Resource Availability Drives Patterns of Productivity Rather than Biodiversity for Local-Scale Temperate Forests

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RESOURCE AVAILABILITY DRIVES PATTERNS OF PRODUCTIVITY RATHER THAN BIODIVERSITY FOR LOCAL-SCALE TEMPERATE FORESTS

By

Kaitlyn Ann Baillargeon
B.S. Environmental Science, University of New Hampshire, 2018

THESIS

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the Requirements for the Degrees of

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in
Natural Resources: Forestry

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This thesis was examined and approved in partial fulfillment of the required for the degree of
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On November 17th, 2021

Approval signatures are on file with the University of New Hampshire Graduate School
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ABSTRACT

In short-lived, grassland ecosystems, biodiversity and productivity have been found to be positively correlated. However, studies in long-lived, forested ecosystems have found mixed results. Biodiversity in forests has primarily been measured using indices of species diversity, but recent studies have shown that biodiversity is more complex than simply quantifying the number of species occupying an area. Biodiversity can also be represented by other measures of diversity such as functional, phylogenetic, and structural diversity; all three of which have been shown to be more strongly correlated to productivity than species diversity alone. Here, we examined the relationship between four biodiversity measures (species, functional, phylogenetic, and structural diversity) and their respective relationship with productivity at a local scale for two northeastern United States temperate forests. Biodiversity indices were calculated using site specific inventory data while productivity was calculated using measured wood growth. Overall, patterns were similar between sites; indices of species, functional, and phylogenetic diversity were strongly to moderately correlated with each other while indices of structural diversity were not correlated with the other three diversity measures. All four biodiversity components were found to be either negatively or weakly correlated to productivity. After accounting for site conditions, such as nitrogen availability and topography, foliar nitrogen was found to be the only variable significantly correlated to productivity while the biodiversity measures were not significantly correlated. Therefore, at these long-lived, local-scale temperate forest sites, there was not a direct, significant relationship between biodiversity and productivity.
INTRODUCTION

A long-standing goal in ecology has been to understand the relationship between biodiversity and functional properties of ecosystems, such as productivity. A widely held assumption is that biodiversity is positively correlated with productivity. This hypothesis has been supported in short-lived grassland experiments (Tilman et al. 1997b; Hector et al. 1999; Tilman et al. 2001), but evidence in longer-lived, forested system has been mixed, showing either positive (Paquette and Messier 2011), negative (Edgar and Burk 2001), or unimodal relationships (Chen and Klinka 2003; Zobel and Pärtel 2008).

Several hypotheses have been proposed to explain why forests have shown inconsistent biodiversity-productivity relationships (BPR), such as the size of the spatial and temporal scale considered or the effect of co-varying environmental conditions (Thompson et al. 2018; Jactel et al. 2018). Much of the evidence for a strong, positive BPR has come from regional to global studies (Chase and Leibold 2002; Paquette and Messier 2011; Zhang et al. 2012; Liang et al. 2016) which has been attributed to complementarity effects where the addition of species is expected to result in higher rates of productivity (Tilman et al. 1997b; Loreau 2000; Turnbull et al. 2013). In theory, as spatial extent increases, the number and variety of available species and traits should increase, which in turn leads to increases in productivity through niche partitioning and facilitation.

Further, BPR have also been found to be driven by latitudinal and climatic gradients, where BPR shift from positive relationships in the tropics to unimodal or negative relationships in temperate and boreal forests (Pärtel and Zobel 2007; Zobel and Pärtel 2008). As climatic conditions become more stressful moving from the tropics to the poles, diversity may become
limited by species dispersal or evolutionary history (Zobel and Pärtel 2008). This can lead to BPR in northern regions to be driven by the selection effect (Mayfield et al. 2010), where the productivity of a site is determined by a few species with traits adapted to specific environmental conditions.

Variations between BPR may also be driven by differences in environmental conditions across climatic regions (Mori 2018). Both biodiversity and productivity have been shown to be influenced by temperature (Stevens and Gavilanez 2015) and precipitation gradients (Churkina and Running 1998). In addition, productivity has also shown to be strongly correlated to nutrient availability (Bergh et al. 1999; Ollinger and Smith 2005). What is unclear is how interactions between environmental conditions, biodiversity, and productivity influence the direction and strength of BPR.

Another factor that has confounded the strength and direction of observed BPR has been differences in the methodology, specifically, how studies have characterized biodiversity (Cavanaugh et al. 2014; Dănescu et al. 2016; Park et al. 2019). Early BPR studies mainly focused on using measures of species diversity, such as species richness (Noss 1990). More recently, studies have begun considering other components of biodiversity, arguing that species diversity alone is not enough to fully capture the relationship between biodiversity and productivity (Dănescu et al. 2016; Bagousse-Pinguet et al. 2019; LaRue et al. 2019). Diversity in functional traits, phylogeny, and canopy structure have been the most common diversity measures used to complement simple biodiversity estimates. Each type of diversity measure is thought to play an important role in driving community productivity, and together may be better predictors of productivity than species diversity alone (Ferris and Humphrey 1999; Díaz and Cabido 2001; Swenson 2011).
Functional diversity describes the number, type, and distribution of functional traits (e.g. leaf type, nutrient content, wood characteristics) among organisms within a community (Díaz and Cabido 2001; Petchey and Gaston 2006) and has been linked to key ecosystem services (Díaz and Cabido 2001; Botta-Dukát 2005; Petchey and Gaston 2006; Mouillot et al. 2011; Valencia et al. 2015; Gross et al. 2017; Bagousse-Pinguet et al. 2019). Functional diversity is thought to be strongly correlated to productivity as it is able to account for functional traits directly related to production such as resource acquisition, resource use efficiency, and photosynthetic capacity (Paquette and Messier 2011; Tobner et al. 2016; Correia et al. 2018).

Phylogenetic diversity describes the evolutionary relationships among species (Faith 1992; Cadotte et al. 2008, 2010). These relationships have been used to improve understanding of the mechanisms that drive patterns of co-occurrence of species (Webb 2000; Silvertown et al. 2006; Cadotte et al. 2010). Phylogenetic diversity has also been linked to several processes, such as extinction (Purvis et al. 2000; Winter et al. 2013), ecosystem functioning (Flynn et al. 2011; Cadotte et al. 2012), and ecosystem services (Faith et al. 2010; Winter et al. 2013). Phylogenetic diversity may also account for unmeasured traits not directly used to calculate functional diversity (Hao et al. 2018; Bagousse-Pinguet et al. 2019).

