Influence of variations in remotely quantified functional traits and diversity on gross primary productivity

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1. Introduction

Traits associated with structural (morphological) diversity are an important subset of plant functional traits, the morphological or physiological characteristics that are functionally relevant for growth, reproduction and survival (Ma et al. 2019) and are at the crossroads between responses to the environment and ecosystem properties (Díaz et al. 2013). Functional traits influence forest ecosystem carbon dynamics. Metrics that quantify canopy structural diversity are much more strongly associated with forest productivity than traditional biodiversity measures like species richness and phylogenetic diversity (Aponte et al. 2020).

Theories that have emerged to explain the influence of functional traits on productivity include niche complementarity (Tilman et al. 1997) and the mass ratio hypothesis (Grime 1998). Niche complementarity is the idea that co-existing species within the forest will use different resources, and that high species diversity will increase the variability of functional traits and increase ecosystem function and productivity. The mass ratio hypothesis (Grime1998) states that "immediate controls are in proportion to inputs to primary production" and "are determined to an overwhelming extent by the traits and functional diversity of the dominant plants and are relatively insensitive to the richness of subordinates and transients." Mass ratio has been shown to be more related to forest productivity than niche complementarity in numerous within- and across-biome forest ecosystem studies (e.g., Watt et al. 2020), particularly outside the humid tropics (Madrigal-González et al. 2020).

Both the mean and dispersion of functional traits at a given scale are typically quantified. The mean is most often weighted by the abundance of constituent species or other taxonomic groupings, the *community weighted mean*. Descriptors of dispersion of functional traits represent the *functional diversity* (Wang and Gamon, 2019) within a community, landscape, or coarser spatial scales (Ma et al. 2019). Forest productivity has been shown to be associated with community-weighted means (Ammer 2019). Being able to quantify status and changes in functional diversity is increasingly important as both pressures on, and the needs for, forests continue to increase. Plant functional traits vary both across and within species (Schneider et al. 2017) and can be mapped using remote sensing (Schneider et al. 2020).

Both physiological and morphological traits are needed for full characterization of functional diversity using remote sensing (Schneider et al. 2017, Ma et al. 2019), necessitating the use of sensors enabling quantification of canopy structure (Aponte et al. 2020) as well as function. Further, high-spatial resolution (or other comparable) data enabling quantification of canopy structure is needed to address multiple scattering and contrasting illumination and to control for varying amounts of vegetation percentage cover in fine spectral resolution measurements (Wang and Gamon 2019). Considering the natural circadian dynamics in photosynthetic function, observation of daily rhythms must be accelerated.

Improved articulation of carbon exchange between forest ecosystems and the atmosphere thus requires diurnal and seasonal observations combining the mean and dispersion of *functional traits*, morphological and physiological characteristics relevant for growth.

2. Objective

Our overall objective is to determine how gross primary productivity is influenced by variations in remotely quantified functional traits and their diversity across space and time.

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3. Methods

3.1 Study Sites

The study sites are two AmeriFlux tower sites in Virginia, USA, Sweet Briar Land-Atmosphere Research Station (AmeriFlux site US-SB1) and National Ecological Observatory Network (NEON) Mountain Lake Biological Station (AmeriFlux Site US-xML). Sweet Briar is an evergreen needleaf forest (managed loblolly pine), and Mountain Lake a deciduous broadleaf forest, the two principal forest types in the southeastern United States.

3.2 Eddy Covariance Data and Site Characterization

Since the two sites are in the AmeriFlux network, standardized sets of measurements are collected to describe ecological processes, including continuous (every 30 minutes) eddy covariance measurements of canopy photosynthetic uptake. Photosynthetic function responds to environmental stresses, such as low or high temperatures or water availability, along with seasonal growth patterns. In addition to CO_2 fluxes, flux towers collect meteorological measurements including air temperature, humidity, incident photosynthetically active radiation (PAR), precipitation, and net radiation that provide information on environmental conditions.

3.3 Airborne Data

Data from both small unmanned aerial systems (sUAS) and manned aircraft (from the hyperspectral and lidar NEON Airborne Observation Platform acquisition in 2021 at the Mountain Lake site) are being used. Optical sUAS data are collected using Cubert FireflEYE snapshot hyperspectral imaging system (HIS) camera mounted on a SkyFish M6 with a total wavelength range of 450 to 998 nm with spectral band widths (FWHM) ranging from 4 nm at 450 nm to 29 nm at 988 nm. A second focal plane provides high resolution panchromatic observations. The integrated pan camera has a ground resolution of 0.03 m and shares the same front-end optics with the HIS camera. These data are used to produce canopy surface reflectance hyperspectral cube (HIS), sunlit and shaded canopy fractions, and canopy surface models using structure from motion. A YellowScan lidar system mounted on a Vapor 35 helicopter is used to collect ultra-high-density airborne laser scanning (ALS) data over each site once per growing season. The NEON Level 3 Ecosystem Structure product (1 m x 1 m canopy height model) is being used from the 2021 NEON Airborne Observatory acquisition over the Mountain Lake site.

