). Finally, average similarity among plots belonging to different block was 41% (ranging from 17 to 73%).

The relatively low similarity between litterfall and vegetation species composition at the scale of plots was also evident in other analyses: neither the Mantel test comparing vegetation and litterfall distance matrices, nor the one comparing matrices of physical

against compositional distances were significant (standardized Mantel statistic = 0.23, $P = 0.26$ for vegetation vs. litterfall; Mantel statistic = 0.158, $P = 0.202$ for physical vs. compositional distances). According to the PCA (Fig. 5), the two main factors accounting for 28.7% of the variation among plots roughly corresponded to sample origin (i.e., litterfall vs. standing vegetation) and spatial distribution of vegetation (i.e., samples from blocks A, B, or C). It is interesting that block B appears as quite distinct from the other two blocks (check Fig. 1 for relative location of blocks over the study area). Finally, vegetation and litterfall samples from the same plots were not grouped together in the MDS ordination space. On the contrary, vegetation samples tended to cluster together while litterfall samples were scattered around (Fig. 5).

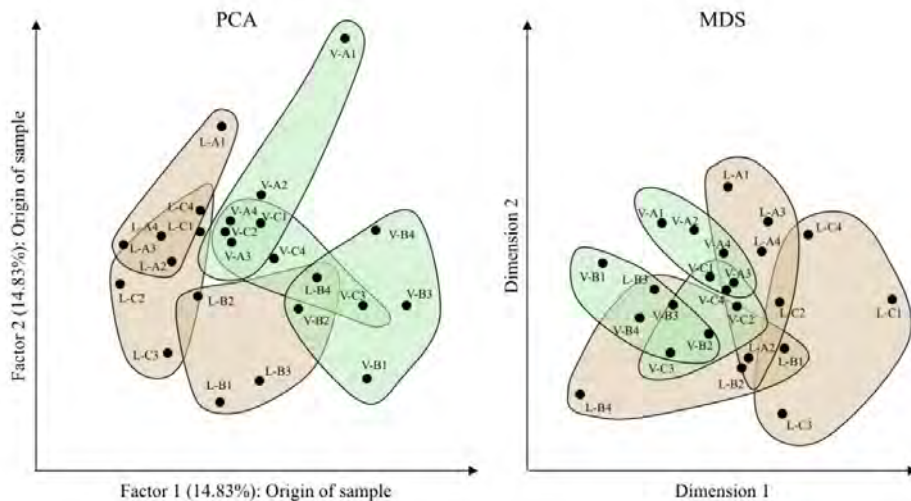


Fig. 5. PCA and MDS ordinations for vegetation in circular plots and litterfall collected in traps located at the center of plots. Codes refer to L = litterfall, V = vegetation, blocks (A, B, and C) and plots (1-4). Shading colors refer to vegetation (green) and litterfall (brown).

4. Discussion

Results from the regression analysis point to the significance of tree height and crown area as main factors determining litterfall composition and thus support ballistic models of leaf dispersal in which both wind and tree height are taken into account (e.g., Jonard et al., 2006). Ballistic models represent leaf dispersal as parabolic trajectories. This means that, even though distance is undoubtedly an important factor determining leaf dispersal, there might not be a simple inverse relation between leaf fall and distance from the source, as traditional models of leaf dispersal imply (e.g., Ferrari & Sugita, 1996). However, comparisons of litterfall and vegetation across scales indicated that patterns of leaf litter dispersal have an important random and wide-ranged character. In addition to the lack of correlation between distance matrices according to the Mantel test, the poor clustering of litterfall and vegetation samples in the MDS ordination space, and the separation of litterfall and vegetation samples along the first axis of the PCA (cf., Fig. 5), a case-based analysis of particular species provided further support for the thesis of a random and wide-ranged leaf dispersal in the

forest studied. For example, the species *Clusia clusioides* and *Clusia rosea* were present in litterfall samples but not in any of the vegetation plots. These species of trees, however, have been recorded in the Luquillo Forest Dynamic Plot (cf., Fig. 1 for the location of this plot. See http://luq.lternet.edu/research/projects/forest_dynamics_description.html for detailed description of this plot) suggesting that litter traps could have collected leaves coming from much farther than 10 m.

Furthermore, the fact that height and crown size were the main factors determining composition of litterfall samples also suggests that small to medium size understory trees can be under-represented in litterfall samples. Such could have been the case for two species of small to medium size tree species –*Palicourea croceoides* and *Ixora ferrea*– which were absent in litterfall samples in spite of being well represented in both the surrounding and adjacent plots. Underestimation of certain components of vegetation in litterfall samples can have important implications for the estimation of forest and ecosystem parameters based on litterfall such as net primary productivity (Clark et al., 2001) and leaf area index (e.g., Vose et al., 1995). According to Clark et al. (2001) failure in the collection of big leaves in litterfall samples can lead to an up to 25% under-estimation of net primary productivity. Such under-estimation might be even greater if the failure to collect leaves from small understory trees is also accounted.

