
The Relationship Between Diversity and Productivity in Selected Forests of the Lake States Region (USA): Relative Impact of Species Versus Structural Diversity

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Abstract.—Ecological theory suggests that diversity and productivity (at some measure) are positively correlated, presumably because individuals engage in niche partitioning to occupy any unclaimed growing space. We examined this theory using inventory information from the U.S. Department of Agriculture, Forest Service, Forest Inventory and Analysis program. The study uses plot-level data from inventories of the Lake States region conducted between 1999 and 2005. Relationships between diversity and biomass productivity in two contrasting forest cover types—aspens and sugar maple-beech-birch—were examined using two measures of diversity. We expected aspen productivity to increase with increasing species diversity and sugar maple-beech-yellow birch productivity to increase with increasing height diversity, reflecting the niche occupancy of each type and reasonable strategies for differentiation. On a landscape level, matching diversity and productivity would better allow us to predict change as a result of management actions, ecological succession, or other factors.

Neither hypothesis was supported by the data. For aspen stands, the increase in competing, more shade-tolerant species apparently constrained aspen growth more than they added to total stand productivity. For sugar maple-beech-yellow birch stands, the freeing of growing space due to height differentiation did not result in a dramatic response by the individual trees capable of occupying that space. Forest managers faced with mandates to enhance biodiversity while maintaining productivity must be aware of what is

and is not possible. Our results suggest that there are fundamental limitations in how managers can simultaneously manage for these two attributes.

Introduction

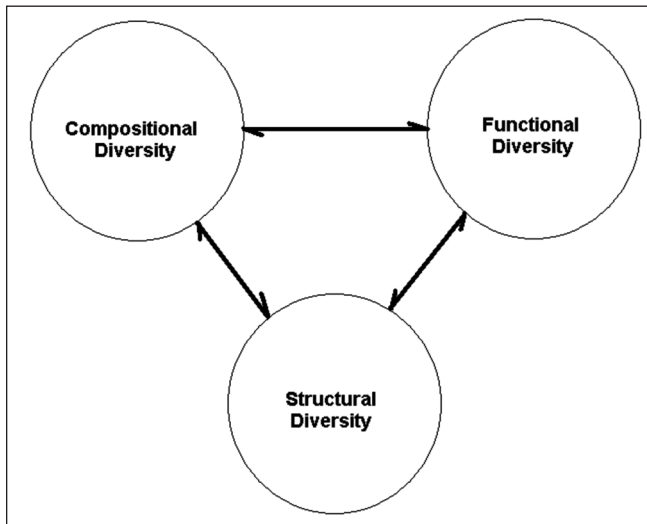
Forests may represent the most diverse ecosystems in the world. Forests provide a wide array of goods and services, both timber and nontimber resources, and play a critical role in carbon storage. Simultaneously, forests provide livelihoods and social and cultural benefits for millions of people throughout the world (Convention on Biological Diversity 2005). Biodiversity has long been considered an important concept in the analysis of ecosystems. Forests are critical areas for managing and protecting biodiversity (Probst and Crow 1991). These ecosystems are defined by the presence and composition of the tree species that inhabit them. A mental construct of such a system might start with the picture of the trees as the “skeleton” upon which one hangs the many attributes of the ecosystem, whether they are wildlife habitat, carbon storage, or nutrient cycling (Odum 1965). To paraphrase, a more diverse forest may offer many different pathways for each of these “skeletal ornament” systems, thus allowing a certain amount of redundancy in the face of disturbances, expected and unexpected.

Although diversity has frequently been described by measures of species or age, other accepted metrics, including ecosystem function, spatial arrangement, and height and diameter differentiation, exist (fig. 1). All have been shown to add value to the ecosystem in some way (Crow *et al.*, 1994). Spies (1998) also stated that particularly important components of forest structure include (1) tree size/age distribution, (2) vertical foliage distributions, (3) horizontal canopy distribution, and (4) dead wood.

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Figure 1.—Components of ecological diversity (from Crow et al. 1994).



The public strongly supports maintaining and enhancing biodiversity, an important component of forest health (Patel *et al.* 1999, but see Rapport 1998). Forest managers are expected to consider the impacts of management actions upon biodiversity. Public land managers, in particular, are susceptible to pressure in this regard.

