The use of productivity and decomposition to address functional redundancy in the Neotropics

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Abstract: Past inability to come to a consensus about the degree of functional redundancy in ecosystems may be due, in part, to different definitions of ecosystem function and different investigative methodologies. Here I define ecosystem function, using the largely plant-based functions of aboveground productivity and decomposition of 10 common early successional trees found in Puerto Rico, and then use two different multivariate techniques to define functional groups. I found that: (1) multivariate statistical methods worked well to sort out the test species on axes defined primarily by productivity, which may have more redundancy than decomposition, and initial leaf nutrient content, (2) there were four plant functional groups defined by species (i) *Psychotria berteriana*, (ii) *Cecropia schreberiana*, (iii) *Inga vera,* and (iv) a group containing the other seven species, and (3) the plant traits of nitrogen-fixing capacity and mycorrhizal strategy mapped better onto these groups then those of seed size, wood density, shade tolerance or successional status. Finally, implications for key plant structures and for conservation of Neotropical areas are discussed.

Abbreviations: PCA - Principal Components Analysis.

Nomenclature: Liogier and Martorell (1982).

Introduction

Ongoing debate over the role of species in ecosystem function and structure (Odum 1977, Schulze and Mooney, 1993) has recently focused on functional redundancy (Walker 1992, Lawton and Brown 1993, Gitay et al. 1996, McGrady-Steed et al. 1997, Naeem and Li 1997, Tilman et al. 1998). The basic question asked is: assuming that species have functions or roles in ecosystems, are there functions that many species can perform equally well, thereby making some species redundant (Tilman and Downing 1994)? This investigation is important because it (1) examines the degree to which species control ecosystem functioning, (2) shows how to preserve function when species are lost to extinction, and (3) can identify important species for conservation efforts aimed at maintaining ecosystem function. This potential loss of species is a real concern in the species-rich Neotropics, because the functions of these ecosystems may be heavily species and species-interaction dependent (Orians et al. 1996). Consequently, the Neotropics is a good place to investigate both species control of function and species redundancy.

However, redundancy studies have been focused mainly in the temperate zone, and the degree of functional or species redundancy has been shown to depend on how ecosystem function is defined and what methods are used. For example, researchers have suggested low functional redundancy (removing species leads to a significant change in function) for mycorrhizal fungi (Allen et al. 1995) and shown it for old-field plants (Ostfeld et al. 1997). Alternatively, researchers have shown high functional redundancy (removing species has little effect on function) for litter decomposition (Wardle et al. 1997) and belowground detritus-driven systems (Lawton et al. 1996), and suggested it for productivity (Schulze and Mooney 1993). A common approach has been to examine the role of different species at the same trophic level. This has shown functional equivalence for pond predators (Morin 1995), functional difference between old field mammalian seed and seedling predators (Ostfeld et al. 1997), and an increase in redundancy (as defined as the average number of taxa in each trophic niche) for freshwater plankton communities after copper addition (Havens 1994). In general, a high degree of redundancy has been suggested for many communities (Lawton 1991) with exotic and keystone species least likely to be redundant (Myster and Pickett 1992, Chapin 1997).

Plant-based processes are key ecosystem functions in terrestrial ecosystems because plants (1) are the conduits for the vast majority of energy and nutrient dynamics (Vitousek and Hooper 1993, Tilman et al. 1997), especially in the tropics where most available nutrients stay in the plant biomass and form loops through decomposition and uptake (Vitousek and Sanford 1986), (2) comprise the bulk of the biomass (Hairston et al. 1960), and (3) may control soil nutrient availability (Wedin and Tilman 1990). Further, those plant-based functions should be productivity and decomposition (Watt 1947). Consequently plant functional types (Grime 1973, Diaz and Cabido 1997) may best be seen as those plant groups of similar productivity and decomposition responses within an ecosystem, and not only groups of similar plant physiological and morphological structures (e.g., Tilman et al. 1997).

Therefore in order to understand redundancy and the role of species in ecosystem functions, I sampled and analyzed 10 common tree species for the key traits of productivity and decomposition. In this study, productivity redundancy refers to similarities in the rates of carbon fixation, not in any other species-specific processes. Similarly, decomposition redundancy refers to similarities in the rate at which nutrients and chemical energy are released to the decomposer community, and not to the decomposer species themselves. Finally, it is critical to remember that species have multiple functions and roles within ecosystems. Therefore here, where the same plant species serve for both of the functions of productivity and decomposition, multivariate analysis is employed. This analysis, based on variance patterns of species responses, is needed to show functional similarity and redundancy.

