Productivity/Turnover and Richness/Turnover relationships in a Puerto Rican pasture

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Abstract: Species turnover is a key parameter influencing dynamics of species in a community. Here I explore relationships between temporal species turnover and productivity and between temporal species turnover and richness in an abandoned pasture in Puerto Rico. Permanent plot data collected in the pasture over the first 10 years after abandonment were used to generate linear regressions, which were then used to test two hypotheses about how productivity and richness relate to turnover, as this pasture reverts back to rainforest. I found (1) productivity had a slight positive relationship (small positive slope) with turnover in years two and three after abandonment, but a large negative relationship (large negative slope) in year four and afterwards, and (2) richness had a negative relationship with turnover in every year which increased (slope became more negative) with time. Because both productivity and richness had a negative relationship with turnover, species loss decreased with time even when species productivity and richness continued to increase or level off; turnover consists mainly in the loss of less productive species. I suggest restoration strategies that managers may follow to either increase or decrease that most basic successional parameter, turnover.

Key words: LTER, lower montane forest, Neotropics, permanent plot.

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Introduction

Communities are dynamic and variation in species composition is central to community-wide changes. These compositional changes are commonly measured as species turnover (Diamond 1969; Phillips & Gentry 1994) which may relate to the "invasibility" of a community (Davis *et al.* 2000; Vitousek *et al.* 1996). The monitoring of species turnover is critical both for efforts to conserve individual species (including exotics and rare species) and for the general maintenance of species richness in communities. "Turnover" can be either spatial - a change in species composition when the same or different communities are measured over spatial gradients (e.g., going up a mountain: Whittaker 1972), or temporal - a change in species composition compared to an initial sampling period, if the same community is measured over time (e.g., recovering after abandonment from agriculture: Myster & Pickett 1994; Shugart & Hett 1973).

Researchers have been interested not just in measuring turnover, but also in the relationship between turnover and ecosystem functions (e.g. productivity: Chalcraft *et al.* 2004; Lonsdale 1999; Loreau *et al.* 2001) and between turnover and community structures (e.g. species richness: Lonsdale 1999). Their motives were either to understand the control and causal effect of turnover itself in communities, or in using turnover to understand other patterns such as those between productivity and richness (Chalcraft *et al.* 2004; Myster 2009) and those associated with invasion by exotic species and their persistence (Yurkonis & Meiners 2004).

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Turnover, productivity, and richness are all well-studied structures and functions of tropical rainforests (Myster 2009; Phillips *et al.* 1994; Myster *in press*), where the relationships among them may be studied with some ease because ecosystem functions there are greatly dependent on the species present and the interactions among them (Orians *et al.* 1996). In particular, examination of rainforests after disturbance presents a unique opportunity to observe and measure the relationships among turnover, production, and richness as the forests recover over successional time. Indeed, the ubiquity of pastures in the tropics (Myster 2003; Myster 2007b) suggests that focusing on pastoral disturbance - clearing of the rainforest, cropping, various cattle effects - can help scientists throughout the tropics not only to understand the relationships among turnover, productivity, and richness, but also to develop a deeper understanding of pastures and the regeneration of rainforest.

A key component to restoration of abandoned pastures is the restoration of structure. To assist in that process, this study examines three common structural parameters in pastures and how they relate to each other over time. In order to explore relationships between productivity and species richness on the one hand and species turnover on the other (Shurin 2007), I tested the following two hypotheses using data collected in permanent plots established in a Puerto Rican pasture, as it recovers to Neotropical rainforest.

Hypothesis 1. High production will be positively correlated (positive slope) with high species turnover (Chalcraft *et al.* 2004; Chase & Leibold 2002; Phillips *et al.* 1994) and this dependence will increase (the slope become more positive) as pasture succession proceeds.

Hypothesis 2. High species richness will be negatively correlated (negative slope) with high species turnover (Bakker *et al.* 2003; Lonsdale 1999; Shurin 2007), and this dependence will increase (the slope become more negative) as pasture succession proceeds.

Methods

The study site is a pasture that borders the Luquillo Experimental Forest (LUQ) of northeastern Puerto Rico USA (18º 20'N, 65º 45' W) which receives 3.8 m rainfall per year, and has an average temperature of 18 ºC. The LUQ is a

tropical long-term ecological research (LTER) site of the U. S. National Science Foundation, and its plant communities are dominated by tropical lower montane wet forest (Ewel & Whitmore 1973) containing tabonuco (*Dacryodes excelsa*)[1], ausubo (*Manilkara bidentata*) and motillo (*Sloanea berteriana*) below 600 m where the sampling took space.

