Disentangling cross scale ecological processes on tree leaf and structural trait distributions.

Introduction

Functional traits are central to how organisms perform under different environmental conditions, interact with other species, and influence the ecosystems to which they belong (McGill 2006). For individual organisms, traits influence core demographic parameters including survival and reproduction. At the species level, traits can influence species distributions and how they respond to changes in land use and climate. Traits influence ecosystems biogeochemical cycles and habitat availability for other species (e.g., Fisichelli et al., 2015). Given their central role across multiple levels of organization, understanding how traits vary within and among species, and at different environments is essential to understand many areas of ecology and predict how ecosystems will change in the future (McGill 2006, Valladares et al., 2014).

Historically, studying plant functional traits has relied on collecting samples of a few leaves from a small number of trees to estimate average trait values at the species level (Wright et al., 2004; Santiago and Wright, 2007; Diaz et al., 2016). Depending on the purpose of the original studies, sample design can be biased with respect to health status, size, species, or environment making it challenging to correctly infer patterns and processes at large scales. As a result, it has been suggested that trait data contains less information than species data on the relationship between plant communities and their environment (Clark, 2016).

An alternative approach that allows continuous estimation of traits across the landscape is to use data collected in the field to derive spatially continuous data from remote sensing (Homolova et al. 2013, Houborg et al., 2015). However, remote sensing estimates for ecological features are typically generated at the pixel level, rather than at the level of the individual tree crown (the primary biological unit and the one typically sampled in the field). Generating Information at the level of individual tree crowns (ITC) is fundamental to integrating derived ecological data with other field censuses and retaining information on community structure and interactions networks (Anderson 2018). This extensive derived data can be fused with other geospatial information such as climate, meso-environment and topography, making it possible to investigate the role of different ecological processes on realized leaf and structural traits composition.

In this project I will integrate field collected trait data with remote sensing to produce derived information for each ITC within 14 different forest ecosystems at landscape scales within the eastern US. These derived data will be used to (1) evaluate patterns of leaf and structural trait distributions in different ecosystems; (2) investigate the role of intra and inter species variability on patterns of leaf traits and their correlation structure; (3) investigate the role of biological interactions on trait distributions and trade-offs across space.

Research plan

Objectives: The primary object of this study is to better understand how leaf functional trait tradeoffs vary with species, environment and biological interactions across the Eastern US, and make predictions for trait distributions that can become the basis of monitoring and forecasting tree function changes in space and time. To do so I will address the following three specific aims:

Aim (1): **Develop methods for generating individual level derived leaf trait data for millions of individual trees and use this data to understand leaf trait patterns at the landscape scale.**

Aim (2): **Determine the relative importance of the environment, inter-species variability and intra-species plasticity for leaf trait trade-offs and distributions across Eastern US.**

Aim (3): **Identify limits and potential .**

Field Data: Leaf chemical traits collected from the field are rare, and typically do not cover a wide spectrum of traits from the same individual tree. I will fuse a combination of field and remote sensing data from local to sub-continental scales into a comprehensive database of individual tree crowns and their ecological information. Field data will include tree species identity, leaf and structural traits. I will use (1) the **Plant Foliar Physical and Chemical Properties** from the National Ecological Observatory Network (NEON) which provides information of LMA, chlorophyll, carotenoids, lignin, and elements (i.e. C, N, P, Ca, Mg, S, B, Zn) for about 300 trees in 14 forest ecosystems across the Eastern US (fig. 1); (2) leaf traits from the **Dimensions of Biodiversity** dataset, which provides information for LMA, N, C, and P for another 300 trees (Graves et al., 2018). Both datasets consist of sun-lit foliage collected at the same time as the remote sensing data. Tree structural traits and species identification will come from (3) the NEON **Vegetation Structure** dataset: field measures of stem diameter (DBH), total stem height (H), canopy diameter (CD), species identity, and location of the measured stems. Coordinates, measurements, identifiers, and species identity collected for all qualified stems with DBH >10 cm in ~1000 20x20 m plots.