Lastly, structural diversity describes the variation in physical arrangement of trees in three-dimensional space (Ishii et al. 2004; Dănescu et al. 2016; Park et al. 2019; LaRue et al. 2019). Structural diversity has been shown to enhance productivity by increasing light absorption and improving light use efficiency (Ishii et al. 2004; Yachi and Loreau 2007; Hardiman et al. 2011, 2013; Gough et al. 2019). These two functions are mainly controlled by differences in light penetration to leaves under varying light environments, which allow canopies to absorb more light and thus become more productive (Niinemets 2012; Gough et al. 2019).
For this study, we explored the relationships between different measures of biodiversity (species, functional, phylogenetic, and structural diversity) as well as their relationship with productivity. In addition, we also investigated how these relationships were influenced by environmental conditions, such as nutrient availability. This was done by using inventory data from two local-scale (i.e., < 10,000 acres), temperate forests in the White Mountain National Forest of New Hampshire, USA. These two sites were chosen because of their extensive network of inventory plots and for their similarity in environmental conditions.
METHODS

Study Sites

Bartlett Experimental Forest (BEF; 44° 03’ N, 71° 17’ W) and Hubbard Brook Experimental Forest (HBEF; 43° 56’ N, 71° 45’ W) are northern hardwood forests located approximately 40 km apart in the White Mountain National Forest in New Hampshire, USA. Both sites have similar climates, experiencing 1,300 mm and 1,400 mm of annual precipitation, respectively, and continuous winter snowpack typically from mid-December to mid-April. Average temperatures range from roughly 19 °C in July to -9 °C in the January. Soils are spodosols and inceptisols developed from glacial till. Elevations range from 207 m to 915 m at BEF and 222 m to 1,015 m at HBEF. Both sites are dominated by similar species including American beech (Fagus grandifolia), yellow birch (Betula alleghaniensis), sugar maple (Acer saccharum), red maple (Acer rubrum), paper birch (Betula papyrifera), red spruce (Picea rubens), and eastern hemlock (Tsuga canadensis).

Both forests were heavily logged towards the end of the 19th century and again for hurricane salvage in the early 20th century. Since then, HBEF has not had any major disturbances except for experimental harvests on several small watersheds, which were not included in this study. Conversely, much of the research at BEF focuses on understanding timber management practices, and several silvicultural prescriptions have been applied across the forest. Only about 45% of the area has remained unmanaged since the early 1900s.

A network of long-term inventory plots has been established at both sites. BEF’s inventory network consists of 427, 0.1 ha square inventory plots, spaced on an approximately 200 m x 100 m grid. During plot inventories, all trees greater than 3.8 cm were surveyed, but for
this study we only included species with a DBH of 10 cm or greater to be consistent with the DBH cutoff used for HB. For this study, the most recent publicly available inventory (2001-2003) was used (Leak et al. 2017).

HBEF’s inventory network consists of 371 0.05 ha circular inventory plots placed along 15 north-south transects separated at 500 m intervals. Along each transect, plots are spaced either 25, 100, or 200 m apart. HBEF inventory plots do not include the highest elevation regions of the valley and are separate from watershed manipulation plots. All species with a DBH greater than 10 cm were surveyed. The most recent publicly available inventory (1995-1998) was used (Battles and Fahey 2019).

**Biodiversity Estimates**

Measures of species, functional, phylogenetic, and structural diversity were represented by three to five indices commonly found in the literature. Chosen indices measured either the richness, evenness, or the variation of each diversity measures (Table 1). Every index was calculated using the abundance of species within a plot; therefore, abundance was represented by the relative basal area (BA) per species per plot. Indices were calculated in R version 3.6.0 (R Core Team 2019).
**Table 1**: Indices used to represent the four measures of biodiversity (species, functional, phylogenetic, and structural diversity). Each measure is represented by at least one index of richness, evenness, variation.

<table>
<thead>
<tr>
<th>Index</th>
<th>Equation</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Species Diversity</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shannon’s Entropy</td>
<td>$H' = \sum_{i=1}^{n} p_i \times \ln p_i$</td>
<td>(Shannon 1948)</td>
</tr>
<tr>
<td>Richness</td>
<td>$S =$ number of unique species within a community</td>
<td>(McIntosh 1967)</td>
</tr>
<tr>
<td>Evenness</td>
<td>$J = \frac{H'}{\ln S}$</td>
<td>(Pielou 1966)</td>
</tr>
<tr>
<td><strong>Functional Diversity</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Functional Richness</td>
<td>$\text{FRic} =$ Volume of a convex hull where the vertices of the hull are traits based on present species.</td>
<td></td>
</tr>
<tr>
<td>Functional Evenness</td>
<td>$\text{FEve} = \frac{\sum_{i=1}^{S} \min \left(P_{\text{E}W_i} \frac{1}{S-1} \right) - \frac{1}{S-1}}{1-\frac{1}{S-1}}$</td>
<td>(Villéger et al. 2008)</td>
</tr>
<tr>
<td>Functional Divergence</td>
<td>$\text{FDiv} = \frac{\Delta d + \bar{d}G}{\Delta</td>
<td>d</td>
</tr>
<tr>
<td>Functional Dispersion</td>
<td>$\text{FDis} = \frac{\sum a_j x_j}{\sum a_j}$</td>
<td>(Laliberté and Legendre 2010)</td>
</tr>
<tr>
<td>Rao Quadratic Entropy</td>
<td>$\text{RaoQ} = \sum_{i=1}^{N} \sum_{j=1}^{N} d_{ij} p_i p_j$</td>
<td>(Botta-Dukát 2005)</td>
</tr>
<tr>
<td><strong>Phylogenetic Diversity</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Faith’s Phylogenetic Diversity</td>
<td>$\text{PD} = (N - 1) + \text{No. of branching points on the minimum spanning path}$</td>
<td>(Faith 1992)</td>
</tr>
<tr>
<td>Phylogenetic Species Richness</td>
<td>$\text{PSR} = n \times \text{PSV}$</td>
<td></td>
</tr>
<tr>
<td>Phylogenetic Species Evenness</td>
<td>$\text{PSE} = \frac{\text{m} \text{diag}(C)^{1/2} \text{M-M'CM}}{m^2-m_i m}$</td>
<td>(Helmus et al. 2007)</td>
</tr>
<tr>
<td>Phylogenetic Species Variability</td>
<td>$\text{PSV} = \frac{\text{n} \text{trC-} \sum C}{n(n-1)}$</td>
<td></td>
</tr>
<tr>
<td>Phylogenetic Species Clustering</td>
<td>$\text{PSC} = 1 - \frac{\sum_{i=1}^{n} \max (c_{i-})}{n}$</td>
<td>(Helmus et al. 2007; Emerson and Gillespie 2008)</td>
</tr>
<tr>
<td><strong>Structural Diversity</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Quadratic mean</td>
<td>$\text{DBHq} = \sqrt{\frac{\sum \text{DBH}_i^2}{n}}$</td>
<td>(Curtis and Marshall 2000; Lei et al. 2009)</td>
</tr>
<tr>
<td>Standard deviation of DBH or height</td>
<td>$\text{DBHsd or ht_sd} = \sqrt{\frac{\sum (x_i - \bar{x})^2}{N}}$</td>
<td>(Lei et al. 2009)</td>
</tr>
<tr>
<td>Shannon’s Index</td>
<td>$\text{DBH}_H' \text{or ht}<em>H' = \sum</em>{j=1}^{m} p_j \times \ln p_j$</td>
<td>(Shannon 1948; Park et al. 2019)</td>
</tr>
<tr>
<td>Richness</td>
<td>$\text{DBH}_S \text{or ht}_S =$ number of unique DBH/height classes within a stand</td>
<td>(McIntosh 1967)</td>
</tr>
<tr>
<td>Evenness</td>
<td>$\text{DBH}_J \text{or ht}_J = \frac{\text{DBH}_H'}{\ln \text{DBH}_S}$</td>
<td>(Pielou 1966)</td>
</tr>
<tr>
<td>Canopy Surface Roughness</td>
<td>$\text{Rumple} =$ ratio of canopy outer surface area to ground surface area</td>
<td>(Parker and Russ 2004; Kane et al. 2010)</td>
</tr>
</tbody>
</table>
Species Diversity