Forest management has traditionally focused on productivity as a measure of success (Assmann 1970). Although past generations may have defined productivity in terms of some economically useful product, or some other “output” such as water yield or wildlife populations, current thinking bases measures of productivity on some measurable quantity, such as volume or biomass. Regardless of how one measures it, productivity is still used as a yardstick for evaluating the progress in meeting management goals.

Given the public interest in and value for diversity, and the use of productivity as a scale against which we measure success, we ask, “What exactly are the tradeoffs, and how do they vary between different geographic, ecosystem, or management situations? How can the results from an investigation into these relationships be translated into reasonable, understandable management guidelines?”

To begin to answer these questions, we chose two cover types common in the Lake States region: aspen and sugar maple-beech-yellow birch. The aspen forest type is composed primarily of quaking aspen (*Populus tremuloides*) and/or bigtooth aspen (*Populus grandidentata*), both of which are shade-intolerant (Baker 1949), relatively short-lived species that historically existed on the forest-prairie ecotone, which was subjected to frequent fires (Laidly 1990, Perala 1990). Disturbance, old-field abandonment, and deliberate management action have resulted in the species’ establishment throughout the region. The sugar maple-beech-yellow birch forest type (often referred to as “northern hardwoods”) is a late successional forest type found in the cold-temperate forests of eastern North America (Eyre 1980). Primarily composed of sugar maple (*Acer saccharum*), American beech (*Fagus americana*), and yellow birch (*Betula allegheniensis*), this forest type is characterized by more shade-tolerant (Baker 1949), longer lived species than the aspen forest type and generally thrives on more mesic, richer sites that experience frequent but low-severity disturbances. In terms of forest type longevity and cohesion, and the physiological performance required by inhabitants of their relative ecological niches, these two forest types should present stark contrasts in their stand dynamics and response to variations in composition, structure, and disturbance.

Literature

Diversity and Forest Management

Many studies have examined the relationship between species mixture and productivity. Pretzsch (1997) looked at a series of stands ranging from pure Norway spruce to pure beech and different combinations of the two. He found that mixed stands are able to compensate for density reductions due to thinning by increased growth within the remaining stand. The greater elasticity of growth against a reduction in stand density can be attributed to the multilayer stand structure in mixed stands.

Any positive or negative deviations from average stand density, due to lack of treatment or unplanned disruption of stand canopy, could be more easily buffered in mixed stands. Kelty (1986) looked at productivity of mixed hardwood stands and

mixed hardwood-hemlock stands. He found that stands with hemlock were more productive without any material reduction in growth of the hardwoods. Edgar and Burk (2001) examined stands in northeastern Minnesota with a range of species mixtures. Although they expected pure aspen stands to be the most productive, they found that the two most productive stands were both vertically stratified aspen-balsam fir-paper birch mixtures.

Using forest inventory and analysis (FIA) data, Caspersen and Pacala (2001) found that successional composition has a significant relationship to forest ecosystem function: early successional stands were more productive than late successional stands. They concluded that successional diversity was positively correlated with productivity, as was species diversity. This result suggests that a forest managed in such a way as to maintain species diversity would maximize the function of interest.

Structural diversity in forested ecosystems has also been studied. MacArthur and MacArthur (1961) documented the relationship between height diversity and bird species diversity. Proponents of “new forestry” have pointed to diversity in tree size and canopy structure as one advantage of old growth forests (Franklin *et al.* 2002). For shade-intolerant forest types, such as longleaf pine, structural diversity can reduce overall productivity (Farrar 1996), but even in these situations, managed-forest structural diversity maintains the ecological benefits largely unchanged over time (Moser *et al.* 2002). In forests where species exhibit substantial niche overlap, structural diversity and temporal advantage can dictate both the species’ proportion and the overall productivity (Oliver and Larson 1996). One study found a pattern of reciprocal replacement, suggesting the importance of structural diversity and species location in maintaining forest composition (Woods 1979).

Growing space is a holistic concept encompassing the availability of factors influencing growth, including sunlight, water, nutrients, oxygen, and carbon dioxide (Oliver and Larson 1996). Where one factor is limiting, its availability controls growth and the ability of a tree to use another resource (Assmann 1970). Tree species can exist on the same site if

their minimum requirements and opportunities for capture of growing space differ (Oliver and Larson 1996).