Remote sensing data: The **NEON Airborne Observation Platform (AOP)** collects remote sensing data from aircraft at ~1000 m altitude along multiple 15 km long flight lines. Each site's flight footprint covers an area of more than 100 km^2. Data are collected once per year, at the peak ecosystem productivity. I will use: (1) **NEON LiDAR** point cloud elevation data with < 1 m^2 resolution, provided in 1 km^2 tiles (.laz format). The number of data points per m^2 varies, averaging ~4 points per m^2; (2) **Digital Terrain Model (DTM), Slope and Aspect** raster products (Geotiff) at 1 m^2 resolution to provide topographic features;

Fig.1 Study area (orange line) and NEON sites (orange and grey dots)

and (3) **NEON Hyperspectral** reflectance data, for 426 five nm wavelength bands ranging from 380 to 2500 m (visible light through near infrared). Reflectance in regions from 1345 to 1430 nm, from 1800 to 1955 nm, and from 2482 to 2512 nm will be discarded because they are strongly affected by water in atmosphere. Finally, I will use the **NASA Daymet** dataset (.ncdf) to retrieve long term monthly trends of meteorological data at 1 km^2 spatial resolution for temperature, precipitation, solar radiation, vapour pressure and snow depth.

Approach:

Aim (1): **Develop methods for generating individual level derived leaf trait data for millions of individual trees and use this data to understand leaf trait patterns at the landscape scale.**

Ecological studies are generally designed to collect information from individual organisms, hard to acquire systematically at scales of 100 ha or more (Anderson-Teixeira et al. 2015). Although information on individual trees is fundamental to integrating derived ecological data with other field censuses, few studies have attempted to model leaf traits using remote sensing at the crown level (but see Chadwick & Asner 2016, Martin et al., 2018). Even when crown level models are developed, the resulting leaf trait predictions are made for pixels, not crowns, due to the challenges in aligning LiDAR and hyperspectral products. Consequently, ecology lacks the large scale individual level trait estimates that are necessary to fully understand relationships between traits, species, and the environment. **I will develop a pipeline to (a) estimate crowns size and shape, (b) align field data to remote sensing, (c) and infer structural**

and chemical traits at both pixel and crown level, and compare these two approaches for building large scale derived datasets of tree structural and chemical traits.

The use of *NEON AOP* data combined with field measures of ITC geometry and leaf traits from *Dimensions in Biodiversity* project provides an ideal opportunity to build such pipeline, test the uncertainty in each step, and make predictions for millions of derived crowns at landscape scales. To do so, I will compare three image segmentation methods to infer crown geometries (Dalponte et al., 2018, Silva et al., 2016, Pau et al., 2010). Methods will be compared using the Jaccard index (Raul & Vargas, 1996) between predicted and measured crown polygons (Marconi et al, 2019). I will use pixels extracted from field crowns to build models relating remote sensing to field measurements of leaf mass area, nitrogen, carbon, and phosphorus content. I will use partial least squares generalized linear regressions (Bastien et al., 2005) that provide better estimates of the uncertainty in predictions than traditional approaches (Kysely, 2008, Leire et al., 2018). I will compare models built on (a) individual pixels, (b) their ensemble, and (c) their aggregation to crown level. I will compare models built on remote sensing data extracted from field-based crown delinations and automated segmentation methods to assess the effects of uncertainty in segmentation and alignment.

Finally, I will use the resulting pipeline to create a dataset of millions of derived trees at landscape scales, and link them to topographic, climatic, leaf and structural trait information. I will focus on two mixed forest NEON sites in the south-east US, Ordway Swisher Biological Station (OSBS) and Talladega (TALL). Data will be distributed and visualized through a flexible web application developed R shiny (Chang et al., 2018). Providing this data as a downloadable data product will allow researchers to conduct individual level research at scales over 100 times greater than current field based datasets.

Crown delineation algorithms currently have high levels of uncertainty (Marconi et al., 2019). This uncertainty is likely to have greater effects on models built on single pixels. Ensembles of pixels within individual crowns should reduce this effect by reducing outliers and false positive pixels (fig. 2), resulting in more reliable estimates of both point estimates and uncertainties (Wagstaff et al., 2008, Choudhury et al., 2018). I expect landscape patterns to follow general trait patterns including the leaf economic spectrum (Wright et al., 2005). I also expect that derived landscape scale data will show different distributions of traits than field samples, because of biases in sampling across edaphic conditions and forest structure (Yang et al., 2018).
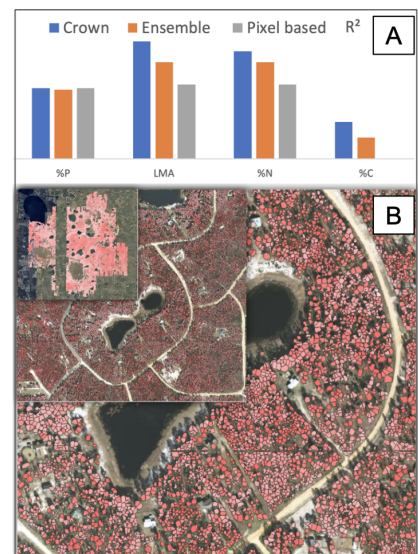
Fig. 2 (A) Performance (held out R^2) for different approaches; (B) example of derived crowns data for 215 km^2.