COVID restrictions on field work restricted us to only one sUAS acquisition in the summer of 2020. All these restrictions have now been lifted in Virginia, so the full suite of acquisitions is taking place in 2021, including two sets of diurnal measurements in both sunlit and shaded conditions for both study sites using the FireflEYE and one ultra-high-density ALS acquisition for each site.

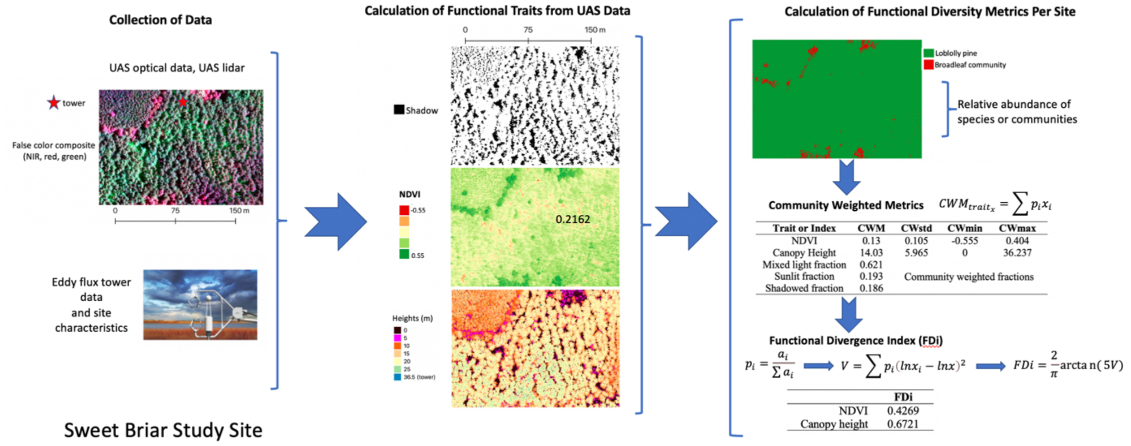
3.4 Functional Diversity Metrics

We are using two relatively simple metrics based on the relative contributions of species at the sites: Community weighted means (CWM) of each functional trait (as well as standard deviations, minimums, and maximums) and the functional divergence index (FDi), which describes the variation in functional traits, proportioned by species (1):

$$FDi = \frac{2}{\pi}\arctan(5V), V = \sum p_i(\ln x_i - \overline{\ln x})^2, p_i = \frac{a_i}{\sum a_i} \tag{1}$$

where V is the weighted variance of functional trait x, a_i is the relative cover of each community type at the site. FDi ranges from 0-1 with no units.

Space precludes listing each site-level trait and its corresponding citation. Physiological traits include indices associated with live green vegetation, vigor, the xanthophyll cycle, light use efficiency, leaf water, and chlorophyll content. Structural traits include LAI quantiles, canopy height and canopy height quantiles, and shadowed and sunlit fractions. Figure 1 shows a partial example of the metric derivation workflow using a limited set of functional traits derived from our 2020 sUAS data and airborne lidar.



$CWM_{trait_x} = \sum p_i x_i$

Trait or Index	CWM	CWstd	CWmin	CWmax
NDVI	0.13	0.105	-0.555	0.404
Canopy Height	14.03	5.965	0	36.237
Mixed light fraction	0.621			
Sunlit fraction	0.193	Community weighted fractions		
Shadowed fraction	0.186			

$p_i = \frac{a_i}{\sum a_i} \longrightarrow V = \sum p_i (lnx_i - lnx)^2 \longrightarrow FDi = \frac{2}{\pi}\text{arcta n}(5V)$

	FDi
NDVI	0.4269
Canopy height	0.6721

Figure 1: Workflow describing the calculation of functional traits, community-weighted functional diversity metrics, and functional divergence indices.

3.5 Statistical analysis to explore functional diversity and productivity across sites

The community-weighted metrics and functional divergence indices are being used to (1) compare the functional diversity throughout the course of a day in for a sunny and cloudy day at each site during the peak of the growing season, and (2) examine the effects of the functional traits on gross primary production.

4. Impact

The recently released IPBES-IPCC workshop report on biodiversity and climate change (Pörtner et al. 2021) makes it clear that limiting global warming and protecting biodiversity are necessary and mutually supporting goals. Developing means by which the combined structure and function of forested ecosystems can be monitored, from canopy to global scales, is becoming vital to human well-being.

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