Diversity Measurement Tools

In this article, we will examine species composition and aspects of the vertical and horizontal distributions within the forest. Metrics that quantify structural and species diversity in forests have existed for over a century. Some are distance independent and manipulate counts of species or sizes (“mixtures”). Some are distance dependent on an ordinal scale, where they compare a subject tree to some number of “nearest” trees (“differentiation”). Finally, there are quantitative distance-dependent methods (“positioning”) that require knowledge of the actual positions of each tree in a group of trees.

Mixtures can be evaluated with counts, such as species richness; proportional measures, such as importance factors; or its opposite, evenness; or some combination of both, such as the Shannon or Simpson indices (Magurran 1988). In this study we focused on the Shannon index

$$H' = -\sum_{i=1}^n p_i * \ln(p_i)$$

where p_i is the proportion of the total number of individuals that belong to a particular category.

Mixtures can also be evaluated with some summary of categorical variables. One example of this type of tool is a measure of mingling (v. Gadow 1999). Mingling measures are based on the proportion of trees (usually totaling three) with characteristics different from the selected sample tree (Graz 2006). To evaluate the extent of horizontal, distance-independent diversity, we calculated mingling indices for species and height at the subplot level. The species mingling index M_i for a given sample tree, i , using n neighbors, is defined as

$$M_i = \frac{1}{n} \sum_{j=1}^n m_{ij}$$

where:

$$m_{ij} = \begin{cases} 1, & \text{if the tree is of another species} \\ 0, & \text{if the tree is of the same species} \end{cases}$$

If three neighbors are used to determine M_p , the index may be one of four possible values:

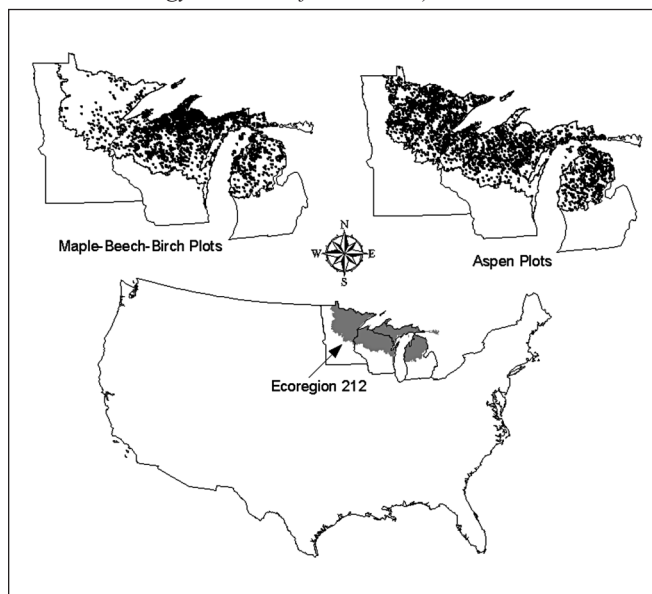
1. 0/3 if none of the neighbors is of a different species.
2. 1/3 if one of the neighbors is of a different species.
3. 2/3 if two of the neighbors are of a different species.
4. 3/3 if all of the neighbors are of a different species.

Mingling values close to 0 suggest that trees of the reference species or height category occur in groups, implying a high degree of aggregation. Higher values of mingling closer to 1 suggest that trees of the reference species or height category do not occur together (Graz 2006).

Objectives

This study examines the relationship between species and height diversity in two representative forest cover types: early successional aspen stands and late successional sugar maple-beech-yellow birch stands, in Ecoregion 212 (fig. 2). The forest types chosen represent endpoints on both single species: multiple species and shade-intolerant/shade-tolerant gradients for this ecoregion.

Figure 2.—Location of Ecoregion 212 and sample plots for the forest types studied before the truncation of the data set; see the “Methodology” section of this article).



Hypotheses

The following hypotheses were evaluated:

1. H_0 : There is no difference in productivity due to species or height diversity.
2. H_1 : High species diversity in aspen stands is associated with high productivity.
3. H_2 : High height diversity in sugar maple-beech-yellow birch stands is associated with high productivity.