The soil (fertile and volcaniclastic in origin), slope, and climate, are typical of pastures abandoned in the area (Thomlinson *et al.* 1996). The history of this pasture is well known and it has been the site of many LUQ LTER studies (e.g., Aide *et al.* 1995; Liu & Zou, 2002; Myster 2003; Myster 2007b; Myster 2009; Myster 2010; Myster 2012a; Myster & Malahy 2008) allowing greater synthesis.

Permanent plot sampling

In the Spring of 1995, two months after the study pasture was abandoned after decades of cattle grazing, a plot of dimension 25 m × 10 m was laid out bordering the LUQ, with the long side parallel to the forest/pasture border in order to facilitate comparative analysis with post-agricultural plots in New Jersey USA (i.e., the Buell-Small successional study: Myster 1993). The plot did not have any large remnant trees or visible tree roots within it at this time. For sampling purposes, the plot was then sub divided into twenty-five 5 m × 2 m contiguous sub plot which have proven sufficient to capture diversity in this pasture (Myster 2003). Starting in Spring of 1996 when the field had been abandoned for one year, and continuing annually for nine more years after that, every tree stem and all stems for every shrub at least 1m tall were measured for height, and for basal diameter at ground level in each subplot. Each stem was also identified to species (for nomenclature see Liogier & Martorell 1982). These data are archived as LTERDBAS#97 and may be visited on the LUQ web site (http://luq.lternet.edu). Production of above-ground biomass was dominated by woody species very soon after abandonment.

Data compilation

After ten years of sampling, above-ground biomass equations were developed (Myster 2002) for each of the ten most abundant tree and shrub

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1. Authorities for all species names will be found in Table 1

species found in the plots as an estimate of production. The whole study was limited to these ten species. This was justified because these species contributed over 90 % of the total stems and over 90 % of the total basal area to the entire woody sampling (Myster 2003). To generate the biomass equations, I collected ten to twelve stems (with their leaves) of each of these species from LUQ pastures and road sides (all within the same range [0.2cm - 6.5cm] of basal diameters as in the subplots). I first measured each stem for height and basal diameter, and then cut each stem at ground level. The total above-ground biomass of each of these stems was found by first drying them at 65 °C, with repeated weighing until constant weight was attained. Multiple linear regression analysis was then performed on these data in order to construct allometric equations for each of the ten species, relating above-ground biomass (the dependent variable) to height and basal diameter (the two independent variables) (Scatena *et al.* 1993; Uhl *et al.* 1988: see Table 1 for more details).

For each subplot and each year of sampling, above-ground woody standing crop was then estimated using the allometric equations, and the basal diameter and the height of all stems recorded in each subplot and year for the ten study species. For each subplot and sampling year, I also computed tree and shrub species richness and tree and shrub species turnover where turnover (Myster & Pickett 1994) at year x = $(N_{1996-x} + N_{x-1996}) / (N_x) - N_{1996}$ and x, where N_{1996-x} is the number of plant species present in the subplot at year 1996 but not present in the subplot at year x, N_{x-1996} is the number of plant species present in the subplot at year x but not present in the subplot at year 1996, N_x is the plant species richness at year 1996 in the subplot and N_{1996} and x is (plant species richness at year x in the subplot- the number of plant species invading the subplot between 1996 and year x). Production was standardized into grams m^{-2} yr^{-1} by dividing the standing above-ground biomass by 10 (area of the subplots) and also dividing it by the number of years since abandonment. This was treated as the annual production for that year because production and standing crop are highly correlated in early succession (Nascimento & Laurance, 2001). Testing of the three study variables - turnover, richness, production - did not suggest any autocorrelation (Durbin & Watson 1971).

I used the turnover, richness, and production computed for each of the 25 subplots and each individual year to compute linear regressions. For each year (1997 - 2006), two linear regressions were calculated (1) with production as the dependent variable and turnover as the independent variable, and (2) with richness as the dependent variable and turnover as the independent variable. Variance assumptions (e.g. of normality) were tested and accepted for each regression. Slopes from these regressions were first tested for significance and then, if significantly non-zero, for differences between years with one degree of freedom (SAS 1985; Sokal & Rohlf 1981). Due to the large number of tests, a sequential Bonferroni test was employed (Durbin & Watson 1971) and it determined that no significant results should be viewed with suspicion. Finally, with this data set I could only investigate patterns among turnover, richness, and productivity, not what is causing them. The amount of data was insufficient for other analyses such as time series analysis.

Results

Turnover was greatest at year 2 and then declined monotonically until year 10. Each of the ten common tree and shrub species showed highly significant allometric biomass regressions (all P values < 0.001, Table 1), and the most productive species were *Syzygium jambos*, *Miconia impetiolaris*, *Miconia prasina*, *Calophyllum calaba*, and *Clibadium umbella* (Table 2). Production was highest in the first two years after abandonment at 0.5 kg m^{-2} yr^{-1}, then declined to about half its maximum level in year three, and stayed there for the remaining years. Richness increased in year two and stayed at that level (~7 species in each subplot) for the remaining years.

