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Mesoscale assessment of changes in tropical tree species richness across a bioclimatic gradient in Panama using airborne imaging spectroscopy

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ABSTRACT

We used imaging spectroscopy to perform a top-down mesoscale analysis of tropical tree species richness across a bioclimatic gradient in Panama. The expressed precipitation gradient from the wet Caribbean side to the dry Pacific side makes Panama an excellent study area for performing a mesoscale assessment of climate effects on tropical tree species richness. Spatial patterns in local spectral variability (expressed as the coefficient of variation) and spectral similarity (expressed as the spectral similarity index) were used as proxies for species area curves and species distance decay curves. Our analysis revealed significant spectral changes along the precipitation gradient. Highest spectral diversity was observed for moist forest sites while lowest diversity was observed for the driest forest sites. Most of the spectral variation came from changes in the visible (VIS) and shortwave-infrared (SWIR) reflectance. Variation in the VIS was significantly higher for the dry compared to the moist and wet forests, while the opposite was true for the NIR and SWIR reflectance. Our spectral mesoscale analysis extends previous results suggesting that niche differentiation with respect to soil water availability is a direct determinant of both local- and regional-scale distributions of tropical trees. A next step would be to test the accuracy and scalability of our results with lower spatial resolution spectrometer data, simulating the observing conditions that will be achieved with future satellite missions such as the European Union's EnMap and NASA's HyspIRI missions.

1. Introduction

Anticipated changes in regional and global climate could drive shifts in the geographic extent, composition and condition of tropical forest canopies (Collwell, Brehm, Cardelus, Gilman, & Longino, 2008; Wright, 2005). Biologists, conservationists and policy makers therefore raise concerns about alterations in the functioning of tropical forests and their capacity to sustain environmental services such as carbon storage and water provisioning (FAO, 2007; Foster, 2001). A need for thorough understanding of how the composition, structure and function of tropical forest canopies will respond to changing environmental conditions will increase as the rate of change accelerates (Schimel, Asner, & Moorcroft, 2013).

The evidence for a pantropical response to global anthropogenic forcing comes almost exclusively from relatively small-scaled censuses of tree plots (Wright, 2005). Although these networks of observations provide valuable insights to the fundamental processes governing canopy function, they lack scalability due to the extremely diverse nature of tropical canopies in terms of both floristic and structural variation, as well as their non-random or systematic placement across tropical land-cover types. An understanding of how tropical forests respond to environmental change requires scaling up our observation capability to the landscape level that captures entire forest communities and transitions between communities. Yet, our ability to measure, scale up and predict basic ecosystem function in tropical forests remains weak. This is strongly linked to practical and logistic difficulties in the often inaccessible tall forest canopies and the overwhelming local-scale (alpha) and regional-scale (beta, gamma) diversity of many tropical systems (Asner, 2013). The majority of work at the landscape scale has thus focused on general description of forest physiognomy, relatively small spatial domains, subsets of common species, or family-level taxonomy (e.g. Higgins et al., 2014).

Until recently, air- and spaceborne remote sensing was most useful for determining the spatial extent and dynamics of vegetation cover. However, technical developments in sensors and instrumentation have vastly improved the quantity and quality of information that can be obtained remotely, and advances in understanding how light interacts with plant canopies have made remote sensing increasingly useful for detecting patterns and analyzing processes related to the composition and functioning of vegetated ecosystems. Imaging spectroscopy, a

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remote sensing technology capable of measuring the earth's reflectance as a continuous spectrum of dozens to hundreds of narrow spectral bands across the visible and near-infrared spectral domain, has shown great potential to map the structure, function and composition of ecosystems at the "mesoscale" (e.g. Jusoff & Ibrahim, 2009; Ustin, Roberts, Gamon, Asner, & Green, 2004). The measured reflectance spectra are sensitive to the structural organization of, and variations in chemical constituents in, canopy components. These physico-chemical-to-spectral linkages provide a means of detecting species and/or functional types (e.g., Asner & Martin, 2009; Asner & Vitousek, 2005; Clark, Roberts, & Clark, 2005; Somers & Asner, 2012; Ustin & Gamon, 2010), and can even provide information about the biogeochemical heterogeneity (e.g. Townsend, Asner, & Cleveland, 2008; Vitousek, Asner, Chadwick, & Hotchkiss, 2009) and species richness of tropical forest canopies (e.g., Asner, Nepstad, Cardinot, & Ray, 2004; Carlson, Asner, Hughes, Ostertag, & Martin, 2007; Feret & Asner, 2013; Kalacska et al., 2007; Nagendra & Rocchini, 2008; Somers and Asner, 2013).

The remote mapping of biological and/or functional diversity is often done by analyzing variation of a particular spectral signal or spectral feature (Gould, 2000). This *Spectral Variation Hypothesis* (SVH) relies on the positive relationship between biological diversity and environmental heterogeneity, and has been used to map or detect biodiversity hotspots (alpha-diversity) and species turnover (beta-diversity) within and between a variety of ecosystems and communities (e.g., Gillespie, Foody, Rocchini, Giorgi, & Saatchi, 2008; Nagendra & Rocchini, 2008; Baldeck & Asner, 2013). Despite progress in the use of spectral variation to estimate biological diversity at different ecological scales, we still lack approaches needed to yield consistent and comparable biodiversity information across different ecosystems. This is particularly true in tropical regions where, for example, vegetation communities may vary from dry to humid forests often over short distances due to strong regional climate gradients (Condit, Ashton, Bunyavejchewin, et al., 2006). With global climate change, it is expected that the current environmental gradients under which forest assemblages formed may shift, and plant communities will be altered in response to those shifts. However, the extent, pattern, and rate of change in forest composition remain unknown, and most dynamic vegetation models lack the fine-scale geographic and biological resolution needed to predict plant community changes over time (Schimel et al., 2013).

