Relationship Between Aboveground Biomass and Diversity in Northern Great Lakes Forests

BIOS 569: Practicum in Field Biology

Natasia Poinsatte

Advisor: *Sam Pecoraro*

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Abstract

The forests of northern Wisconsin and the upper peninsula of Michigan have witnessed a period of re-growth over the past 60 years as they have recovered from logging and other human disturbances. The species composition of these successional forests bears little resemblance to the primary stands that preceded them. Understanding the relationship between diversity and productivity in these forests can help us predict their carbon sequestration potential as species composition shifts towards increased homogeneity. Although niche differentiation appears to drive a positive diversity-productivity relationship (DPR) globally, we predicted that the unique climate, land-use history and species composition of the upper Great lakes area would cause competitive exclusion to outweigh the benefits of niche differentiation within the region. We therefore hypothesized a negative linear relationship between species diversity and productivity in these forests. To test this hypothesis, we ran a linear regression between Shannon diversity index and total aboveground live biomass in twelve 0.05 hectare plots. Significant negative relationships were found between diversity and productivity (R2 = 0.50, p = 0.007) and between the proportion of codominant trees and diversity (R2 = 0.54, p = 0.004). A significant positive relationship between the proportion of codominant trees and biomass was found (R2 = 0.45, p- = 0.01). These results support our conclusion that competitive exclusion allows the regionally dominant species *Acer saccharum* to achieve enhanced productivity, thus driving a negative relationship between diversity and productivity.

Introduction

Carbon fixation in forests affects climate change mitigation and planning, as growing forests remove carbon dioxide from the Earth's atmosphere. The northern woods of Wisconsin and the upper peninsula of Michigan have witnessed a period of re-growth over the past 60 years as they have recovered from logging and other human disturbances (Rhemtulla et al. 2009a). The species composition of these successional forests bears little resemblance to the primary stands that preceded them (Rhemtulla et al. 2009b). A legacy of repeated clear-cuts until 1920, combined with browsing pressure from white-tailed deer, fire suppression and other management policies have decreased the regional prevalence of coniferous trees and increased the abundance of shade tolerant hardwood species, especially sugar maple (*Acer saccharum)* (Bragg et al. 2004). These processes have decreased overall species diversity within the Great Lakes region (Rhemtulla et al. 2009b).

The relationship between species diversity and productivity is an active area of research, given the recent, rapid losses in biodiversity worldwide and the importance of plant productivity in carbon cycles that drive global climate change (Vance-Chalcraft et al. 2010). However, the relationship between diversity and productivity in forest ecosystems remains contentious (Jennings et al. 2005). Past studies have found relationships ranging from positive linear (Sagar & Singh 2006) to negative linear (Larpkern et al. 2011), unimodal (Vance-Chalcraft et al. 2010) and non-significant (Vila et al. 2003). A 2012 meta-analysis of 54 studies analyzing the diversity-productivity relationship (**DPR**) in forest ecosystems (Zhang et al. 2012) found an overall positive relationship between productivity and diversity, with 23.7% higher productivity in polycultures compared with monocultures (Zhang et al. 2012).

According to Zhang et al. (2012), the niche complementarity hypothesis is the cornerstone of DPR empirical studies. This hypothesis states that the “positive diversity effect is due to increased resource use and nutrient retention via niche differentiation or partitioning and interspecific facilitation” (Zhang et al 2012). In other words, a higher diversity of species minimizes competition because species’ resource requirements overlap less. Resources are then more completely utilized, which maximizes productivity. Interspecific facilitation occurs when an individual benefits from the presence of a neighbor of a different species (Levin 2009). As supported by Zhang et al., niche complementarity may be a driver of positive DPR globally and across a variety of biomes. However, their meta-analyses did not include an empirical study focused on the forested Great Lakes region.

