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Does biodiversity make a difference? Relationships between species richness, evolutionary diversity, and aboveground live tree biomass across U.S. forests

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ABSTRACT

Biodiversity conveys numerous functional benefits to forested ecosystems, including community stability and resilience. In the context of managing forests for climate change mitigation/adaptation, maximizing and/or maintaining aboveground biomass will require understanding the interactions between tree biodiversity, site productivity, and the stocking of live trees. Species richness may not be the most appropriate tree biodiversity metric in this context as it weights all species as equally important. Measures that account for evolutionary relationships among species should be more biologically meaningful surrogates of functional diversity within forest communities, given that more phylogenetically distinct species should contribute more to the diversity of traits within a community. Using data from approximately 79,000 permanent and standardized forest inventory plots across the United States, we assessed trends in live aboveground tree biomass (LAGB) in relation to metrics of forest tree biodiversity at national and regional scales, controlling for site productivity and live tree stocking. These metrics included four measures of evolutionary diversity associated with distinct components of functional variation. In certain situations and locations across the U.S., evolutionary diversity metrics supply additional information about forest stands beyond that provided by simple species richness counts. This information can potentially include critical insight into tree functional attributes inherently related to evolutionary diversity. Relationships nationally between LAGB and most biodiversity metrics weakened with increasing site productivity and with increasing live tree stocking: The greater the site productivity and tree stocking, the less likely that higher biodiversity was associated with greater LAGB. This is consistent with the expectation that the coexistence of functionally different species increases forest productivity in less productive and more stressful environments, while dominant and highly productive species are able to competitively dominate in more productive habitats. Phylogenetic species clustering (PSC) was increasingly correlated with LAGB as live tree stocking increased on low-productivity sites, suggesting that the co-occurrence of tree species more widely distributed across the phylogenetic tree of life, and therefore likely possessing a wider variety of functional attributes, resulted in greater biomass accumulation on poorer sites. PSC and species richness appear to be the best biodiversity predictors for LAGB on the low-productivity sites likely to be most important for carbon/biomass management. These biodiversity metrics will be important for maximizing biomass/carbon for future carbon sequestration or bioenergy needs and should serve as indicators of forest function in forest resource assessments.

1. Introduction

The fundamental importance of biodiversity to forest management and forest health monitoring at a national scale is recognized by its incorporation into indicators of forest sustainability, including the Criteria and Indicators for the Conservation of Sustainable Management of Temperate and Boreal Forests (Montréal Process Working Group, 2009). Experimental and observational studies have revealed numerous functional benefits of biodiversity to natural ecosystems (Loreau et al., 2001; Hooper et al., 2005; Balvanera et al., 2006). These include attributes of community stability, such as the ability to reduce the susceptibility of the ecosystem to invasion after disturbance (Chapin et al., 1997) and the ability to enhance ecosystem reliability, the probability that the ecosystem will provide a consistent level of performance for a given function over time (Naeem and Li, 1997). A link also exists in many cases

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between ecosystem primary productivity, defined as the rate of plant biomass production (Tilman, 2001), and biodiversity (Naeem et al., 1994; Chapin et al., 2000; Tilman et al., 2001; Cardinale et al., 2007). Much research (e.g., Loreau and Hector, 2001; Gross et al., 2007; Warren et al., 2009) indicates that this relationship can result from "complementarity" between different species that are able to exploit different resources as a result of possessing different traits, ensuring that the efficiency of resource exploitation increases with the addition of new species to a community. One mechanism of complementarity (Loreau and Hector, 2001) is niche differentiation, which is the separation of species by habitat that can result in a more efficient use of resources when a broader range of species traits is present in a more diverse community (Tilman, 1999, 2001). Another complementarity mechanism is facilitation, which occurs when a species modifies the environment in a way that benefits a co-occurring species and which should be more prevalent when greater number of species coexist (Vandermeer, 1989; Fridley, 2001). Biodiversity may also affect ecosystem productivity through the sampling effect, which is the increased statistical probability that, with greater species diversity, species are present that will have a dominant effect on a given community or ecosystem process such as productivity (Huston, 1997; Tilman et al., 1997). Conversely, the coexistence of a greater number of species provides insurance against the loss or poor performance of some species (Folke et al., 1996).