Study area

This study took place in the Luquillo Experimental Forest (LEF) of northeastern Puerto Rico, USA (18° 20'N, 65° 45'W) which is the tropical long-term ecological research (LTER) site of the National Science Foundation (Myster and Fernandez 1995). The climate of the LEF is dominated by trade winds that produce moisture-bearing clouds year round with a total water input between 2 and 5 meters per year. The wettest months are between July and October, and the driest between January and April. The forest is subtropical wet rainforest and characterized by tabonuco (*Dacryodes excelsa)*, ausubo (*Manilkara bidentata*) and motillo (*Sloanea berteriana*) below 600 m, palo colorado (*Cyrilla racemiflora*) and palm (*Prestoea montana*) between 600 m and 850 m, and cloud forest above 850 m to 1080 m (Ewel and Whitmore 1973). Also, mean air temperatures vary between 23°C at the lower elevations and 18.7°C at the highest (D. Schae-

fer, pers. comm.). The dynamics of the LEF includes the four disturbance types of treefall gaps, hurricanes, landslides and human activity laid on this distinct altitudinal gradient. Vegetation after these disturbances include *Cyathea arborea, Gleichenia bifida, Cecropia schreberiana, Miconia racemosa, Inga vera, Guarea guidonia, Schefflera morototoni* and *Nepsera acuatica* (Myster and Walker 1997). Finally, soils are mainly derived from volcanoclastic primary substrate that has weathered into clay ultisols.

Methods

I first measured, harvested, dried and weighed 15 sapling size individuals (1-2 cm basal diameter and 15-20 cm height) of 10 common and widely distributed early and mid-successional tree species (these species comprise more than 90% of the stems in successional LEF plots; Myster and Fernandez 1995, Myster and Walker 1997) growing on several LEF roadsides having different environmental conditions. Because these tree species and genera are found throughout the Neotropics, they probably assume major functional roles there and make good study organisms. I then used these data to construct an allometric equation for each of the species, relating height and basal diameter (the independent variables) to above-ground biomass (leaf and wood biomass as the dependent variable; Scatena et al. 1993). In addition, 15 individual stems (1-2 cm basal diameter with similar initial heights) of each of the 10 test species, growing in Puerto Rican successional areas, were measured (height, basal diameter) over a year's time (March 1997-March 1998). Small stems were used because turnover of small successional saplings and trees dominates tree dynamics in these areas. By using the allometric equations, I generated a mean net initial and mean final total above-ground biomass and a mean above-ground productivity rate (g/yr) for each species. Total above-ground biomass included both living and senescent leaves, branches and stems.

For decomposition species parameters, I harvested 20 g of leaf biomass and 20 g of wood biomass of each species from 5–10 individuals (5 replicates). Fallen leaves were not used because they would already be partially decomposed (as much as 25% organic matter loss within a few days; Myster and Schaefer, unpub. data). Ten grams of leaf biomass and 10 g of wood biomass were analyzed fresh for carbon, nitrogen (N), phosphorus (P) and potassium (K) content for each species, with 5 replicates and using means for the analysis, which represents the accumulation of nutrients in the above-ground biomass during the growth captured by the productivity rates. This initial litter of each species was dried, milled to 1.0 mm mesh,

Table 1. Values of all the variables used to define the matrix in the multivariate analysis, given by species (see Figure 1, for abbreviations), with mean and standard error.