Species diversity was represented using three indices: the Shannon’s Entropy Index (H’; Shannon 1948), species richness (S; McIntosh 1967), and species evenness (J; Pielou 1966). H’ represents a ratio between the number of species present relative to their importance within the plot. It is a function of species richness, the number of species present, and evenness, the relative abundance of species (Magurran 1988).

H’ was calculated using the fractional basal area of each species. S was determined by counting the number of unique species found on a plot and J was calculated using Pielou’s evenness index (Table 1).

Functional Diversity

Functional diversity was represented by five indices: functional richness (F Ric), evenness (FEve), divergence (FDiv; Villéger, Mason, and Mouillot 2008), dispersion (FDis; Laliberté and Legendre 2010), and Rao’s Quadratic Entropy (RaoQ; Botta-Dukát 2005) (Table 1). Indices were calculated using the R package FD (v. 1.0.12; Lalibert, Legendre, and Shipley 2014).

Seven species-specific functional traits associated with three key components of plant functioning (light, water, and nutrients) were selected to calculate the functional diversity indices. Six of these traits, mycorrhizal fungi type, leaf type, xylem type, waterlogging tolerance, drought tolerance, and shade tolerance, were obtained from the TRY plant database (Kattge et al. 2020). Values for the seventh trait, mean, mass-based foliar nitrogen (N), were obtained from the Northeastern Ecosystem Research Cooperative (NERC) database (Northeastern Ecosystem Research Cooperative 2010) (Table 2).
<table>
<thead>
<tr>
<th>Species</th>
<th>Nutrient Traits</th>
<th>Light Traits</th>
<th>Shade Tolerance</th>
<th>Xylem Type</th>
<th>Drought Tolerance</th>
<th>Waterlogging Tolerance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abies balsamea</td>
<td>Ectomycorrhizae</td>
<td>Needle-leaf</td>
<td>5.01</td>
<td>Non-Porous</td>
<td>1.00</td>
<td>2.00</td>
</tr>
<tr>
<td>Acer pennsylvanicum</td>
<td>Arbuscular mycorrhizae</td>
<td>Broadleaf</td>
<td>3.56</td>
<td>Diffuse Porous</td>
<td>2.00</td>
<td>1.00</td>
</tr>
<tr>
<td>Acer rubrum</td>
<td>Arbuscular mycorrhizae</td>
<td>Broadleaf</td>
<td>3.44</td>
<td>Diffuse Porous</td>
<td>1.84</td>
<td>3.08</td>
</tr>
<tr>
<td>Acer saccharum</td>
<td>Arbuscular mycorrhizae</td>
<td>Broadleaf</td>
<td>4.76</td>
<td>Diffuse Porous</td>
<td>2.25</td>
<td>1.09</td>
</tr>
<tr>
<td>Acer spicatum</td>
<td>Arbuscular mycorrhizae</td>
<td>Broadleaf</td>
<td>3.31</td>
<td>Diffuse Porous</td>
<td>2.00</td>
<td>2.00</td>
</tr>
<tr>
<td>Amelanchier</td>
<td>Ectomycorrhizae</td>
<td>NA</td>
<td>2.86</td>
<td>Diffuse Porous</td>
<td>2.52</td>
<td>1.39</td>
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<td>Betula alleghaniensis</td>
<td>Ectomycorrhizae</td>
<td>Broadleaf</td>
<td>3.17</td>
<td>Diffuse Porous</td>
<td>3.00</td>
<td>2.00</td>
</tr>
<tr>
<td>Betula papyrifera</td>
<td>Ectomycorrhizae</td>
<td>Broadleaf</td>
<td>1.54</td>
<td>Diffuse Porous</td>
<td>2.02</td>
<td>1.25</td>
</tr>
<tr>
<td>Betula populifolia**</td>
<td>Ectomycorrhizae</td>
<td>Broadleaf</td>
<td>1.50</td>
<td>Diffuse Porous</td>
<td>2.34</td>
<td>1.00</td>
</tr>
<tr>
<td>Fagus grandifolia</td>
<td>Ectomycorrhizae</td>
<td>Broadleaf</td>
<td>4.75</td>
<td>Diffuse Porous</td>
<td>1.50</td>
<td>1.50</td>
</tr>
<tr>
<td>Fraxinus americana</td>
<td>Arbuscular mycorrhizae</td>
<td>Broadleaf-Compound</td>
<td>2.46</td>
<td>Ring Porous</td>
<td>2.38</td>
<td>2.59</td>
</tr>
<tr>
<td>Fraxinus nigra**</td>
<td>Arbuscular mycorrhizae</td>
<td>Broadleaf-Compound</td>
<td>2.96</td>
<td>Ring Porous</td>
<td>2.00</td>
<td>3.50</td>
</tr>
<tr>
<td>Juglans nigra*</td>
<td>Arbuscular mycorrhiza</td>
<td>Broadleaf-Compound</td>
<td>1.93</td>
<td>Ring Porous</td>
<td>2.38</td>
<td>1.83</td>
</tr>
<tr>
<td>Ostrya virginiana*</td>
<td>Ectomycorrhizae</td>
<td>Broadleaf</td>
<td>4.58</td>
<td>Diffuse Porous</td>
<td>3.25</td>
<td>1.07</td>
</tr>
<tr>
<td>Picea rubens</td>
<td>Ectomycorrhizae</td>
<td>Needle-leaf</td>
<td>4.39</td>
<td>Non-Porous</td>
<td>2.50</td>
<td>2.00</td>
</tr>
<tr>
<td>Pinus resinosa*</td>
<td>Ectomycorrhizae</td>
<td>Needle-leaf</td>