It is interesting that distance to traps was not a significant factor determining the relative abundance of species in litterfall samples. Here again specific cases are illustrative. For example, *Ardisia glauciflora* was absent in litterfall in spite of being mostly located close to the litterfall traps (the highest IV was recorded at distance class <5 m). In contrast, leaf litter of *B. tetraphylla* was higher than expected from the regression model given the height and crown size recorded for this species, despite the fact that most of the trees were located at distance class 8-10 m. These observations agree with previous studies in which proximity of big trees to litter traps was no warranty for catching leaf litter in the closest traps (e.g., Burnham, 1997; Lowman, 1988). Thus, if proximity to litter traps does not solve the problem of under-representation of small trees, it might be the case that in addition to a higher number of litter traps, litter traps should be placed at lower heights. Litter traps are commonly placed at 1 m above ground level (e.g., John, 1973; Kitayama & Aiba, 2002; Lam & Dudgeon, 1985; Martinez-Yrizar & Sarukhan, 1990; Newbould, 1970), although studies using traps at 0.4-0.8 m height (e.g., Kavvadias et al., 2001; Lowman, 1988; Rai & Proctor, 1986) and at 1.2-1.5 m height (e.g., Hirabuki, 1991; Hughes, 1971; Ukonmaanaho & Starr, 2001) are also quite common. However, there is rarely any explicit indication about the reason why a particular height is chosen. Results from this study suggest that at least the vertical structure of the forest should be considered to determine the optimal height at which traps are to be placed. We recommend a litterfall trap height lower than 1.3 m (the one used in this study), yet further studies are needed to establish exact canopy/litter trap height parametrization.

The comparison between litterfall samples and vegetation from the surrounding and adjacent plots proved to be informative for the experimental design of future studies employing litterfall traps. According to our results, studies in which the species composition of litterfall samples is a relevant parameter (e.g., decomposition and litterfall dynamics studies) should use litterfall traps located in the center of the studied plots, whereas studies focusing on general characterization of primary productivity at scales higher than 10⁴ m² can use either central or lateral traps.

Even though we did not find a significant effect of leaf size over leaf litter samples composition, regression analysis suggested a trend in which small-leave trees were over-estimated whereas big-leave trees were under-estimated (cf., Fig. 3). We believe that further studies should investigate this trend by including either specific leaf area (SLA) or specific leaf weight (SLW) in the analyses. For example, *Alchornea latifolia* and *Micropholis garciniifolia* were slightly under-represented (cf. residues < -1 in Fig. 3) and both have relatively low SLA values (51 and 48.7 cm²/g respectively; data from Tanner & Kapos, 1982; Weaver & Murphy, 1990), suggesting that litter traps did less well at catching bigger and heavier leaves, and not simply bigger leaves. An approach based on SLA and/or SLW might also be promising in the study of specific patterns of horizontal mobility of leaf litter as were inferred in this study from the Spearman correlations. In addition, other factors such as wind pattern, animal distribution, and seasonal effects (Zalamea & González 2008) on litterfall patterns should be considered in future studies.

5. Conclusion

Higher height and a wider crown were more important determining relative abundance of species in litterfall samples. Trees with small leaves tended to be over-estimated. While distance to traps was not a significant factor determining the relative abundance of species in litterfall samples. The decreasing similarity between litterfall and vegetation from the scale of the forest stand down to the scale of sampling blocks and plots, plus the compositional differences among blocks inferred from the PCA indicates that sampling units at scales around 10⁴ m² do not necessarily constitute proper replicates of units at bigger scales such as the forest stand (see for instance Williams et al., 2002 for the implications of scaling up highly spatially heterogeneous parameters), and that estimates at the forest stand scale should be calculated by pooling data coming from all the sampling units. Therefore, care must be taken when scaling up from small to intermediate sampling units such as plots and block respectively, due to the high variation of leaf litter dispersal at scales lower than 10² m².

6. Acknowledgment

This research was performed under grant DEB-0218039 from the National Science Foundation to the Institute of Tropical Ecosystem Studies, University of Puerto Rico (UPR), and the U.S. Department of Agriculture -Forest Service (USDA-FS), International Institute of Tropical Forestry (IITF) as part of the Long-Term Ecological Research Program in the Luquillo Experimental Forest. Additional support was provided by USDA-FS and UPR. We are thankful to the litterfall sorters: Yadira Ortíz, Omar Ortíz, Juan Ramírez, Marcos Rodríguez, Alberto Rodríguez, Vivian Vera, and Ivan Vicens. Aaron Shiels, Jill Thompson, and Eda Meléndez kindly provided unpublished and raw data on CTE plots vegetation and Luquillo Forest Dynamic Plot. El Verde technicians (especially John Bithorn) helped collecting litterfall samples. Maya Quiñones of the IITF GIS Remote Sensing Laboratory helped with figure 1. Finally, we are grateful to two anonymous reviewers whose comments helped to significantly improve the manuscript.

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