Variable	Cs	Gs	Hc	Iv	Mr	Pr	Pg	Ph	Pb	St	mean	SE
productivity g/yr	391	75	89	268	30	77	10	10	157	49	115.6	124.13
% leaf remaining	44	31	29	59	44	26	28	21	15	15	31.2	14.03
% wood remaining	47	80	68	64	68	68	48	67	52	51	61.30	11.04
initial leaf P mg/g	1.1	0.5	0.5	1.0	0.5	0.6	0.9	1.1	0.9	1.7	0.88	0.37
initial leaf K mg/g	12.1	12.1	9.7	8.8	6.5	14.6	23.5	21.1	21.8	18.6	14.88	6.00
initial leaf N mg/g	20.7	13.4	15.4	34.2	17.6	20.8	27.3	39.4	28.3	32.1	24.92	8.66
initial wood P mg/g	0.6	0.2	0.2	0.5	0.5	0.9	0.4	0.3	0.3	0.6	0.45	0.21
initial wood K mg/g	13.1	5.3	4.1	5.4	5.5	10.8	12.0	13.1	5.0	9.4	8.37	3.66
initial wood N mg/g	8.2	5.4	4.1	13.5	7.4	7.3	12.9	8.0	5.6	7.5	7.99	3.03
final leaf P mg/g	0.9	0.6	1.0	0.6	0.8	1.4	0.8	1.2	1.0	0.8	0.91	0.25
final leaf K mg/g	1.9	1.7	2.7	1.5	2.7	2.8	2.1	1.3	2.2	1.5	2.04	0.55
final leaf N mg/g	35.2	25.8	28.1	34.8	26.0	45.8	42.0	63.1	50.9	38.2	38.99	11.89
final wood P mg/g	0.6	0.1	0.5	0.2	0.2	0.0	0.4	0.3	0.7	0.4	0.34	0.22
final wood K mg/g	1.9	0.8	1.7	1.1	1.4	0.0	1.3	0.8	2.3	1.7	1.30	0.65
final wood N mg/g	14.0	6.2	8.6	12.2	4.5	6.6	16.4	8.0	11.0	8.7	9.62	3.73

and subsamples consumed in a furnace (550°C for 12 hr) to determine ash-free dry weight and percent of the organic matter remaining. Chemical analyses of subsamples were done for total N by combustion analysis and, for P and K by inductively-coupled plasma spectroscopy after acid digestion. This analysis cannot distinguish between different forms of these nutrients. These data were converted to percentage of the initial organic matter and nutrient remaining (see Zou et al. 1995).

The remaining plant biomass was put in 100 litter bags (20 cm x 20 cm 0.01 mm mesh synthetic cloth [bottom] with 1 mm steel mesh [top]), one bag with 10 g leaf material and one bag with 10 g wood material for each of the ten species with five replicates, and set out in a LEF successional area until the majority of the biomass was decomposed (this took 16 weeks as in other LEF successional studies; Zou et al. 1995, Myster and Schaefer, unpub. data). The bags were then collected, with the contents analyzed as before representing species-specific carbon and nutrient losses in leaf and in wood biomass. A decay rate of % of the original 10 g of leaf biomass remaining for each bag was calculated.

This field experiment included both a litterbag decomposition experiment and a natural harvesting of saplings where both productivity and decomposition were measured and evaluated in a natural setting. I chose to measure the natural growth and decay parameters of indi-

vidual tree saplings in the field, instead of varying species groups in a greenhouse. This generated real response data that were then used in multivariate statistical analysis for a better investigation of similarity/dissimilarity and relationships between both plant functions. Also, the focus on the top ten species taken one at a time assumes an individualistic perspective (Myster and Pickett 1988) on ecosystems, where plant growth is dominated by within-species tolerances and life-history traits (Myster and Pickett 1992).

The multivariate techniques compare and contrast all data and, therefore, ratios among nutrients are included in the analysis. The productivity data and the decomposition data were combined in a matrix with the 10 species defining rows. Column variables were: above-ground biomass (leaf + wood) accumulation or rate of net productivity per average stem (g/yr), the rate of leaf decomposition (% of the original 10 g of leaf biomass remaining in litterbags), the rate of wood decomposition (same computation as leaf biomass), initial levels of P, K, N (all three expressed as mg/g) in the leaf tissue, initial levels of P, K, N in the wood tissue, P, K, N levels in the leaf biomass after 16 weeks in the field, and P, K, N levels in the wood biomass after 16 weeks in the field (Table 1). The complete matrix (10 rows x 15 columns) was used in two multivariate analyses: principal components analysis (PCA) using the correlation matrix of variables and (2) cluster analysis

giving the actual clustering metric (Euclidean distance). Single-linkage sorting was used as the clustering algorithm; this procedure is known to detect well-separated clusters since cluster-to-cluster distance is defined as the smallest distance between the points (SAS 1997). Therefore, redundancy is approached in terms of similarity or dissimilarity among the key variables. Finally because the same species are used to define both productivity and decomposition, multivariate analyses must be used and thus this is a new approach to the problem of functional redundancy.