A large-scale study by Paquette and Messier (2011) also identified a strong, positive and significant effect of biodiversity on forest ecosystem processes, but in contrast to the meta-analysis performed by Zhang et al., their study contained an important caveat: “The effects of biodiversity and climate on productivity were barely significant within the southerly, more stable and more productive temperate biome that is dominated by sugar maple” compared with more stressful boreal forest environments (Paquette and Messier 2011). Jiang et al. (2009) found a disparity between the results of short-term diversity-manipulation experiments and small-scale observational analyses of DPR. While the former tends to reveal a positive relationship, the latter often finds a negative DPR (Jiang et al. 2009).

According to these studies, the effects of complementarity are overwhelmed by competitive exclusion when a) forests are located in temperate climates and dominated by sugar maple (Paquette and Messier 2011) and b) small-scale, natural plots are observed rather than diversity-manipulated experimental plots (Jiang et al. 2009). Our experiment fulfills both qualifications of location and methodology. According to the competitive exclusion principle, dominant, highly productive species might take over in habitats that are productive in terms of nutrient and water availability and at late successional stages in natural habitats where "realistic species rank-abundance patterns" have had time to develop (Jiang et al 2009, Paquette and Messier 2011).

According to the pattern accumulation hypothesis, regional diversity-productivity relationships are determined by local-scale processes summing to a more general pattern (Guo and Berry 1998, Scheiner et al. 2000). Therefore, an analysis of DPR in multiple localized plots can help us understand the relationship between diversity and productivity within the northwoods more broadly. This is particularly important given the trend towards increased species homogeneity among regenerating northern forests and the importance of these secondary forests in sequestering large quantities of carbon from the Earth's atmosphere, which is currently mitigating global climate change (Rhemtulla 2009a).

Two factors can be used to describe species diversity—richness and evenness. Richness is a simple count of the number of species present within a given area. Evenness measures the relative abundance of rare and common species within an area (Hill 1973). Species richness alone is an inadequate measure of diversity because it does not address the impact of the relative abundance of species on interspecific competition (Zhang et al. 2012). We therefore incorporated both evenness and richness in diversity calculations.

Several measurements can function as proxies for productivity, including aboveground live biomass, volume and diameter at breast-height (**DBH**). We chose to use total estimated aboveground live biomass as a surrogate for productivity within our plots because biomass was the most prevalent surrogate in the literature reviewed (Zhang et al. 2012). It is superior to DBH alone because it is a three dimensional metric, and by using allometric scaling, it accounts for geometric differences in species shape and height as well as differences in wood density (Jenkins 2004).

We sampled plots at the University of Notre Dame Environmental Research Center (UNDERC), a site chosen by the National Ecological Observatory Network (NEON) as representative of the greater Great Lakes region. Because the unique climate, land-use history and species composition within the region may allow competitive exclusion to outweigh niche differentiation, we hypothesized a negative linear relationship between species diversity and productivity.

Materials and Methods

The University of Notre Dame Environmental Research Center is a 3055 hectare reserve in the northwoods which was clear-cut in the early 20th century, selectively logged until 1968 and formally established as a restricted-access Ecological Reserve in 1980. The late-successional forests covering 80 % of the property are dominated by sugar maple (UNDERC Program Review 2009).

Forest stands within the UNDERC property were selected to control as closely as possible for endogenous factors that might alter or obscure the impact of stand-level diversity on productivity. We accomplished this by classifying site quality variables including slope, elevation, aspect and topographic convergence index (TCI). GIS mapping was used to overlay these site quality variables on the UNDERC property and break the property down into 8 site types (Figure 1). Each site type represents 12.5 percent of the total variability across these four factors (Sam Pecoraro personal communication 2013).

All of our plots fall within the same site-type according to the overlay (Figure 1). Within this site-type, we selected plots removed from the road that represented a range of diversity in terms of evenness and richness. We then marked off twelve 0.05-hectare circular plots and inventoried all trees larger than 5 cm diameter at breast-height, within each plot. For each tree, DBH (in cm), species, canopy class, and distance and azimuth from the center of the plot were recorded. Canopy class was determined based on observation, with trees being labeled codominant if they competed with neighboring trees for light rather than emerging above them or falling within their shadow. Aboveground live biomass for each tree was calculated using allometric regressions for North American tree species derived from a compilation of all published literature predicting over-dry biomass of individual tree species based on DBH (Jenkins 2004). The aboveground biomass of all live trees recorded was summed to estimate total aboveground live biomass (in Kg) in each plot. The Shannon diversity index was used to quantify diversity, as it incorporates both richness and evenness and gives equal emphasis to both dominant and rare species within a plot (Liang et al. 2007).