Aim (2): **Determine the relative importance of the environment, inter-species variability and intra-species plasticity for leaf trait trade-offs and distributions.**

Trait-based ecology has traditionally focused on identifying trade-offs in leaf traits that define constraints on species function and quantify functional relationships in ecosystem models (Wright et al., 2004, Mokany et al. 2008, Boulangeat et al. 2014, Stahl et al. 2014). One approach models trait syndromes directly from environmental conditions (independent of species identity), based on the idea that traits themselves are most important for predicting and understanding the structure and function of ecological communities (McGill et al. 2006, Lebrija-Trejos et al. 2010, Lamanna et al. 2014, Violle et al. 2014). Alternatively, it has been proposed that knowing how the distribution of species responds to the environment provides more information on trait variation than focusing on trait patterns alone (Clark et al.

2016). Despite these two competing perspectives little is known about how the relative importance of the environment and taxonomy changes with trait, ecosystem type, and ecological region (Liu et al., 2019, Messier et al., 2017, Anedregg et al., 2018). **Combining the two approaches in a unified framework will allow me to integrate inter & intra species effects on trait distributions, and explore the relative importance of taxonomy, climate and topography on joint leaf trait distributions across forests in the Eastern US.**

The integration of remote sensing and field data from *NEON AOP* and *TOS* represents a unique opportunity to address this problem. Field data provide information on species identity and a variety of leaf traits for hundreds of trees, that can be used to integrate field data with remote sensing and environmental data. Climate, soil and topography are the main environmental drivers used both in predicting species distributions (Clark, 2016), and determining intra-species variability in traits (Maire et al., 2015, Wüest et al., 2018). The remote sensing data can be used to (1) identify the amount of intra and inter species variability information captured by spectral reflectance (Schweiger et al., 2018), and (2) assess the effect of uncertainty in species classification on inter-species variability when using remote sensing to derive species identity. I will build joint trait regression models in a multi-level, multivariate, fully bayesian framework (Clark et al., 2017, Burkner, 2017, 2018). Models will be trained using any combination of species, reflectance, climate, soil and topography information. I will include inter-species effects by using relationships across species in a phylogenetic comparative framework (Garamszegi, 2014).

To address the relative importance of each group of variables I will calculate intra-class correlation coefficients, and will quantify unique and shared variance components by comparing the bayesian predicted R^2 on held-out data for all models (Gelman et al., 2018). To explore the connections between each class of predictors, I will build structural equation models for each analyzed trait, and compare the relative weight of different paths (Merckle and Rosseel, 2018). To identify how the relative importance of taxonomy and the environment vary geographically and across traits, I will explore patterns in variance partitioning on the full model for each NEON site independently. Finally, I will update the Chapter 1 pipeline to create derived-data for millions of ITCs per NEON site, with inferred species identities (Anderson, 2018).

I expect species identity to dominate variance in leaf traits like LMA, where there is a high range of global variation and single species cover narrower ranges (Asner et al., 2011, Fajardo & Siefert, 2016). In contrast, I predict that traits like leaf pigments vary highly with the environment, because of their more rapid turnover and direct relation to radiation dynamics (Keenan & Niinemets, 2017, Aneece et al., 2017). I expect reflectance to capture mainly variation in leaf characters shared by climate and species (fig. 3). Uncertainty in species identity derived from remote sensing may strongly affect traits estimates if species effects are assumed to be independent. However, including phylogenetic covariance among species should reduce this effect, because misclassifications are more likely to occur among closely related species (Ballanti et al., 2016).
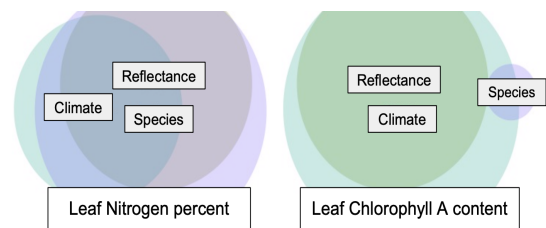

Fig. 3. Variance partitioning among species, reflectance and climate for 2 out of 16 traits, produced by marginalizing the full model.