Results

Table 1 shows the values for all variables, for all species used in the analysis with means and standard errors. Using these data, PCA separated the species very well with the first two axes explaining 98% of the total variance (axis I is most important at 66%, axis II explains 32%) among the species. PCA axis I was defined by a significant positive correlation with productivity (r = 0.999, p<0.0001). PCA axis II was defined by significant positive correlations with initial leaf P (r = 0.6606, p = 0.0376), initial leaf K (r = 0.8757, p = 0.0009), initial leaf N (r = 0.6974, p = 0.0250) and final leaf N (r = 0.8595, p = 0.0014), and with a significant negative correlation with percent wood biomass remaining (r = -0.66524, p = 0.0358; Table 2). In addition, correlation among variables was suggested when they correlated with the same axis.

Table 2. Loadings of each variable on the first two PCA axes.

| Variable	PCA I	PCA II
productivity	0.999	0.115
% leaf remaining	0.345	0.265
% wood remaining	0.471	-0.665
initial leaf P	0.556	0.660
initial leaf K	0.288	0.875
initial leaf N	0.129	0.697
initial wood P	0.282	0.461
initial wood K	0.582	0.552
initial wood N	0.439	0.256
final leaf P	0.381	0.235
final leaf K	0.601	0.178
final leaf N	0.527	0.859
final wood P	0.456	0.264
final wood K	0.324	0.599
final wood N	0.127	0.163
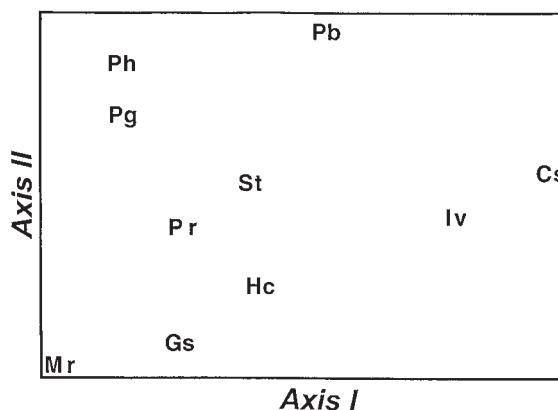
Figure 1. Scatter plot of species locations in ordination space as defined by Principal Components Analysis. Species are abbreviated as: *Cecropia schreberiana* (Cs), *Gonzalagunia spicata* (Gs), *Heterotrichum cymosum* (Hc), *Inga vera* (Iv), *Miconia racemosa* (Mr), *Palicourea riparia* (Pr), *Piper glabrescens* (Pg), *Piper hispidum* (Ph), *Psychotria berteriana* (Pb), *Solanum torvum* (St).
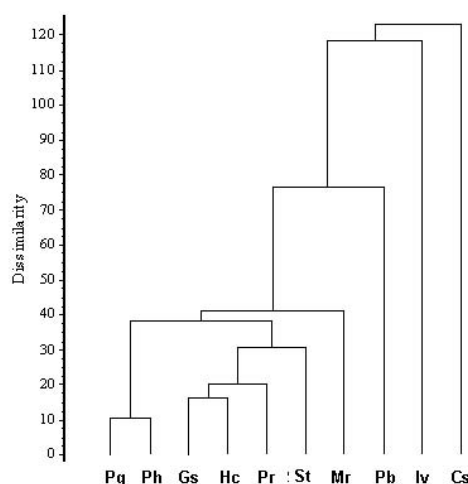

Figure 2. Results from single-linkage cluster analysis using the first two principal component scores of the ten test species to compute Euclidean distances. See Figure 1, for abbreviations.

Figure 1 shows the scores of the ten test species on the first two PCA axes, whereas Figure 2 is dendrogram of species as derived by single linkage clustering from the PCA scores. A well-separated large cluster contains species *P. glabrescens, P. hispidum, S. torvum, M. racemosa, P. riparia, G. spicata* and *H. cymosum*, fused by species *P. berteriana, C. schreberiana* and then *I. vera* as separate clusters.