Statistical analysis was completed in R (R Core Team 2013). We ran linear regressions with Shannon diversity index as a predictor of aboveground live biomass across all 13 plots. An initial regression of Shannon diversity against aboveground live biomass violated the assumption of normality of residuals, and two data points exhibited undue leverage on the model. Therefore, we log transformed the response variable to satisfy all assumptions. In order to better understand potential competitive exclusion mechanisms at work within the plots, we ran a linear regression between the proportion of codominant trees and diversity as well as proportion of codominant trees and total live biomass. Again, total live biomass was log transformed to satisfy the assumptions.

Results

Shannon diversity index yielded values ranging from zero to 1.405 across the twelve plots. The values did not fall evenly along this range; 9 of the 13 values were above 0.9 and the other 4 were below 0.6. Total live biomass ranged from 4,470 kg to 19,062 kg.

A linear regression yielded a significant negative relationship between diversity and aboveground live biomass ($p = 0.007$, $R^2 = 0.50$ on 11 df; Figure 2). The relationship between diversity and proportion of trees codominant was also negative and significant ($p = 0.04$, $R^2 = 0.33$ on 11 df; Figure 3). Finally, the relationship between proportion of trees codominant and live biomass was significant and positive ($p=0.01$, $R^2=0.33$ on 11 df; Figure 4).

Discussion

Our results support our hypothesis that there is a negative relationship between diversity and aboveground live biomass of adult trees within 0.05 ha plots on the UNDERC property. These results agree with the findings of Larkpern et al. (2011) that evenness is negatively correlated with productivity in woody communities. However, that study asked how productivity influences evenness, whereas our study analyzed how diversity (including evenness) drives differences in productivity between plots (Larkpern et al. 2011). This distinction delineates two major branches of research related to the diversity-productivity relationship (**DPR**). Framing the analysis with productivity as the independent variable assumes changes in productivity, for example due to climate change or anthropogenic forcing, and questions how that impacts species composition. Our analysis "assumes the ongoing problem of biodiversity loss and asks how such losses could affect ecosystem services" (Jennings et al. 2005). According to some studies, climate change will impact the future of northern forests, but land-use and fire suppression policies leading to species homogenization will remain the driving forces of change within the region (Rhemtulla et al. 2009, Schulte et al. 2007). Therefore, we consider the question of how changes in species diversity impact productivity to be more relevant to northern forests.

Still, the DPR within UNDERC is likely driven by competitive exclusion. Competitive exclusion occurs when a species capitalizes on resource availability at the expense of other species, and it is likely to outweigh niche differentiation in nutrient abundant environments (Paquette and Messier 2012, Jiang et al. 2011). Larkpern et al. (2011) considered small-scale variations in productivity, but the analysis done by Paquette and Messier (2011) indicates that the impact of productivity on DPR may in fact play out at much larger scales. In stressful environments, such as boreal forests where nutrients and water are strongly limiting, species may benefit more from niche differentiation and facilitation, because they avoid the stress of competition and associated detrimental impacts. However, less stressful biomes favor "few dominant, highly productive species" (Paquette and Messier 2011).

It may be that this relationship is highly specific to the particular biome and forest type of the northwoods; all four of the least diverse plots in our study were heavily dominated by sugar maple, and it is possible that sugar maple is a species that particularly benefits from competitive exclusion. Further research into sugar maple physiology would help us understand its ability to capitalize on abundant resource availability. Further, our study does not address the underlying question of why some plots are so heavily dominated by sugar maple while others remain more diverse.