Aim 3: **Understand how biological interactions influence the distribution of traits and their tradeoffs, at scales from neighbouring trees to landscapes.**

Biological interactions have an important role on ecosystem function (Chi et al., 2015, Chamney et al., 2016; Fahey et al., 2015). For example, competition for light modulates microsite quality and stand

structure, which influences trade-offs in tree allocation strategies in leaf traits (Zhang et al., 2016; Kaitaniemi, P. & Lintunen, 2010). Understanding the nature and ramifications of these networks of interactions remains an open area of research (Sutherland et al., 2013). **I will investigate the role of tree interaction networks on joint distributions of leaf chemical traits across the Eastern US.** I will build and analyze the structure of plant-plant networks (Saiz et al., 2017; 2018, 2019) from local to landscape scales using data on millions of trees within each NEON site. There network analyses are typically difficult at large scales because documenting the size and position of every possible interaction in the landscape scales is difficult or impossible using field data (Jordano, 2016). The dataset derived from Chapters 1 and 2 is a unique opportunity to circumvent this challenge using derived data on every tree at each NEON site. To reduce the effect of environmental heterogeneity (Getzin et al., 2008), I will first divide each site into contiguous environmentally equivalent subregions. Each subregion will be divided in adjacent plots of 0.1, 1 and 10 ha. To determine whether interactions primarily affect taxonomy or tree plasticity, I will build networks on both (a) taxonomic groups (observed species), and (b) an equivalent number of functional groups (pseudo-species). Species and pseudo-species identity will be determined using methods from Anderson (2018) and hierarchical clustering (Legendre and Legendre, 2012). To reduce the effect of uncertainty in crown density and shape, I will measure interaction weights, sign, and significance by calculating plot level canopy cover covariance for each pair of species (Saiz et al., 2016; 2019).

For each network I will calculate the: (a) link density, which represents the level of spatial connections within the network (Lau et al., 2017); (b) link weight mean, which describes whether the community is dominated by facilitative (positive value) or competitive (negative value) relationships; (c) heterogeneity, which measures how interactions are heterogeneous in magnitude and sign (Saiz et al., 2017); and (d) global network balance, which measures the nested structure of the network, and hence the presence of distinguished patches within the same community (Lau et al., 2017, Saiz et al., 2018). I will finally build a multilevel model as in Chapter 2 including these metrics to identify the relative contribution of biotic interactions over climate, topography, and taxonomy.

In closed canopies I expect interactions to affect traits distributions by either (1) stimulating intra-species diversification of co-occurring functionally similar species, to reduce competition by partially diversifying their niches (Bennett et al., 2015); or (2) favoring coexistence of species using specific divergent trait spaces, leading to to clustered communities with little variance in traits distributions (Kunstler et al. 2012). I expect similar traits underdispersion in sparse canopies with strong environmental filtering (Kunstler et al, 2016).

Significance and broad impacts

Understanding the processes driving trait tradeoffs and distribution is essential for scaling from individuals to ecosystems, modeling ecosystem function, and linking traits to ecological services (Bloomfield et al., 2018, Fajardo & Siefert, 2016). However, trait data are limited to one or few traits per individual, for a small number of trees in a region. These limitations reduce the scope of studies focusing on functional traits (Yang et al, 2018). I aim to circumvent these limitations by inferring trait information for millions of trees and for a large number of traits, which will allow me to explore how trait tradeoffs and distributions are affected by taxonomy, environment, and biotic interactions from site to sub-continental scale. This information will provide insights into how forest communities assembly and their potential to adapt to (and mitigate) environmental changes (Adler et al., 2013). Because NEON data is collected annually, these analyses will help provide short to mid-term time series of plant traits, making it possible to conduct pioneering studies of tree traits dynamics and forecasting. The models produced can be used to infer

traits from the Forest Inventory Analysis, allowing the investigation of cross-scale patterns from local to continent scales.

Making derived data on a wide number of traits available for millions of trees will allow the broader scientific community to explore numerous macroecological questions that have not been previously possible. To facilitate this, I will create two broader impacts designed to improve the development and use of derived trait data at broad scales: (1) create web applications to facilitate data visualization, subsetting, analysis and downloading of this derived data and (2) develop and run data science competitions on converting remote sensing into ecological information.

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