Discussion

These results add to the redundancy debate suggesting that the majority of the 10 tree species were redundant (within the same clusters) for the functions productivity and decomposition. In addition, PCA axis I shows the dominance of productivity and growth rate in defining plant functional groups (Cornelissen et al. 1996), suggesting it is a key trait in defining tropical tree life histories. PCA axis II suggests an important role in defining function for initial leaf nutrient concentration as well, and shows that high nutrient tissue decays fastest. Also, results for productivity and leaf N suggest that nutrient use-efficiency (defined as productivity/leaf N) may be relatively constant for the test species. Because the PCA axes separated the two functions well, with productivity on axis I and decomposition on axis II, this allows closer examination of overlap and linkage in redundancy. For example, (1) *Psychotria berteriana* may not be a separate cluster if viewed on the productivity axis alone and (2) the 10 species seem to be evenly spread out on the decomposition axis (Wardle et al. 1998) suggesting that redundancy is more common for productivity than for decomposition (McGrady-Steed et al. 1997).

The functional clusters of Figures 1 and 2 allow some investigation into tree structural similarities and differences, which may be important in causing these functional differences, by mapping plant structures thought to be key traits onto the species within these groups. Although the data for tropical trees is limited, I found that the traits: shade tolerance (*Piper* sp. and *Solanum torvum)* differ greatly in shade tolerance but are in the same cluster; Smith 1970, Devoe 1989), seed size (species in the same clusters differ greatly in seed size, over several orders of magnitude; Francis and Rodriguez 1993, Myster 1997) and wood density (Reyes et al. 1992) were not consistent inside clusters. However, there is a degree of correspondence for species that alter or increase nutrient availability: (1) for species of similar Arbuscular-Mycorrhizae (AM) fungal dependency strategy (obligate species *Psychotria berteriana* defines a cluster, and the facultative species *Cecropia schreberiana* defines another cluster; Calderon-Gonzalez 1993) and (2) for N-fixing species (*Inga vera* is a N-fixing species). Furthermore, redundant structures may be identified as those morphological, anatomical or physiological structures (Tilman et al. 1997) that the plants in each cluster do not have in common even if they are needed to realize the ecosystem functions of productivity and decomposition, or, as those structures that the plants have in common within clusters but cannot be tied to productivity or decomposition. For the ten test species, I suggest that (1) specific leaf area, gas exchange structures, root to shoot ratio, leaf and stem architecture (as seen by the correlation between PCA axis I and productivity; N. Fetcher, pers. comm.) and (2) root structures adapted for N and P uptake (consistent with the functional clusters), may be key plant structural traits controlling productivity and decomposition for these successional species.

Results which highlight species with special nutrient roles also point to known successional patterns where patches may have limited AM spores (Myster and Fernandez 1995). PCA axis II again shows the importance of plant strategies involving phosphorus, nitrogen and AM to Neotropic ecosystems (Allen et al. 1995, Myster and Fernandez 1995). Furthermore, the plant clusters reflect successional colonization well because species ranks, when they enter and dominate during succession based on permanent plot sampling, are consistent within the functional groupings (Myster and Walker 1997). Individual species data were consistent with those previous Puerto Rican studies that also studied individual tree growth and decay. For example, Scatena et al. (1993) found twice as much N and P in leaves compared to wood with similar K levels between leaves and wood, *Palicourea riparia* had higher levels of all nutrients than *Cecropia schreberiana* especially in the wood of *Cecropia*, and a growth rate for *Cecropia* 2-3 times as high as for *Palicournea*. Also, Zou et al. (1995) found decomposition rates for mixed-species litterbags in the same ranges as these single species litterbags.

Finally, there are at least two caveats to remember for this study and others of species and ecosystem function: (1) species interactions may be a controlling factor in determining how species cluster in functional groups because species could be excluded from groups by other species and not by their inability to perform certain functions, and (2) patterns may be the result of other factors correlated with species richness (Huston 1997) not the species themselves, or even a factor that simply varies in a consistent way either spatially or over successional time. However unlike past studies that sought functionality indirectly by examining and grouping plant morphological and physiological traits, this study used key functional response data and multivariate analysis to define plant functional groups. This has led to a more objective species grouping and investigation of redundancy, which may be particularly important in tropical ecosystems where loss of habitat makes decisions about which species and functions to conserve critical both now and into the future.

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