New methods and technologies are critically needed to map and monitor changes in the functional and biological composition of ecosystems through time. Nowhere does this seem more critical than in tropical regions, such as Panama, where climate change and land use come together to place maximum pressure on forests and the ecological services they provide to society. Here we use airborne imaging spectroscopy to perform a top-down mesoscale analysis of changes in tropical tree species richness across a bioclimatic gradient in Panama. The expressed precipitation gradient from the wet Caribbean side to the dry Pacific side makes Panama an excellent study area. We sought to answer these specific questions: (i) Can we use airborne imaging spectroscopy to study spatial patterns in local (alpha) and regional (beta) tree species richness across tropical forests? (ii) Can we reveal significant changes in forest canopy spectral patterns, and thus canopy composition and diversity, along a precipitation gradient in Panama?; and if so (iii) are there specific spectral regions or wavelengths that dominate the spectral variation? In this study we seek to determine if imaging spectroscopy can be used to scale up previous results from plot-based studies providing a technology to track shifts in species richness due to climate change over broad spatial scales.

2. Material

2.1. Study area

The isthmus of Panama is dominated by a strong environmental gradient in climate, topography and geology. Average annual precipitation ranges from less than 1600 mm/yr on the Pacific side of the isthmus gradually increasing to over 3100 mm/yr on the Caribbean coast. At the highest elevations along the Caribbean coast precipitation can reach 4000 mm/yr (Rand & Rand, 1982). Rainfall is seasonal with a dry season from January through March, showing marked variation across sites, with an annual extreme moisture deficit around 500–600 mm at the driest sites but only between 300 and 400 mm in the wettest sides (Condit, Engelbrecht, Pino, Pérez, & Turner, 2013). The weathering pattern produced by the strong precipitation gradient has resulted in a complex geological terrain composed of either dense, relatively impermeable volcanic rock or porous, chemically unstable sedimentary rocks and volcanic mud flow deposits (Dietrich, Windsor, & Dunne, 1982).

Due to the variation in rainfall, Panama harbors a great diversity of tree species. The isthmus can broadly be divided into three general bioclimatic regions. On the wettest Caribbean slopes, there is enough moisture throughout the year to support evergreen tropical forests. In contrast, on the Pacific side many of the slopes have hard, dry soil by April. On this south-western side, many species are dry-season deciduous. In the middle of the country, lies moist tropical forest where the community transitions from dry to wet along the precipitation gradient. The trees increase in size and the occurrence of deciduousness lessens compared to dry forests, but does not disappear entirely (Condit, Pérez, & Daguerre, 2010). We selected a representative site of approximately 400 ha in each of the three bioclimatic regions (dry forest site: 7°26′50″N, 80°10′45″W; moist forest site: 9°4′32″N, 79°39′12″W; wet forest site: 9°16′50″N, 79°58′44″W) where both airborne imagery (see Section 2.3) and ground reference data (see Section 2.2) were available (Fig. 1).

2.2. Floristic data

For this study we used publicly available species lists collected from 18 permanent sampling forest plots (10 plots of 1 ha and 8 plots of 0.4 ha, Table 1) maintained by the Smithsonian Institution's Center for Tropical Forest Science (Condit, 1998; Pyke, Condit, Salamon, & Lao, 2001). For each plot all tree stems ≥ 10 cm DBH were identified and listed. These data were used to validate the spectral proxies for species richness and turnover (cf. Section 3.1.).

2.3. Remote sensing data and preprocessing

For each of the three study sites (Fig. 1) we used data collected from the Carnegie Airborne Observatory-2 Airborne Taxonomic Mapping Systems (CAO-2 AToMS; Asner et al., 2012). The imagery was acquired during January–February 2012 (i.e. the early dry season). AToMS includes a Visible-to-ShortWave InfraRed (VSWIR) imaging spectrometer and a dual laser, waveform LiDAR (Asner et al., 2012). These subsystems are boresight aligned onboard a Dornier 228-202 aircraft. Data were collected from an altitude of 2000 m above ground level, providing imagery with a 2 m spatial resolution, at an average flight speed of 55–60 m s^{-1} and a mapping swath of 1.2 km.

The VSWIR spectrometer collects data in 480 contiguous spectral bands spanning the 252–2648 nm wavelength range with a spectral resolution of 5 nm. The VSWIR data were radiometrically corrected using a flat-field correction, radiometric calibration coefficients, and spectral calibration data collected in the laboratory. Apparent surface reflectance was derived from the radiance values using the ACORN-5 atmospheric correction model (Imspec LLC, Palmdale, CA). To improve aerosol corrections, ACORN-5 was run iteratively with different visibilities until the reflectance at 420 nm (i.e. almost constant for vegetation) was 1%. The reflectance data were further corrected for cross-track brightness gradients using a bidirectional reflectance distribution function model (Colgan, Baldeck, Féret, & Asner, 2012). Full details on the preprocessing of the VSWIR data can be found in Asner et al. (2014) and Colgan et al. (2012).