<td>1.89</td>
<td>Non-Porous</td>
<td>3.00</td>
<td>1.00</td>
</tr>
<tr>
<td>Pinus strobus*</td>
<td>Ectomycorrhizae</td>
<td>Needle-leaf</td>
<td>3.21</td>
<td>Non-Porous</td>
<td>2.29</td>
<td>1.03</td>
</tr>
<tr>
<td>Populus grandidentata</td>
<td>Arbuscular &amp; Ectomycorrhizae</td>
<td>Broadleaf</td>
<td>1.21</td>
<td>Diffuse Porous</td>
<td>2.50</td>
<td>2.00</td>
</tr>
<tr>
<td>Populus tremuloides</td>
<td>Arbuscular &amp; Ectomycorrhizae</td>
<td>Broadleaf</td>
<td>1.21</td>
<td>Diffuse Porous</td>
<td>1.77</td>
<td>1.77</td>
</tr>
<tr>
<td>Prunus pensylvanica</td>
<td>Arbuscular mycorrhizae</td>
<td>Broadleaf</td>
<td>2.46</td>
<td>Diffuse Porous</td>
<td>3.02</td>
<td>1.06</td>
</tr>
<tr>
<td>Prunus serotina</td>
<td>Arbuscular mycorrhizae</td>
<td>Broadleaf</td>
<td>2.46</td>
<td>Ring Porous</td>
<td>3.02</td>
<td>1.06</td>
</tr>
<tr>
<td>Quercus rubra*</td>
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<td>Broadleaf</td>
<td>2.75</td>
<td>Ring Porous</td>
<td>2.88</td>
<td>1.12</td>
</tr>
<tr>
<td>Sorbus americana</td>
<td>Arbuscular &amp; Ectomycorrhizae</td>
<td>Broadleaf-Compound</td>
<td>2.59</td>
<td>Ring Porous</td>
<td>1.77</td>
<td>1.27</td>
</tr>
<tr>
<td>Tilia americana**</td>
<td>Ectomycorrhizae</td>
<td>Broadleaf</td>
<td>3.98</td>
<td>Ring Porous</td>
<td>2.88</td>
<td>1.26</td>
</tr>
<tr>
<td>Tsuga canadensis</td>
<td>Ectomycorrhizae</td>
<td>Needle-leaf</td>
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<td>Non-Porous</td>
<td>1.00</td>
<td>1.25</td>
</tr>
<tr>
<td>Ulmus americana*</td>
<td>Arbuscular mycorrhizae</td>
<td>Broadleaf</td>
<td>3.14</td>
<td>Ring Porous</td>
<td>2.92</td>
<td>2.46</td>
</tr>
</tbody>
</table>
To calculate functional diversity indices, a matrix of functional traits was used to create an n-dimensional space based on n-axes, where n represents the number of traits used. FRic was used to represent the amount of functional space filled by a community (Villéger et al. 2008) or the number of species within a particular niche (Goswami et al. 2017). FEve represented the evenness in which species filled functional trait space or the evenness of the distribution of species abundances in niche space (Mason et al. 2005; Villéger et al. 2008). FDiv determined how species abundances are spread along a functional trait axis within a community (Villéger et al. 2008). Lastly, both FDis and RaoQ measured the degree of functional trait dissimilarity between species within a community (Botta-Dukát 2005; Karadimou et al. 2016).

**Phylogenetic Diversity**

Five indices were selected to represent phylogenetic diversity: Faith’s Phylogenetic Diversity index (PD; Faith 1992), phylogenetic species variability (PSV), phylogenetic species richness (PSR), phylogenetic species evenness (PSE), and phylogenetic species clustering (PSC; Helmus et al. 2007) (Table 1). To calculate these indices, a dendrogram was created based on the species’ taxonomic rankings, and branch lengths were given a value of one unit per segment (Figure 1). These indices were calculated using the R package *picanate* (v.1.8; Kembel et al. 2019).

Faith’s PD was calculated by summing the branch lengths of the dendrogram between all species found within the community (Faith 1992; Helmus et al. 2007; Cadotte et al. 2010). PSV summarized the degree to which species in a community were related, where increased relatedness resulted in decreased variability. PSR was a combined measure of the variability between species phylogenies and species richness within a community. PSE was calculated by
accounting for the phylogenetic divergence within a community and the difference in abundances among the species (Helmus et al. 2007). Lastly, PSC measured the degree at which co-occurring species were related to each other (Emerson and Gillespie 2008). As PSC approached one, species were more closely related, which was the opposite of PSV (Helmus et al. 2007; Emerson and Gillespie 2008).

**Figure 1**: Phylogenetic dendrogram used to calculate phylogenetic diversity based on the taxonomic classification of species. An arbitrary length of 1 unit was used for each of the branch segments. * Species only found at BEF. ** Species only found at HBEF.

