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Community patterns of tropical tree phenology derived from Unmanned Aerial Vehicle images: intra- and interspecific variation, association with species plant traits, and response to interannual climate variation

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Phenology is a key life history trait of plant species and critical driver of ecosystem processes. There is strong evidence that phenology is shifting in temperate ecosystems in response to climate change, but tropical forest phenology remains poorly quantified and understood. A key challenge is that tropical forests contain hundreds of plant species with a wide variety of phenological patterns, which makes it difficult to collect sufficient ground-based field data to characterize individual tropical tree species phenologies. Satellite-based observations, an important source of phenology data in northern latitudes, are hindered by frequent cloud cover in the tropics. To quantify phenology over a large number of individuals and species, we collected bi-weekly images from unmanned aerial vehicles (UAVs) in the well-studied 50-ha forest inventory plot on Barro Colorado Island, Panama. The objective of this study is to quantify inter- and intra-specific responses of tropical tree leaf phenology to environmental variation over large spatial scales and identify key environmental variables and physiological mechanisms underpinning phenological variation.

Between October 2014 and December 2015 and again in May 2015, we collected a total of 35 sets of UAV images, each with continuous coverage of the 50-ha plot, where every tree $\geq$ 1 cm DBH is mapped. UAV imagery was corrected for exposure, orthorectified, and then processed to extract spectral, texture, and image information for individual tree crowns, which was then used as inputs for a machine learning algorithm that successfully predicted the percentages of leaf, branch, and flower cover for each tree crown (r2=0.76 between observed and predicted percent branch cover for individual tree crowns). We then quantified cumulative annual deciduousness for each crown by fitting a non-parametric curve of flexible shape to its predicted percent branch time series and calculated the area under the curve. We obtained the species identities of 2000 crowns in the images by linking the crowns to stem tags in the field, thus producing a time series of cumulative annual deciduousness for 65 species.

Deciduousness showed continuous variation among species rather than distinct phenological categories (ie evergreen and deciduous) that are commonly used in physiological, ecosystem and modeling studies. Some species labelled as evergreen by expert-based classification had annual deciduousness higher than those labelled as deciduous. We found significant, positive relationships between species mean deciduousness and species' leaf phosphorous, photosynthetic capacity and adult relative growth rate, suggesting that higher deciduousness is associated with greater resource acquisition. Comparing May 2015 (during an El Nino drought) and May 2014 (an non El Nino year with normal rainfall), mean deciduousness values for nearly all species was greater in 2015 but with differing levels of intraspecific variation. We discuss how the variation in deciduousness among species, its relationship with plant traits and response to the drought might be incorporated into terrestrial biosphere models of tropical forests to more accurately represent phenology and understand the consequences of community-level variation in phenology for ecosystem processes.