According to Schulte et al. (2007) and Rhemtulla et al. (2009b), changes in forest composition are occurring over time, so it may be that the current variation of diversity across the UNDERC property is a snapshot of a process occurring over both time and space. If that is the case, the proportion of plots dominated by sugar maples may become more abundant as driving factors—sugar maple resistance to deer browsing, fire suppression and gap dynamics in late successional forests—continue to alter forest composition across the region (Bragg et al. 2004).

The principle of competitive exclusion as posited by Paquette and Messier (2011) and Jiang et al. provides one possible explanation for the relationship between productivity and diversity on UNDERC (Paquette and Messier 2011, Jiang et al. 2009). We did not directly measure utilization of resources within plots. Still, observational analyses can help us understand the mechanisms that might allow plots approaching zero diversity to achieve greater productivity.

During our field work, we noticed that plots heavily dominated by sugar maples tend to have specific characteristics—stems appear less dense and more uniformly spaced. Less diverse plots also appear to have less structural complexity, with little understory and a mostly even canopy. This observation is supported empirically by the significant negative relationship between species diversity and proportion of codominant trees within a plot. It is possible that sugar maple monocultures achieve high levels of productivity in part due to their ability to support multiple successful individuals within the same canopy layer, thus capitalizing on available light resources. This could also function as a competitive exclusion mechanism, as these dense canopy layers exclude shade intolerant and light-seeded species (Burton et al. 2009). This conclusion is further supported by the positive linear relationship between proportion of codominant trees and aboveground live biomass.

The observed lower density and uniform distribution within the sugar maple-dominant plots may also enable efficient resource use, if physical spacing between each tree allows individuals to capitalize on the nutrients in the surrounding soil without suffering intraspecific competition. Grossiord et al. (2013) tested the impact of species mixture on species-specific and ecosystem-level carbon accumulation within a plantation setting and found that increased species mixture did not impact aboveground biomass of individual trees or plot-level productivity (Grossiord et al. 2013). The wide spacing and relatively even distribution of trees in a sugar maple-dominated monoculture is somewhat reminiscent of a plantation setting. Perhaps this set of plot characteristics buffers the impact of diversity on productivity by decreasing the need for niche differentiation. Additional analysis is required to support this prediction.

Overall, although our results are significant, there are limitations in the breadth and scope of the data. First, diversity values in our plots do not fall evenly across the entire range, but are concentrated at the low and high ends. The significant difference in productivity between these two groups (low and high) appears to drive the negative regression. These results tell us that plots approaching the status of monoculture may be significantly more productive than plots that are much more diverse, but they do not fully support the existence of a linear relationship across all levels of diversity. Filling these data gaps would improve our understanding of DPR across the full range of diversity at UNDERC, but time limitations prevented identification and inventory of more moderately diverse plots within the specified site quality parameters.

Despite these limitations, the significance and strength of the evenness and diversity regressions support the conclusion that DPR in the northwoods may be negative, distinguishing it from global trends identified by Zhang et al. Further analysis into competitive interactions in productive environments dominated by sugar maple would help us better understand the nuances of this relationship and its implications for regional carbon sequestration.