**Structural Diversity**

Several indices were used to characterize structural diversity. For both sites, horizontal structural diversity was represented by the variation in DBH based on measurements from the
inventory data. Indices used include the quadratic mean of DBH (DBHq), standard deviation of DBH (DBHsd), the Shannon’s Entropy Index (DBH_H’), richness (DBH_S), and evenness (DBH_J) (Table 1). For BEF, vertical structural diversity was characterized by measurements of height and canopy surface roughness calculated from discrete return Light Detection and Ranging (LiDAR) data collected in the summer of 2017 by the National Ecological Observatory Network (NEON; (National Ecological Observatory Network 2017). LiDAR points were returned at a density of 1-4 points/m² at a spatial resolution 1 m and processed to create a 1 m resolution canopy height model (CHM). Indices from the LiDAR data include standard deviation of height (ht_sd), canopy surface roughness (rumple; (Parker and Russ 2004; Kane et al. 2010), the Shannon’s Entropy Index (ht_H’), richness (ht_S), and evenness (ht_J) (Table 1). Vertical structural diversity indices were not calculated for HBEF, as comparable LiDAR data collected around the same time frame as the BEF LiDAR was obtained during the leaf-off period.

The DBHq represents the average stand diameter per plot (Curtis and Marshall 2000; Storch et al. 2018) while the DBHsd represented the variation in diameter (Storch et al. 2018). Similarly, ht_sd represented the variation in tree height. For DBH_H’, the number of species was replaced with the number of DBH classes grouped into 3 cm bins while proportions were based on the basal area per DBH class. Richness was based on the number of DBH classes and evenness of the DBH classes was calculated using Pielou’s evenness (Park et al. 2019). Similarly to DBH_H’, Ht_H’ was calculated using 3 m bin height classes from the LiDAR points. Ht_S was based on the number of height classes and ht_J was calculated using Pielou’s evenness. Lastly, rumple was calculated from the CHM using the R package lidR (Roussel et al. 2019) and represents the ratio between the top of the canopy to the ground surface.
Productivity Estimates

Forest productivity was represented using direct measures of wood growth from a subset of 38 plots at BEF and 18 plots at HBEF. The subset of plots was chosen for productivity over the rest of the inventory plots because the subset plots were measured at a higher temporal frequency and included (1) individually tagged trees (which allowed us to determine individual tree growth and mortality) and (2) additional data that was used to represent influencing environmental conditions, such as mass-based foliar nitrogen (N). Foliar N measurements were conducted using methods described in Ollinger et al. 2008. Subset plots were previously chosen and measured by Smith et al. (2002) to collect repeat wood growth measurements. DBH measurements (cm) for every species, living and dead, were converted to wood biomass (g) using species specific allometric equations (Jenkins 2004). Woody biomass was scaled up to the plot level by summing the biomass of all species on a plot and dividing by plot area (g/m²), making sure to carry over trees that died between remeasurement periods. Finally, wood growth (g/m²/yr) was calculated by subtracting the previous year’s measurements from the most recent measurements and dividing by the number of years between measurement periods.

Data Analysis

Because plot sizes for BEF and HBEF were different, the two sites were analyzed individually, as biodiversity has been shown to increase with area (MacArthur and Wilson 1967; Werger 1972). Linear and non-linear regressions were used to explore the relationship between indices of biodiversity measures and their relationship with productivity. Pearson’s coefficient (r) was used to determine the strength and direction of the relationship between variables while
the coefficient of determination (R²) was used to explain the percent of variation explained. Regression P values (P < 0.05) were used to identify the significance of each model.

Relationships between biodiversity indices were also analyzed using principal component analyses (PCA) based on linear correlation matrices. PCAs were used to determine how indices clustered into groups based on the correlative strength between the indices. The PCAs also helped to reduce the variation between the indices into a smaller number of variables known as components. These components were also used in linear regression analyses to examine the relationship between the indices and productivity.

On the subset of plots with measured wood growth, multiple linear regressions were used to analyze the relationships between biodiversity, productivity and site factors including topography (elevation, aspect, and slope; (Fraser et al. 2019) and average plot weighted foliar N. Best models were selected based on the smallest Akaike’s Information Criteria (AIC) and Bayesian Information Criterion (BIC) value. Variables not significant (p > 0.05) to the model were removed until only significant variables remained.

Relationships between biodiversity and measured foliar N from the subset of plots were also explored to examine the impact of nutrient availability on biodiversity. This was done through linear and non-linear regressions. To test how these relationships changed when accounting for all the plots, estimated foliar N concentrations per species were averaged over a plot. These estimated foliar N values were used as a proxy for nutrient availability at all plots because they were strongly and significantly correlated to the measured foliar N values at the subplots (Figure S1) and because foliar N has been shown to be strongly related to N mineralization at these sites (Ollinger et al. 2002).
RESULTS

Relationships Between Measures of Biodiversity

Average values for most of the biodiversity measures were similar, but significantly different between the two sites (Table S1) where biodiversity estimates were higher at BEF due to its larger plot sizes. Additionally, managed and unmanaged plots at BEF did not show a significant difference between most biodiversity indices (Table S2), therefore plots were not analyzed separately based on management history.

Relationships among the biodiversity measures were also similar between the sites. Indices of species, functional, and phylogenetic diversity were significantly (P < 0.05) as well as strongly (r ≥ 0.6) to moderately (0.4 ≤ r < 0.6) correlated with each other, but indices of structural diversity were only weakly (r < 0.4) and often non-significantly (P > 0.05) correlated to the other three measures (Table S3). At BEF, LiDAR structural indices were also weakly and sometimes insignificantly correlated to the other three biodiversity measures (Table S4). Correlation significance, strength, and direction from the linear regression models varied between biodiversity indices. While most of the relationships between species, functional, and phylogenetic diversity indices were significant and positively correlated, the strongest correlations between indices explained less than 50% of the variation. Meanwhile, indices representing structural diversity were weakly correlated to all other indices and were only able to explain 10% or less of the variation (Figure 2).
Figure 2: Example linear regressions between the four measures of biodiversity. Indices of species, functional, and phylogenetic diversity were found to be strongly ($r > 0.6$) and significantly ($P < 0.05$) correlated to each other while indices of structural diversity were found to be weakly ($r < 0.4$) and sometimes non-significantly ($P > 0.05$) correlated to the other three measures.

For PCA analyses, observed patterns were similar to those found in the linear regression models. Generally, indices of species, functional, and phylogenetic diversity were more closely related to each other than they were to indices of structural diversity. Additionally, across biodiversity measures (excluding structure), indices formed groups based on the type of index used, such as richness or evenness.

The first two PCA components captured 54.5% and 50.4% of the variance of the biodiversity indices for BEF and HBEF, respectively (Figure 3). For BEF, the first component explained 34.9% of the variance while HBEF’s first component explained 35.0%. For both sites, the first component was most closely associated with indices for species, functional, and phylogenetic diversity. Meanwhile, the second component explained 19.6% of the variation for
BEF and 15.4% of the variation for HBEF and was most closely associated with indices of structural diversity.