Hypothesis 1

The slopes of the regression lines of productivity vs. turnover were significantly non-zero ($F_{1,240} = 18.48$, $P = 0.005$) and significantly different among years ($F_{8,240} = 13.72$, $P = 0.012$). Years 1997 and 1998 had a slightly positive slope between production and turnover, and year 1999 had a significant negative slope (Table 3) which became more negative with time. All tests met the Bonferroni corrected significance criteria.

Hypothesis 2

The slopes of the regression lines of richness vs. turnover were significantly non-zero ($F_{1,240} = 14.33$, $P = 0.006$) and significantly different among years ($F_{8,240} = 10.98$, $P = 0.040$). Year 1997 showed a slightly negative slope between richness and turn-

Table 1. The results of linear regression analysis using stems from the ten most common tree and shrub species. The model was: total above-ground biomass in grams = a + b*(basal diameter [bd] in cm) + c* (height in cm). N is the number of stems used in the analysis.

Species	N	bd range	P	R^2	a	b	c
Syzygium jambos	12	0.31-2.34	0.0001	0.83	-26.4	-43.8	1.46
Psychotria berteriana	12	1.1-4.8	0.0001	0.88	- 631.6	390.3	-0.1
Piper glabrescens	12	0.88-2.2	0.0001	0.88	-74.0	72.8	0.2
Miconia impetiolaris	11	0.7-3.4	0.0002	0.91	-101.6	143.4	-0.2
Miconia prasina	10	0.55-2.5	0.0002	0.81	-105.0	151.7	-0.2
Calophyllum calaba	12	0.2-1.8	0.0001	0.86	-24.11	-40.89	1.17
Miconia racemosa	10	0.55-2.25	0.0004	0.89	-100.5	154.6	-0.1
Clibadium umbella	10	0.4-2.15	0.0001	0.94	-99.7	99.3	0.48
Piper hispidum	10	0.55-1.9	0.0003	0.91	-38.5	44.3	0.2
Inga vera	10	0.75-6.5	0.0009	0.86	-1499	404.7	5.6

Table 2. The estimates of above-ground biomass (in gm^{-2}) for each of the ten most common tree species in each of the ten years of the study.

Species	yr 1	yr 2	yr 3	yr 4	yr 5	yr 6	yr 7	yr 8	yr 9	yr 10
Syzygium jambos	35.1	202.4	77.7	110.5	102.2	89.9	82.2	76.6	85.7	77.9
Psychotria berteriana	0.8	0.7	1.7	0.7	2.7	3.2	2.9	3.3	4.5	5.8
Piper glabrescens	2.1	8.3	7.6	6.1	12.2	9.8	12.5	9.4	13.6	14.4
Miconia impetiolaris	17.2	37.6	21.8	31.1	25.8	26.6	29.3	33.3	37.6	44.8
Miconia prasina	13.3	53.4	25.6	33.9	26.6	28.4	27.7	36.9	42.2	48.9
Calophyllum calaba	9.5	115.5	36.9	20.6	21.5	20.5	19.9	15.6	22.3	18.8
Miconia racemosa	0.7	3.3	3.4	3.2	2.3	3.3	4.5	4.2	3.1	3.9
Clibadium umbella	21.1	49.4	26.1	38.5	37.9	44.4	48.8	52.2	46.2	54.3
Piper hispidum	1.1	7.3	7.1	6.2	13.7	14.4	14.8	15.7	15.1	16.8
Inga vera	2.2	24.4	2.8	4.1	7.4	9.8	12.2	13.8	15.5	17.7

over (Table 4) which became more negative with time. Once again, all tests met the Bonferroni corrected significance criteria.

Discussion

Turnover levels were similar to those seen in other post-agricultural successions in the Neotropics (Myster 2007a; Myster 2007b; Uhl *et al.* 1988) but higher than temperate old fields of similar ages (Myster & Pickett 1994) where the grass (*Dactylis glomerata*) was planted. Regardless of where the fields were, however, turnover after agriculture in both the temperate zone and the tropics decreases through time as pioneer species are replaced by longer-living species that are more resistant to invasion. Grasses present at abandonment may reduce initial species richness and slow turnover due to a reduction of new

species invasion. In general, production was low in the early years of pasture succession compared to LEF areas after a major hurricane (12.2 kg m^{-2} y^{-1} one year after Hurricane Hugo: Scatena *et al.* 1993) and to the intact LEF itself (11-14 kg m^{-2} y^{-1} which also includes litter production). This is not surprising because Puerto Rican pasture productivity may take 55 years to recover to forest levels (Aide *et al.* 1995). Richness levels were lower than similar plots in Ecuador (Myster 2007a; and also see chapters in Myster 2007b).