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Figures

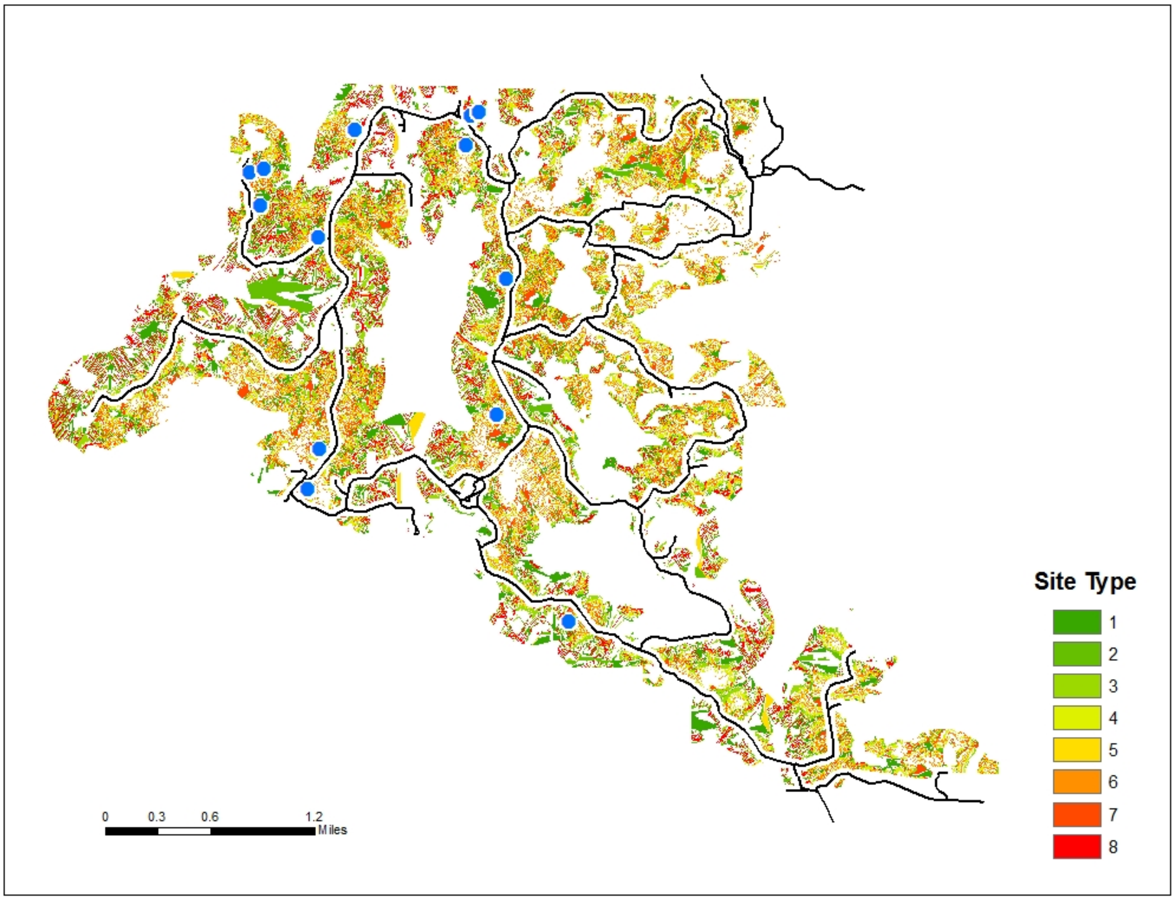

Figure 1: Site quality map of the UNDERC property, with plots marked in blue. Each site type represents 12.5% of the total variability across slope, elevation, aspect and TCI. White indicates aquatic environments or road buffers. All sites selected fall within site type 4.