At BEF, five distinct PCA clusters were formed (Table S5 and Table S6). Cluster 1 contained richness indices as well as phylogenetic clustering and was able to explain 21% of the total variation explained by the indices. Cluster 1 was most strongly represented by species richness. Cluster 2 explained 13% of the variation and contained structural diversity indices. DBHsd most strongly represented cluster 2. Cluster 3 was represented by RaoQ and contained functional diversity indices and phylogenetic variability which together explained 14% of the variation. Cluster 4 contained indices characterizing evenness and species diversity. This cluster explained 15% of the variation and represented by species evenness. Lastly, cluster 5 also contained structural diversity indices and was represented by the evenness of DBH. This cluster only explained 9% of the total variation between indices.

At HBEF, four distinct PCA clusters were formed, similar to those found for BEF. Cluster 1 contained richness indices and phylogenetic variability, explained 21% of the total variation between indices, and was represented by phylogenetic richness. Cluster 2 contained most of the structural diversity indices as well as phylogenetic clustering, was most represented by the quadratic mean of DBH, and explained 15% of the variation. Cluster 3 contained the largest number of indices including evenness, species and functional diversity, and Shannon’s variation of DBH. It was most represented by phylogenetic evenness and explained 23% of the variation. Lastly, cluster 4 only contained one biodiversity index, functional divergence, and explained 6% of the variation.
Figure 3: Results of principal component analyses (PCA) based on correlations between biodiversity indices. Indices were grouped into clusters based on correlation strength. Indices of species, functional, and phylogenetic diversity were more likely to be in a group together while indices of structural diversity did not fall into groups with the other three measures.
**Relationships Between Biodiversity and Productivity**

For the subset of plots with measured productivity rates, linear regressions between wood growth and biodiversity were mostly negative and non-significantly correlated (Table 3). Functional and phylogenetic diversity indices had the strongest correlations with wood growth among the diversity measures, but the correlation coefficients were negative. All positive correlations between biodiversity and wood growth were weak and non-significant.

Relationships between the biodiversity indices and wood growth were also examined using non-linear regressions. For some indices, a quadratic model was determined to be a slightly better fit, but the degree of improvement over the linear model was small (Table S7). In addition, when the biodiversity indices were combined using the first two components from the PCAs, the two components were found to be non-significantly related to wood growth (Table 3).

For multiple linear regressions estimating wood growth using only the biodiversity indices, functional and phylogenetic diversity were the only variables to be significantly correlated to wood growth (Table S8). Meanwhile, multiple linear regressions estimating wood growth using the biodiversity indices and environmental conditions, found that only foliar N was significantly related to wood growth and relationships with the biodiversity indices became insignificant (Table 4).
Table 3: Pearson correlation coefficients and significance for correlations between biodiversity indices, wood growth, and foliar N for the subset of plots and biodiversity indices and foliar N for all the plots at BEF and HEBF.
* P < 0.05, ** P < 0.001, *** P < 0.0001

<table>
<thead>
<tr>
<th>Index</th>
<th>Wood Growth</th>
<th>Foliar N (Subplots)</th>
<th>Foliar N (All plots)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>BEF  HBEF</td>
<td>BEF  HBEF</td>
<td>BEF  HBEF</td>
</tr>
<tr>
<td><strong>Species Diversity</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>H'</td>
<td>-0.05 0.04</td>
<td>0.05 -0.00</td>
<td>0.06 -0.09</td>
</tr>
<tr>
<td>S</td>
<td>-0.07 0.02</td>
<td>-0.00 -0.07</td>
<td>-0.08 -0.09</td>
</tr>
<tr>
<td>J</td>
<td>0.01 -0.04</td>
<td>0.09 0.10</td>
<td>0.19** -0.01</td>
</tr>
<tr>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>FRic</td>
<td>-0.10 -0.17</td>
<td>-0.13 -0.33*</td>
<td>-0.02 -0.12*</td>
</tr>
<tr>
<td>FEve</td>
<td>0.18 0.15</td>
<td>0.27 -0.04</td>
<td>0.18** 0.05</td>
</tr>
<tr>
<td>FDiv</td>
<td>-0.60*** -0.17</td>
<td>-0.60*** -0.31</td>
<td>-0.43*** -0.35***</td>
</tr>
<tr>
<td>FDis</td>
<td>-0.45** -0.41</td>
<td>-0.38* -0.56**</td>
<td>-0.39*** -0.42***</td>
</tr>
<tr>
<td>RaoQ</td>
<td>-0.54** -0.49*</td>
<td>-0.47** -0.62***</td>
<td>-0.45** -0.48***</td>
</tr>
<tr>
<td><strong>Phylogenetic Diversity</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PD</td>
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<td>0.04 -0.06</td>
<td>-0.00 -0.10*</td>
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<td>PSV</td>
<td>-0.63*** -0.18</td>
<td>-0.70*** -0.44***</td>
<td>-0.51*** -0.49***</td>
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<tr>
<td>PSC</td>
<td>-0.03 -0.13</td>
<td>-0.12 -0.12</td>
<td>0.02 0.02</td>
</tr>
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<td>PSR</td>
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<td>-0.18 -0.24</td>
<td>-0.19*** -0.27***</td>
</tr>
<tr>
<td>PSE</td>
<td>-0.32* -0.43</td>
<td>-0.28 -0.50**</td>
<td>-0.19*** -0.45***</td>
</tr>
<tr>
<td><strong>Structural Diversity</strong></td>
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<td></td>
</tr>
<tr>
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<td>-0.11 0.29</td>
<td>-0.05 0.52***</td>
</tr>
<tr>
<td>DBHsd</td>
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<td>0.05 0.42***</td>
</tr>
<tr>
<td>DBH_H'</td>
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<td>-0.38* 0.05</td>
<td>-0.19*** -0.03</td>
</tr>
<tr>
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<td>-0.29 0.04</td>
<td>-0.14** 0.17**</td>
</tr>
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<td>DBH_J</td>
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<td>-0.41* -0.07</td>
<td>-0.21*** -0.35***</td>
</tr>
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<td>0.09 NA</td>
<td>-0.04 NA</td>
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<tr>
<td>ht_H'</td>
<td>0.09 NA</td>
<td>-0.06 NA</td>
<td>-0.13** NA</td>
</tr>
<tr>
<td>ht_S</td>
<td>-0.04 NA</td>
<td>-0.14 NA</td>
<td>-0.04 NA</td>
</tr>
<tr>
<td>ht_J</td>
<td>0.14 NA</td>
<td>0.04 NA</td>
<td>-0.14** NA</td>
</tr>
<tr>
<td>Rumple</td>
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<td>0.09 NA</td>
<td>-0.13** NA</td>
</tr>
<tr>
<td><strong>PCA Components</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PC 1</td>
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<td>-0.31 -0.45*</td>
<td>-0.20*** -0.39***</td>
</tr>
<tr>
<td>PC 2</td>
<td>-0.29 0.24</td>
<td>-0.25* 0.40</td>
<td>-0.21*** 0.41***</td>
</tr>
</tbody>
</table>