Considering biodiversity in policy and management decision-making is essential, especially when making decisions affecting large temporal and spatial scales (Hooper et al., 2005). One prominent example is the management of forests in the context of climate change, for the fostering of stand resilience to global change through the maintenance of diverse mixtures of tree species and stand structures in managed forest settings (Evans and Perschel, 2009; Puettmann et al., 2009), and for the sequestration of additional atmospheric carbon (Malmsheimer et al., 2008). Recently, forest management strategies for maximizing forest volume or biomass have been applied to the maximization of C sequestration (e.g., even-aged, single-species plantations (Jacobs et al., 2009)). Forest management objectives have long centered on the efficient production of roundwood for sawtimber or pulp markets with periodic harvests on productive timberland (Kimmins, 1992). The increased application of forest management for the purpose of maximizing aboveground C storage or biomass will likely encounter novel combinations of tree species compositions, stand densities, and site qualities. At the same time, factors other than biodiversity are also important in defining ecosystem function (Chapin et al., 1997). Most importantly, the functional characteristics of species present in the ecosystem, and the distribution and abundance of those organisms over space and time, act in concert with climate, resource availability and disturbance regimes to influence ecosystem properties (Hooper et al., 2005). The relationship between biodiversity and productivity, therefore, may vary dynamically over both time and space as a result of spatial heterogeneity and disturbance regimes (Cardinale et al., 2000). Specifically, complementarity mechanisms, such as niche differentiation or facilitation, may allow functionally different species to increase overall productivity in less productive and more stressful environments, while in more productive habitats, dominant and highly productive species are able to competitively exclude others (Warren et al., 2009; Paquette and Messier, 2011).

Better understanding the relationship between tree biodiversity and biomass stocking attributes would greatly aid efforts to estimate the effects that various management activities would have on maximizing aboveground C storage or biomass available to bioenergy industries (Woodall et al., 2011a). In the same manner that past silvicultural research of mixed species systems has informed approaches to management for maximizing merchantable volume yield (e.g., Assmann, 1970; Kelty, 2006), it will be important to determine the effect of tree species composition on biomass production and C storage in response to bioenergy and climate change concerns. This is particularly true across regional scales, where biodiversity is expected to be a less important predictor of ecosystem processes than at smaller spatial scales because biodiversity at large scales is a dynamic variable that adjusts to differences in environmental conditions (Loreau et al., 2001), and where abiotic factors therefore may be the main drivers of variation in ecosystem function across environmental gradients (Loreau, 1998). Although analyses of large numbers of forest plots across Sweden (Gamfeldt et al., 2013), Quebec (Paquette and Messier, 2011), and the Midwest of the United States (Caspersen and Pacala, 2001) found relationships between tree diversity and biomass, such large-scale studies are rare, and none have been conducted for the entire contiguous United States.

Determining indicators of biodiversity that correlate with trends in live aboveground forest biomass (LAGB), in the context of site quality and stand density, would assist in the management forest carbon/biomass across broad scales. Biodiversity is not an easy concept to measure, however (Helmus et al., 2007), and it is not clear whether simple species richness counts are the best tree biodiversity metric when attempting to explain variation in forest productivity (Paquette and Messier, 2011). Species richness is a metric that weights all species equally, and therefore may have more limited value than measures that account for evolutionary relationships among species (Vane-Wright et al., 1991). Taxonomically distinct species are expected to contribute more to the diversity of features, including functional traits, present within a community (Faith, 1992), so measurements of evolutionary history within a set of co-occurring species are assumed to represent the diversity of traits present within that community (Faith, 2002). Greater phylogenetic diversity within communities has been linked to nutrient cycling, resistance to invasion, soil carbon accumulation and other ecosystem processes, goods and services, supporting the argument that phylogenetic diversity is more useful than species richness as a conservation criterion for management decisions (Cavender-Bares et al., 2009). Plant phylogenetic diversity also has been found to explain more variation in community productivity in grasslands than other measures of biodiversity (Cadotte et al., 2008, 2009), while phylogenetic diversity and species richness performed similarly well in explaining forest productivity (Paquette and Messier, 2011). Pillon et al. (2006), meanwhile, demonstrated that phylogenetic diversity is a more appropriate measure of biodiversity than species richness because species richness is more sensitive to taxonomic inflation associated with sampling effort. Comparisons of species richness and phylogenetic diversity across thousands of standardized forest inventory and analysis plots in the United States found that the biodiversity metrics can be strongly correlated across national scales, but that important differences exist regionally and locally (Potter, 2012; Potter and Woodall, 2012).

In order to clarify how and under what circumstances tree biodiversity can serve as a useful indicator of potential forest biomass across broad geographic scales, we used data from approximately 79,000 permanent and standardized forest inventory plots across the contiguous United States to examine the relationship between plot-level measures of biodiversity and levels of LAGB, accounting for site productivity and live tree stocking. Specifically, we tested three hypotheses: (1) Plot-level measures of tree evolutionary diversity are not strongly correlated with species richness across broad scales in the United States; (2) measures of evolutionary diversity are better correlated with levels of forest biomass than species richness, within a matrix of site productivity and live tree stocking; and (3) the relationship between biodiversity and LAGB is stronger when site productivity is lower.