Methodology

FIA Data Set

The plot and tree measurements presented here come from paired observations from plots located in Ecoregion 212 in Michigan, Minnesota, and Wisconsin, with final measurements taken from 1999 to 2005. All plots consist of an initial measurement followed by a remeasurement of the plot 5 to 14 years later that accounts for all live trees measured initially and any new trees that have grown onto the plot. Growth and mortality for a plot are recorded based on changes observed over the remeasurement period. Plots are characterized for diversity, age, and current volume based on the second measurement. In cases where three measurements of a plot were available (e.g., a plot measured in 1990, 2000, and 2005), the first two measurements (e.g., 1990–2000) were treated as one plot and the second two measurements (e.g., 2000–2005) were treated as a second independent plot in our data set. These repeated plots at the same location account for 13 percent of the aspen and 23 percent of the sugar maple-beech-birch plots. We restricted measures of diversity to include only live trees on single-condition plots that were entirely on timberland and had not had any removals over the remeasurement period. The measure of productivity was the ratio of all live growth on timberland to current all-live volume on timberland. Complete documentation of the plot design and all measurements can be found at <http://socrates.lv-hrc.nevada.edu/fia/dab/databandindex.html>.

Tree measurements used in this study include species and height (total tree height measured to the nearest foot) and tree location (determined through distance and azimuth measure-

ments from plot center). Height was measured only on trees 5 in in diameter and larger.

Measures of relative growth rates and density are affected by the life-history strategy of the species and the relative stages of stand development. To eliminate the influence that different relative lifespans, high juvenile growth rates, or density declines with advanced age might have on our analysis, we truncated our original data set by removing the oldest 20 percent and youngest 20 percent for each forest type. This tactic reduced the number of aspen forest-type plots from 3,190 to 1,914 and the number of sugar maple-beech-yellow birch plots from 2,440 to 1,464.

We speak of “productivity,” but it is actually a relative growth rate (Blackman 1919), or the annual growth rate ($\text{ft}^3 \text{ ac}^{-1} \text{ yr}^{-1}$) divided by current-year volume ($\text{ft}^3 \text{ ac}^{-1}$). The advantage of this technique is that it matches growth to the volume rather than giving undue weight to stands with large volumes (which might have large growth). One disadvantage is that above-average growth rates occur in the early years of a stand, when they often have lower diversity values (particularly in aspen stands); so there is a confounding of age and diversity. Also, physiologically, we should be comparing active sapwood volume, not total volume, to growth. Still, there is a correlation (albeit lagged in time) between sapwood volume and total volume, and measuring volume is one real-world benchmark of stand performance.

Measures of Diversity

We used the Shannon index to calculate species diversity and diversity of categories of height. To convert a continuous variable-like height into a categorical one, we assigned heights to 3-ft classes. Each class was then treated in the same manner as species in the computation of the index. We calculated the mingling index for each subplot and then averaged the four values for each plot. We used analysis of variance of selected stand structure variables—basal area and stand density index

(SDI), stand age, aspect and diversity indices—at the 95-percent level to test our hypotheses.

Results

Shannon Index

Our results suggested that measures of diversity— H' species and H' height—along with stand age and measures of stand density show a significant relation to productivity.³ When we analyzed the data separately by forest type, we continued to observe a significant relationship between productivity and stand age, basal area, and H' species.⁴ The sugar maple-beech-yellow birch data did not display a significant relationship with H' height where aspen did.⁵

Figure 3 displays growth percentage compared with the Shannon index for the two forest types. Growth percentage for aspen forest types was highest at the lower diversity classes, the opposite of H' , and declined significantly as diversity increased. Sugar maple-beech-yellow birch productivity did increase slightly as diversity increased, with the two lowest classes being significantly less than the three highest diversity classes. The two forest types' productivity levels were not significantly different at the highest diversity level. Figure 4 displays a steady, significant decline in aspen productivity with increasing diversity. Sugar maple-beech-yellow birch productivity did not change significantly across height-diversity categories.

Mingling Index

As opposed to the Shannon index, which is a plot-level calculation, the mingling index reflects the association of each individual tree with its three nearest neighbors. We expected that fine-scale heterogeneity would be more easily detectable using this technique. Overall, the results of our analysis of variance found significant relationships between productivity and overstory density (both basal area and SDI), stand age, and both