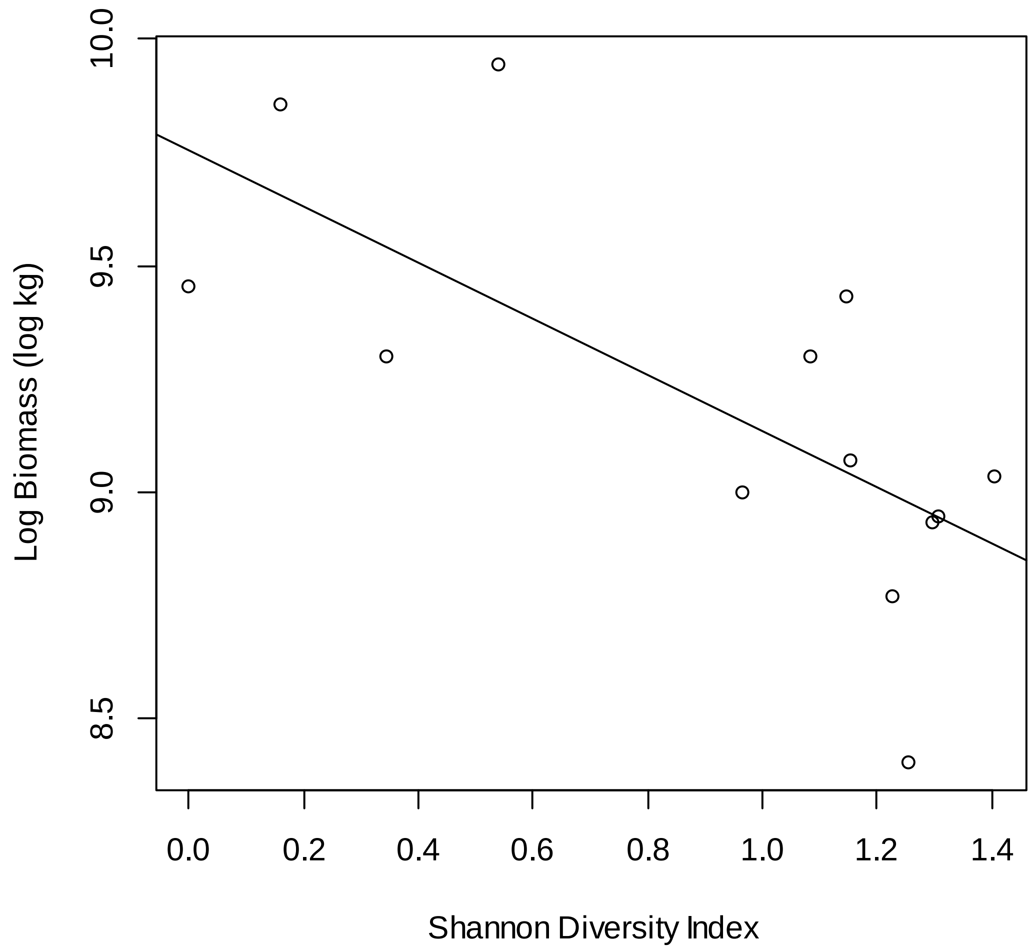

Figure 2: Shannon diversity versus log of biomass (log Kg). There was a significant negative linear relationship between diversity and biomass (R^2 = 0.50, p-value = 0.007 on 11 df).