In tropical forests turnover has been thought to be tied to productivity (Phillips et al. 1994) because the faster a forest grows the more rapid stem turnover it must have (and also species turnover because of low tree densities in tropical forests) and so this pasture should show a greater and greater positive relationship between the two with time. My results are consistent with the idea

Table 3. Linear regressions of productivity (g m^{-2} y^{-1}) on species turnover (per cent per annum) for each year over the ten-year sampling period. Turnover (of the ten main tree species) is expressed as a percentage of species present in Year One. Slope is positive in years 1997 and 1998, negative in year 1999, and becomes more and more negative monotonically with time.

Year	Slope	Y-intercept	R^2	*P-value*
1997	1.11	183	0.89	0.04
1998	0.72	160	0.91	0.04
1999	-0.23	152	0.78	0.03
2000	-0.31	143	0.65	0.01
2001	-0.38	122	0.82	0.04
2002	-0.44	98	0.75	0.02
2003	-0.53	83	0.96	0.02
2004	-0.67	76	0.77	0.03
2005	-0.78	62	0.81	0.02
2006	-0.86	55	0.64	0.01

that unproductive successional plant communities with low rates of competitive displacement and high diversity should have high turnover (Huston 1997). Productive mature plant communities should then have low turnover, because their species are longer-lived, and because those communities are difficult to invade due to their high rates of competitive displacement and dominance by only a few species (Huston 1997). It is thus thought that production may relate to species turnover through the replacement of less productive species by more productive ones, rather than through an increase in the growth of all species. Increases in production during early succession, when most species are already present (Pickett 1982), suggest that any negative relationship between turnover and production could be due to the loss of low production species during succession (Myster & Pickett 1988).

On the other hand, results of this study contrast with studies (Bakker *et al.* 2003; Phillips *et al.* 1994) that showed both spatial turnover (Bellingham *et al.* 1999; Chytry *et al.* 2001) and temporal turnover (Yurkonis & Meiners 2004) were positively correlated with productivity. Whatever the pattern, mechanisms causing turnover to change with productivity may include environmental heterogeneity causing turnover which is positively correlated with productivity, and productivity altering the probability of colonization or extinction because production may

be as much a consequence of colonization as of growth (Chase & Leibold 2002). Indeed, significant regressions could be the result of turnover being influenced, not by productivity or species richness, but by some other factor correlated with them (Huston 1997). In fact, turnover, productivity, and richness of functional groups of Neotropic plant species (e.g., those defined by phosphorus, nitrogen, and mycorrhizal strategies) rather than total plot species may prove critical (Tilman *et al.* 1997). Ultimately, however, a mechanistic explanation of these patterns must be explained by the plant-plant replacement process that leads to the plants found in the plots and by the interactions between species niches and the environment which generate the replacements (Myster 2007b; Myster 2012b).

Table 4. Linear regressions of species richness on species turnover for each year over the ten-year sampling period. Only the ten main tree species are considered for both variables. Turnover is expressed as a percentage of the species present in Year One. Slopes are negative throughout, and do not change monotonically.

Year	Slope	Y-intercept	R^2	*P-value*
1997	-0.51	8.3	0.79	0.05
1998	-0.88	7.1	0.81	0.03
1999	-0.63	5.4	0.86	0.04
2000	-0.64	4.3	0.69	0.04
2001	-0.66	3.9	0.86	0.01
2002	-0.71	3.5	0.75	0.02
2003	-0.73	3.0	0.86	0.01
2004	-0.77	2.5	0.66	0.03
2005	-0.83	1.6	0.93	0.04
2006	-0.83	1.1	0.74	0.03

Tropical forest richness may be positively correlated with tree species turnover as well (Phillips *et al.* 1994) and temperate forests also show a significant relationship between species turnover and richness (Bellingham *et al.* 1999). The spatial scale of observation may not change this relationship between turnover and richness over time (e.g., heathland in the Czech Republic) and even in temperate grasslands, productivity is positively related with both richness and turnover (Bakker *et al.* 2003). Finally, past analysis of similar data from Puerto Rico (LTERDBAS#101) has shown a "hump-shaped" relationship between productivity and richness after agriculture and

pasture in the Neotropics (Myster 2009), and other studies have suggested that increasing temporal scale will not affect this pattern (Chalcraft *et al.* 2004). In summary, results supported both hypotheses by showing an initially positive but later negative relationship between production and turnover, suggesting more individuals or growth from the productive species, and a negative relationship throughout all time periods between richness and turnover.

Acknowledgements

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