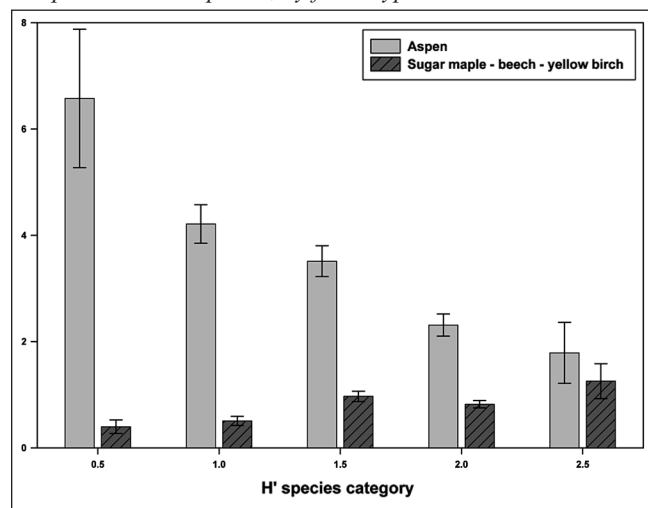
³ Basal area ($F = 42.3$, $p(F) = 0$), stand age ($F = 204.3$, $p(F) = 0$), SDI ($F = 10.4$, $p(F) = 0$), H' species ($F = 8.7$, $p(F) = 0.03$), H' height ($F = 36.7$, $p(F) = 0$).

⁴ Aspen: basal area ($F = 17.3$, $p(F) = 0$), stand age ($F = 49.3$, $p(F) = 0$), SDI ($F = 7.6$, $p(F) = 0.01$), H' species ($F = 7.9$, $p(F) = 0$). Sugar maple-beech-yellow birch: basal area ($F = 3.9$, $p(F) = 0.05$), stand age ($F = 4.8$, $p(F) = 0.03$), SDI ($F = 9.5$, $p(F) = 0$), H' species ($F = 6.6$, $p(F) = 0.01$).

⁵ Aspen: H' height ($F = 20.7$, $p(F) = 0$). Sugar maple-beech-yellow birch: H' height ($F = 0.25$, $p(F) = 0.615$).

mingling indices (species and height).⁶ When only aspen stands were examined,⁷ we found significance in the relationships between productivity and density, and age and the mingling index for species. For sugar maple-beech-yellow birch stands,⁸ however, only density (overstory basal area and SDI) and stand age displayed significant relationships with productivity.

Figure 3.—Growth as a percentage of current live volume compared with H' species, by forest type.



Productivity for aspen stands was significantly larger than sugar maple-beech-yellow birch stands at corresponding mingling index levels except for the highest category (fig. 5). The differential between the two forest types declined as the index increased. Across mingling indices for height, aspen productivity was significantly larger than sugar maple-beech-yellow birch productivity (fig. 6), although, as in species mingling,

Figure 4.—Growth as a percentage of current live volume compared with H' height, by forest type.

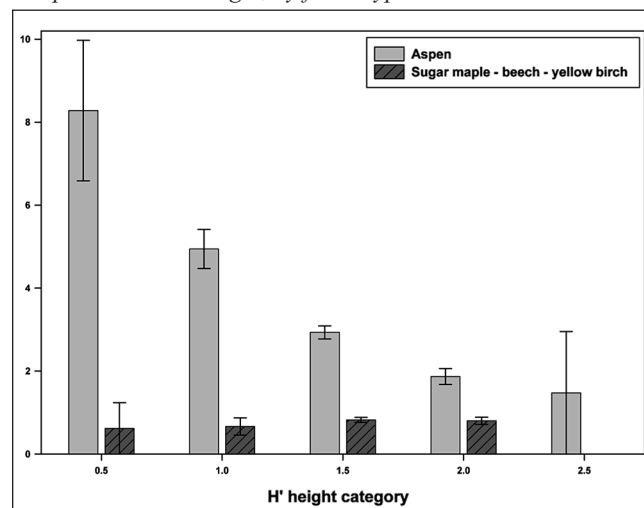


Figure 5.—Productivity (growth/current volume) compared with mingling index for species, by forest type.