Table 4: Standardized coefficients and significance for multiple linear regressions between productivity, biodiversity, topography, and foliar nitrogen (N).

<table>
<thead>
<tr>
<th>Predictor</th>
<th>BEF</th>
<th>HBEF</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Coefficient</td>
<td>P value</td>
</tr>
<tr>
<td>Foliar N</td>
<td>0.87</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Elevation</td>
<td>0.03</td>
<td>0.6841</td>
</tr>
<tr>
<td>Species Diversity (H’)</td>
<td>0.04</td>
<td>0.6605</td>
</tr>
<tr>
<td>Functional Diversity (RaoQ)</td>
<td>-0.15</td>
<td>0.1632</td>
</tr>
<tr>
<td>Phylogenetic Diversity (PSV)</td>
<td>0.01</td>
<td>0.9022</td>
</tr>
<tr>
<td>Structural Diversity (DBHsd)</td>
<td>0.08</td>
<td>0.2720</td>
</tr>
</tbody>
</table>
For relationships between foliar N and biodiversity, measured foliar N was insignificantly related to most of the biodiversity indices with the exception of some indices of functional and phylogenetic diversity, which were negatively correlated with foliar N. For estimated foliar N concentration across all plots, more of the indices were significantly correlated to foliar N, but the majority of these relationships were negative (Table 3). When non-linear models yielded a substantial improvement over linear models (Table S9), most relationships displayed a concave down, unimodal relationship (Figure 4).

**Figure 4**: Example relationship between the biodiversity and estimated foliar N across all BEF and HBEF plots where most indices displayed a concave down, unimodal relationship.
DISCUSSION

The goal of this study was to understand the relationships among species, functional, phylogenetic, and structural diversity indices as well as their respective relationship with productivity. We found significant, positive correlations between indices of species, functional, and phylogenetic diversity, while indices of structural diversity were weakly and sometimes non-significantly correlated to the other three biodiversity measures. In addition, productivity was negatively related to indices of functional and phylogenetic diversity, but once we accounted for environmental conditions such as nutrient availability, the biodiversity measures were not significantly correlated to productivity. Instead, foliar N was found to be the only variable significantly correlated to productivity. In addition, the biodiversity measures were found to be non-linearly related to estimates of foliar N, displaying concave down, unimodal relationships. Given the strong relationship between foliar N and productivity, this likely translates to a unimodal relationship between biodiversity and productivity at these local-scale forests.

Relationships Between Measures of Biodiversity

Index choice likely played an important role in how the different components of biodiversity correlate with each other (Cadotte et al. 2011; Bagousse-Pinguet et al. 2019; LaRue et al. 2019). Indices of species, functional, and phylogenetic diversity require similar information about species composition, likely contributing to their positive correlations and PCA clustering. For example, richness indices showed the strongest correlations because they all describe the number of species present, the only difference being that functional and phylogenetic indices
accounted for the number of species in relation to their respective functional and phylogenetic traits.

Correlations between species, functional, and phylogenetic diversity only explained a maximum of 50% of the variation (Figure 2). While index choice undoubtedly plays a role in the strength of the relationships, it was not the only influencing factor. Trait redundancy between plots – a result of overlapping functional and phylogenetic traits from closely related species (Cadotte et al. 2011) – also likely influenced the strength of relationships among diversity components. Overlapping traits can cause plots sharing similar levels of species diversity to differ in functional and phylogenetic diversity. For example, a plot with high species diversity may have low phylogenetic diversity if all species present are from the same genus. Similarly, functional diversity might also be low if present species shared the same or similar traits. These differences between biodiversity components supports the idea that one form of biodiversity is not enough to capture the full spectrum of ecologically important traits within any given community.

Correlations between structural diversity and the other three diversity measures did not follow the same patterns as those found in other studies (Morin et al. 2011; Park et al. 2019; Thom et al. 2021). For example, previous studies have stated that species diversity should promote canopy heterogeneity through differences in species’ physical crown dimensions in the canopy (Morin et al. 2011). In addition, increased structural diversity is thought to allow different species to occupy different regions of the canopy in order to optimize light use efficiency within the community (Rissanen et al. 2019). In this study, correlations between structural diversity and the other biodiversity measures were weak and mostly insignificant which provides little support for these previous hypotheses. The lack of correlation suggests that
structural diversity captures a completely unique form of diversity which cannot be described by measures of species, functional, or phylogenetic diversity.

**Relationships Between Biodiversity and Productivity**

When biodiversity measures were evaluated separately or combined, we did not find significant, positive BPR at these two local-scale, temperate forests (Table 3). At this spatial and temporal scale, foliar N was found to be more strongly correlated to productivity than biodiversity. Additionally, biodiversity was shown to be non-linearly related to estimated foliar N (Table S9). This indicates that resource availability is more likely a driver of productivity than biodiversity and that it may also impact patterns of biodiversity in these temperate forests at this scale and time period.

BPR are thought to be driven by two major mechanisms: niche complementarity and the selection effect. The complementarity hypothesis proposes that communities with greater diversity can better utilize available resources through niche partitioning and facilitation which in turn allows a community to become more productive (Tilman et al. 1997b; Loreau and Hector 2001; Cavanaugh et al. 2014; Hagan et al. 2021). While this hypothesis has been used to explain situations where biodiversity and productivity are positively correlated, it falls short when explaining unimodal or negative relationships. Negative and unimodal BPR are better explained by the selection effect hypothesis which proposes that productivity may not necessarily be driven by the variety of species, but by a few highly competitive, productive species that outcompete less productive species over time (Loreau and Hector 2001; Mayfield et al. 2010; Cavanaugh et al. 2014; Hagan et al. 2021). For example, in aspen-dominated stands in northern Minnesota, Edgar and Burk (2001) observed a negative relationship between productivity and species
diversity, which they attributed to species specific functional traits and adaptation to the available site resources; thus, pure aspen stands were found to be more productive than mixed species stands.