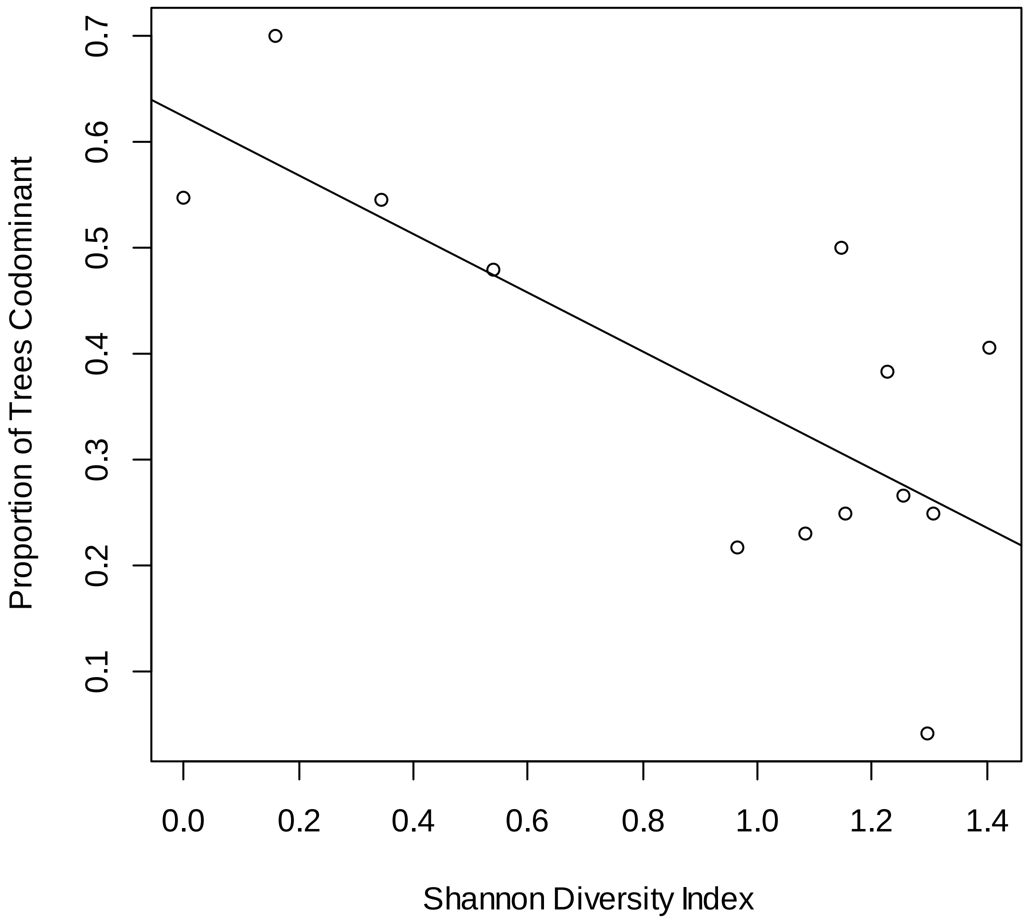

Figure 3: Shannon diversity versus proportion of trees codominant. There was a significant negative linear relationship between diversity and proportion of trees codominant (R^2 = 0.54, p = 0.004 on 11 df).

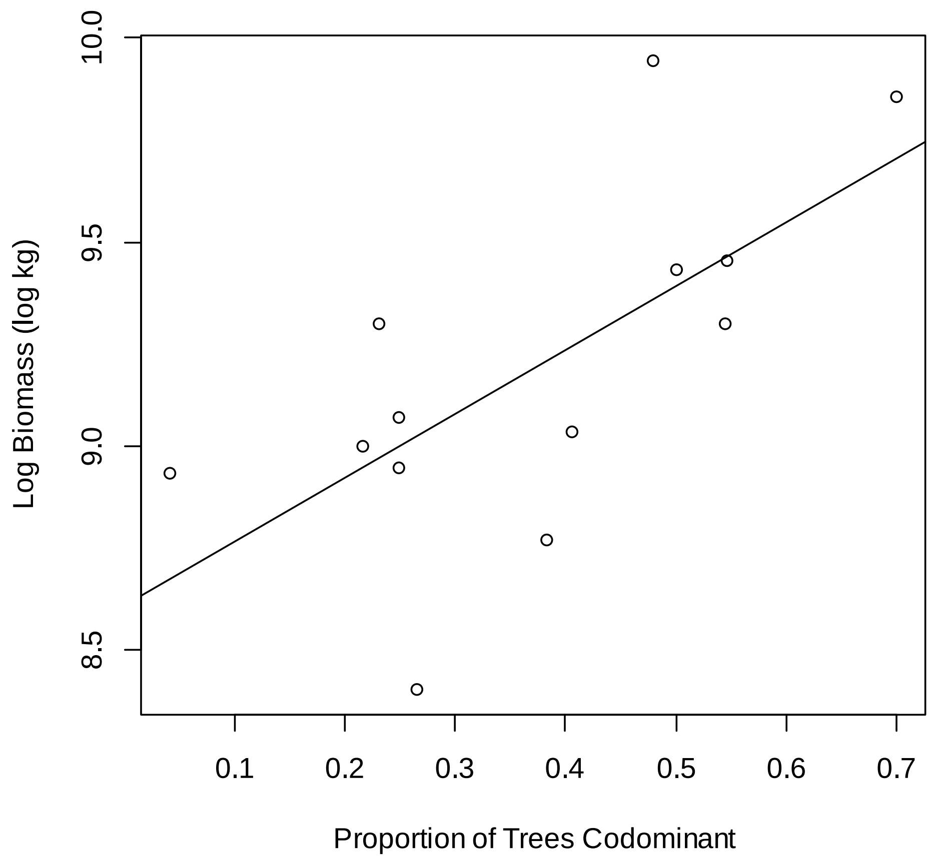

Figure 4: Proportion of Trees Codominant versus log of biomass (log Kg). There was a significant positive linear relationship between diversity and biomass (R^2 = 0.45, p = 0.01 on 11 df).