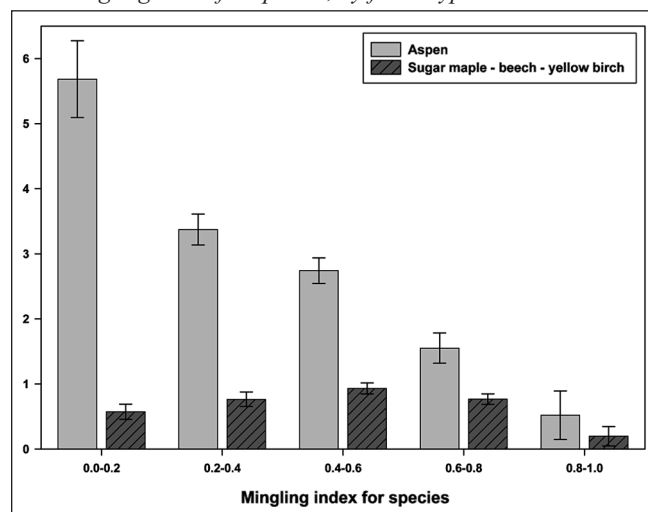
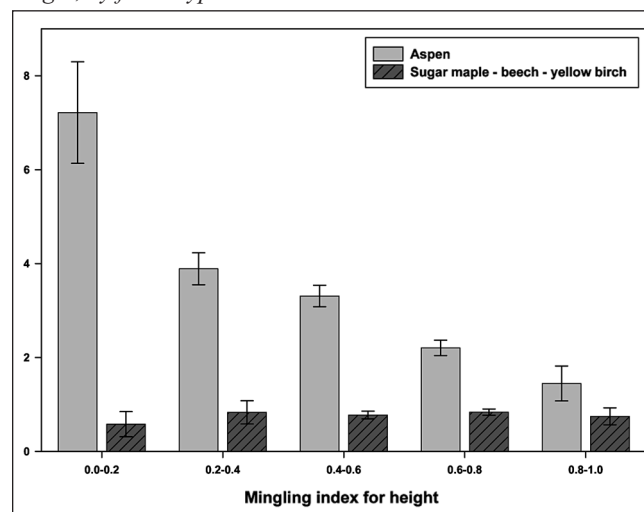


Figure 6.—Productivity compared with mingling index for height, by forest type.



⁶ Overstory basal area ($F = 42.0$, $p(F) = 0$), stand age ($F = 202.9$, $p(F) = 0$), SDI ($F = 10.4$, $p(F) = 0$), Mi-species ($F = 16.4$, $p(F) = 0$), Mi-height ($F = 6.3$, $p(F) = 0.01$).

⁷ Aspen: overstory basal area ($F = 17.2$, $p(F) = 0$), stand age ($F = 48.9$, $p(F) = 0$), SDI ($F = 7.5$, $p(F) = 0$), Mi-species ($F = 12.5$, $p(F) = 0$).

⁸ Sugar maple-beech-yellow birch: overstory basal area ($F = 3.9$, $p(F) = 0.05$), stand age ($F = 4.8$, $p(F) = 0.03$), SDI ($F = 9.4$, $p(F) = 0$).

the difference between the two forest types declined as the mingling index increased.

Discussion

Our original hypotheses were that (1) increased species diversity would increase productivity in aspen stands, and (2) increased height diversity would increase productivity in sugar maple-beech-yellow birch stands. Neither hypothesis was supported by our data. Aspen productivity declined as the Shannon index for species diversity increased. Although aspen productivity was usually higher than sugar maple-beech-yellow birch productivity across species diversity levels, the relative advantage declined as species diversity increased. Apparently, the available growing space in aspen stands is occupied by species that, in time, suppress more aspen growth than they contribute with their own growth. Similar relationships have been observed in mixed pine-hardwood stands in the southern United States, where the hardwood presence suppressed the growth of loblolly pine (Miller *et al.* 2003).

Our second hypothesis was that height diversity would increase sugar maple-beech-yellow birch productivity because the close-niche overlapping northern hardwoods would stagnate without some type of differentiation or release. Our data did not support this hypothesis. Apparently, the niche overlap was not as constricting as we first thought; the stand was not influenced by the increase in height diversity. Another explanation might be that the available growing space in a mixed-height stand was not captured by the remaining trees as dramatically as we had expected.

The mingling indices provided a smaller scale analysis of mixtures than did the plot-level Shannon indices. Mingling should be more sensitive than Shannon to clumping at scales smaller than subplot level. Productivity declined for aspen as M_j -species and M_j -height increased. The sugar maple-beech-yellow birch results for species were not significantly different with respect to the mingling index. Aspen productivity was generally higher than sugar maple-beech-yellow birch productivity. As the mingling indices are ordinal in their tree-to-tree categorization, we had difficulty discovering the influences of

mingling compared with measures of density, although analyses of variance suggested density was a significant influence on productivity.