Figure 5: A) Correlations between measured foliar N and wood growth for the subset of plots. B) Unimodal relationship between estimated wood growth, calculated from the relationship between measured foliar N and wood growth, and species diversity as an example of relationships between productivity and biodiversity across all the plots at BEF and HBEF.

Although we did not find evidence for a positive BPR, we did find evidence for a unimodal BPR based on the relationship between measured foliar N and wood growth (Figure 5A). Using the relationship between measured foliar N and wood growth, we can estimate wood growth across all of the plots. The relationship between biodiversity and estimated wood growth indicates that plots are moderately productive at peak levels of biodiversity and show either low or high productivity at low levels of biodiversity (Figure 5B). This unimodal pattern is consistent with similar patterns found in other local-scale, temperate forest studies (Worm and Duffy 2003; Paquette and Messier 2011; Adler et al. 2011; Fraser et al. 2015).

Unimodal relationships have been attributed to species’ specific evolutionary history, adaptations to available resources and interactions with other species, such as competitive exclusion (Zobel and Pärtel 2008; Paquette and Messier 2011). In temperate forests, there are a
limited number of species adapted to areas with high resource availability. These species are typically fast growing, broadleaf species, such as aspens and birches. On the other hand, there are also a limited number of species adapted to more stressful, resource limited locations. These species are typically evergreen species which have slower growth rates to compensate for resource limitations. Plots with high biodiversity are then moderately productive as these plots contain a mixture of species and traits which work together to fill niche spaces and optimize use of available resources. The effect of biodiversity on productivity at these temperate sites may then be less important than the interactions between species and their environment (Paquette and Messier 2011).

While we did not find direct evidence for significant, positive BPR at these local-scale forests, BPR have been shown to be much stronger across regional and global scales (Cavanaugh et al. 2014; Liang et al. 2016) and over longer time periods (Naeem 1998; Bengtsson et al. 2000; Fargione et al. 2007; Forrester 2014). Across continental to global scales, biodiversity and productivity has been shown to be positively correlated, but the direct role of environmental conditions, such as nutrient availability, is not fully known. Positive correlations between biodiversity and productivity are thought to be driven by patterns of niche complementarity (Tilman et al. 1997a; Díaz and Cabido 2001; Paquette and Messier 2011; Correia et al. 2018) as well as species evolutionary history and dispersal ability (Zobel and Pärtel 2008). Meanwhile, BPR are also expected be stronger over longer time periods as species evolve to optimize their production (Ruijven and Berendse 2005; Fargione et al. 2007).
Conclusion

At BEF and HBEF, two local-scale temperate forests, we examined the relationship between four measures of biodiversity: species, functional, phylogenetic, and structural diversity, as well as their relationship with productivity. Overall, we found that measures of species, functional, and phylogenetic diversity were partially related and structural diversity was weakly correlated to the other three measures. This indicates that each one described a unique portion of variation within the community. For relationships between biodiversity and productivity, we did not see significant, positive relationships. Instead, we showed that productivity may be more closely related to resource availability, such as foliar N and that there may be an indirect link between biodiversity and productivity through their relationship with foliar N. The results of this study suggest that more work should be done to show how interactions between the biodiversity measures and productivity across different spatial and temporal time scales and how resource availability impacts the relationships.
LIST OF REFERENCES


Fraser OL, McGuire KJ, Bailey SW (2019) Hubbard Brook Experimental Forest: 5 meter LiDAR-derived Topographic Metrics, 2018 ver. 1. Environmental Data Initiative. https://doi.org/10.6073/pasta/a24417c8e5a0dc97e35c114e3a1518f2


Park J, Kim HS, Jo HK, Jung IB (2019) The influence of tree structural and species diversity on temperate forest productivity and stability in Korea. Forests 10:.
https://doi.org/10.3390/f10121113


Storch F, Dormann CF, Bauhus J (2018) Quantifying forest structural diversity based on large-scale inventory data: a new approach to support biodiversity monitoring. For Ecosyst 5:34. https://doi.org/10.1186/s40663-018-0151-1


Figure S1: Correlations between measured foliar N at the subset of plots and estimated foliar N taking the average estimated foliar N value per species within a plot.
Table S1: Summary statistics (mean, standard deviation, minimum, and maximum) for the biodiversity measures at BEF and HBEF as well as a comparison of means of the indices between the two sites using the Tukey-Kramer threshold. Positive values indicate that there was a significant difference between the two sites.

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<td>0.75 ± 0.15</td>
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Table S2: Comparison of means for biodiversity indices at BEF between managed and unmanaged plots using the Tukey-Kramer threshold. Positive values indicate the means between managed and unmanaged plots were significantly different.

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Table S3: Pearson correlation coefficients for relationships between species, functional, phylogenetic, and structural diversity indices.

* P > 0.05, ** P > 0.01, *** P > 0.0001

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Table S4: For BEF only, Pearson correlation coefficients for relationships between LiDAR structural diversity indices and indices for species, functional, phylogenetic diversity as well as DBH structural diversity indices. * P > 0.05, ** P > 0.01, *** P > 0.0001

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Table S5: Most representative biodiversity indices for each principal component analysis (PCA) cluster created from correlation strengths between indices.

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<th>Number of Members</th>
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<th>Cluster Proportion of Variation Explained</th>
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<th>Group Classification</th>
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<tr>
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<td>0.14</td>
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Table S6: Biodiversity indices belonging to the PCA clusters created from correlations between the indices.

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Table S7: Coefficient of determination ($R^2$) and root mean square error (RMSE) values for linear and quadratic relationships between the biodiversity measures and wood growth. Models with the smaller standard error are considered to be the better fit model, but in most cases, the relationship between biodiversity and productivity did not improve.

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Table S8: Best multiple linear regression models using only biodiversity indices and biodiversity indices with foliar N and topography. * P > 0.05, ** P > 0.01, *** P > 0.0001

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Table S9: Comparison between linear and non-linear models for correlations between the biodiversity measures and estimated foliar N concentrations across all BEF and HBEF plots. Models with the lower RMSE value were determined to be better fitted to the data.

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