Other explanations of the trends include noise in the data set and unaccounted-for variables. For example, on highly productive sites, aspen may have gotten a good start; the species dominates the site and grows quickly. On other sites, where multiple species occurred during regeneration (possibly due to poor stocking), growth is slow. Also, we were measuring volume, not biomass, which may not account for the differences in converting carbohydrates to a unit of volume at different densities. There was a suggestion that we did not appropriately account for the different sites on which each forest type is traditionally found (i.e., aspen is found on more northerly and colder sites than the sugar maple-beech-yellow birch plots) (Frelich 2007). Although we believed that by restricting our analyses to Ecoregion 212 we might have sufficiently controlled for climate, further analysis with a larger data set might allow us to better explore this issue.

We did observe trends, although not statistically significant, that suggested middle-level diversity in both species and height provided an optimal situation for stand-level productivity in sugar maple-beech-yellow birch stands. Further investigation with a larger data set, perhaps one with linked remeasurements, is needed.

We tried to control for age by eliminating portions of the data at either end of each forest type's age-class distribution. Nevertheless, we did observe trends where diversity increased with age. These trends were particularly visible in aspen stands.

Other Measures Available

Other methods are available to explore some of the relationships we examined in this study.

Diameter Based. The Shannon index for diameters has the advantage of historical validation (deLiocourt 1898), ease of measurement compared to height (Avery and Burkhart 2002), and correlation with other measures of tree size. Although diameter is easier to measure than tree height and is frequently correlated with this variable, diameter growth is lower in priority

than height growth for a tree's allocation of carbohydrates (Kozlowski *et al.* 1991) and therefore presents an imperfect mirror to the structural (height) diversity we seek. In a sense, diameter diversity is more a result of partitioning of growing space than a creator of these partitions (i.e., it is a "post-hoc" measure).

Distance Dependent-Quantitative. Analysis of distance-dependent relationships provides an apparently more precise evaluation of tree-to-tree influences. Some sort of pair-correlation function might be called for here, but an index does not tell us about within-plot clumping. (Are the trees grouped with equal numbers of near and far trees, or are they equally spaced?) Furthermore, edge correction, particularly on the circular FIA plots, is quantitatively challenging and, depending on the radius of the plot, a source of considerable bias.

Clumping. These methods provide measures of clumping, but do not consider differences in particular species or structural diversity. To do this, one must run the calculation separately for different species or size classes.

Aggregation Index. (Clark and Evans 1954) This index compares the mean distances between each tree in a forest stand with an expected mean distance in a stand with random tree locations.

Neighborhood or Contagion Index. (v. Gadow 1999). The neighborhood index looks at the expected equal size of the number of angles framed by n trees, and determines the index as a proportion of the angles less than the equal size. For example, a neighborhood with four trees would have a standard angle size of 90 degrees. The contagion index would calculate the proportion of the angles that are less than 90 degrees. This method necessitates the use of a distance-dependent measure and/or an estimate of density (Graz 2006).

Acknowledgments

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Literature Cited

- Assmann, E. 1970. The principles of forest yield study. New York: Pergamon Press. 506 p.
- Avery, T.E.; Burkhardt, H.E. 2002. Forest measurements. Boston: McGraw-Hill. 456 p.
- Baker, F.A. 1949. A revised tolerance table. *Journal of Forestry*. 47(3): 179-181.
- Blackman, V.H. 1919. The compound interest law and plant growth. *Annals of Botany*. 33: 353-360.
- Caspersen, J.P.; Pacala, S.W. 2001. Successional diversity and forest ecosystem function. *Ecological Research*. 16: 895-903.
- Clark, P.J.; Evans, F.C. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology*. 35(4): 445-453.
- Convention on Biological Diversity. 2006. Convention on biological diversity: implementation in the European Union. Luxembourg: Office of official publications of the European Union. 28 p.
- Crow, T.R.; Haney, A.; Waller, D.M. 1994. Report on the scientific roundtable on biological diversity convened by the Chequamegon and Nicolet national forests. Gen. Tech. Rep. NC-166. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Research Station. 55 p.
- deLiocourt, F. 1898. De l'aménagement des sapinieres. *Bulletin trimestriel, Société forestière de Franche-Comté et Belfort*, juillet 1898, pp. 396-409. English translation Nygren, M.; Nygren, P.; and Larsen, D.R. 2001. On the amelioration of fir forests. (Revised 27 February 2002.)
- Edgar, C.B.; Burk, T.E. 2001. Productivity of aspen forests in northeastern Minnesota, U.S.A., as related to stand composition and canopy structure. *Canadian Journal of Forest Research*. 31(6): 1019-1029.
- Eyre, F.H., ed. 1980. Forest cover types of the United States and Canada. Washington, DC: Society of American Foresters. 148 p.

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- Farrar, R.M. 1996. Fundamentals of uneven-aged management in southern pine. In: Moser, W.K.; Brennan, L.A., eds. Misc. Pub. 9. Tallahassee, FL: Tall Timbers Research Station. 66 p.
- Franklin, J.F.; Spies, T.A.; Van Pelt, R.; Carey, A.B.; Thornburgh, D.A.; Berg, D.R.; Lindenmayer, D.B.; Harmon, M.E.; Keeton, W.S.; Shaw, D.C.; Bible, K.; Chen, J. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecology and Management*. 155: 399-423.
- Frelich, L. 2005. Personal communication. February 21, 2007.
- Graz, F.P. 2006. Spatial diversity of dry savanna woodlands. *Biodiversity and Conservation*. 15: 1143-1157.
- Kelty, M. 1986. Productivity of New England hemlock/hardwood stands as affected by species composition and canopy structure. *Forest Ecology and Management*. 28(3-4): 237-257.
- Kozlowski, T.T.; Kramer, P.J.; Pallardy, S.G. 1991. The physiological ecology of woody plants. San Diego: Academic Press. 390 p.
- Laidly, P.R. 1990. *Populus tremuloides*. In: Burns, R.M.; Honkala, B.H., tech. coords. Silvics of North America, vol. 2, Hardwoods. Agriculture Handbook No. 654. Washington, DC: U.S. Department of Agriculture, Forest Service. 877 p.
- MacArthur, R.H.; MacArthur, J.W. 1961. On bird species diversity. *Ecology*. 42(3): 594-598.
- Magurran, A.E. 1988. Ecological diversity and its measurement. Princeton, NJ: Princeton University Press. 179 p.
- Miller, J.H.; Zutter, B.R.; Zedaker, S.M.; Edwards, M.B.; Newbold, R.A. 2003. Growth and yield relative to competition for loblolly pine plantations to midrotation: a southeastern United States regional study. *Southern Journal of Applied Forestry*. 27: 1-16.
- Moser, W.K.; Jackson, S.M.; Podrázský, V.V.; Larsen, D. 2002. Examination of stands on quail plantations in the Red Hills region of Georgia and Florida managed by the Stoddard-Neel System: an example for forest managers. *Forestry (Oxford)*. 75(4): 443-449.
- Odum, E.P.; Marshall, S.G.; Marples, T.G. 1965. The caloric content of migrating birds. *Ecology*. 46(6): 901-904.
- Oliver, C.D.; Larson, B.C. 1996. Forest stand dynamics. Updated edition. New York: McGraw Hill. 540 p.
- Patel, A.; Rapport, D.J.; Vanderlinden, L.; Eyles, J. 1999. Forests and societal values: comparing scientific and public perception of forest health. *Environmentalist*. 19: 239-249.
- Perala, D.A. 1990. *Populus tremuloides*. In: Burns, R.M.; Honkala, B.H., tech. coords. Silvics of North America, vol. 2. Hardwoods. Agriculture Handbook No. 654. Washington, DC: U.S. Department of Agriculture, Forest Service. 877 p.
- Pretzsch, H. 1997. Analysis and modeling of spatial stand structures. Methodological considerations based on mixed beech-larch stands in Lower Saxony. *Forest Ecology and Management*. 97: 237-253.
- Probst, J.R.; Crow, T.R. 1991. Integrating biological diversity and resource management. *Journal of Forestry*. 89(1): 12-17.
- Rapport, D.J. 1998. Biodiversity and saving the earth. *Environmental Monitoring and Assessment*. 49: 169-175.
- Spies, T.A. 1998. Forest structure: a key to the ecosystem. *Northwest Science*. 72(2): 34-39.
- v. Gadow, K. 1999. Waldstruktur und Diversität (Forest structure and diversity). *Allg. Forst- u Jagd-Zeitung*. 170: 117-122.
- Woods, K.D. 1979. Reciprocal replacement and the maintenance of codominance in a beech-maple forest. *Oikos*. 33: 31-39.

Additional Reading

- Pommerening, A. 2002. Approaches to quantifying forest structures. *Forestry (Oxford)*. 75(3): 305-324.