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Remotely sensed canopy height reveals three pantropical ecosystem states

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Abstract. Although canopy height has long been a focus of interest in ecology, it has remained difficult to study at large spatial scales. Recently, satellite-borne LiDAR equipment produced the first systematic high resolution maps of vegetation height worldwide. Here we show that this new resource reveals three marked modes in tropical canopy height ~40, ~12, and ~2 m corresponding to forest, savanna, and treeless landscapes. The distribution of these modes is consistent with the often hypothesized forest-savanna bistability and suggests that both states can be stable in areas with a mean annual precipitation between ~1,500 and ~2,000 mm. Although the canopy height states correspond largely to the much discussed tree cover states, there are differences, too. For instance, there are places with savanna-like sparse tree cover that have a forest-like high canopy, suggesting that rather than true savanna, those are thinned relicts of forest. This illustrates how complementary sets of remotely sensed indicators may provide increasingly sophisticated ways to study ecological phenomena at a global scale.

Key words: alternative stable states; climate change; desert; rainforest; remote sensing; savanna; tree cover.

Introduction

Some ecosystems have alternative stable states, implying the possibility of critical transitions as they cross a tipping point (Scheffer et al. 2001, 2012). The suggestion that tropical vegetation may have alternative stable states (Hirota et al. 2011, Staver et al. 2011) has attracted much attention, as it implies that climatic change may invoke sharp transitions rather than gradual change between the contrasting vegetation states (Holmgren et al. 2013). Although recent field data confirmed multi-modal distributions of tree cover (Staal and Flores 2015) and tree basal area (Dantas et al. 2016) in tropical areas, this work has mostly been based on the analysis of remotely sensed tree cover, invoking two lines of critique. First, it was suggested that the tree cover modes might be sensitive to the particular algorithm used to compute the tree cover from remotely sensed data (Hanan et al. 2014). Second, vegetation ecologists raised the point that tree cover might not be the most appropriate variable to distinguish between savanna and forest (Ratnam et al. 2011, Torello-Raventos et al. 2013). Indeed, forests and savannas differ not only in average tree cover, but also in other fundamental aspects. For instance, the taxonomic composition of savanna and adjacent forests hardly overlaps (Hoffmann et al. 2012, Charles-Dominique et al. 2015). Savanna trees have traits that help them survive in a fire-dominated system and are typically less tall (Hoffmann et al. 2003). The relatively small size of savanna trees suggests that canopy height might be a feature of additional value to distinguish vegetation states. Indeed, canopy height has been shown to have multi-modal distributions in a latitudinal transect spanning across African vegetation (Hansen et al. 2016) and in global temperate vegetation (Xu et al. 2015). Here we aim to test if the debated tree-cover based distinction of alternative states and their distribution across the tropics is consistent with results from a global analysis of canopy height.

Tree cover proxies (e.g., NDVI) have long been the most widely used remotely sensed indicators of vegetation structure at large spatial scales. However, this situation is changing with increasing availability of satellite-borne Radar and laser instruments. For example, the Geoscience Laser Altimeter System (GLAS) on the

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Ice, Cloud and land Elevation Satellite (ICESat) can provide LiDAR measurements with close to global coverage. Although this remote sensing platform has been in service for over a decade, the ability to systematically retrieve vegetation height at large scales was developed only recently. Using the GLAS laser beams with a diameter of ~40–90 m. it is now possible to reconstruct the height distribution of vegetation globally (Los et al. 2012). To explore whether this fascinating new source of information may help to resolve the above-mentioned critique on tree-cover based classifications of vegetation states, we analyzed the vegetation structure across the tropics using canopy height information and tree cover estimates simultaneously.

Materials and Methods

The global vegetation height product was developed from the Satellite-borne LiDAR measurements by the GLAS/ICESat (Los et al. 2012). All available GLAS land data during 2003–2009 were collected to calculate initial vegetation height (Rosette et al. 2008), which was further calibrated and filtered to eliminate spurious observations in the GLAS data. The resulting estimates of canopy heights ranging from 0 to 70 m in 0.5-m intervals were aggregated in each 0.5° grid cell. As an indicator of maximum height, we took the 90th percentile of canopy height (as it is less sensitive to errors/outliers than taking a straight maximum) within each 0.5° grid cell. We excluded agricultural, urban, water, and bare areas using the 2005 ESA Globcover dataset (categories 11–30 and 190–230) at 300 m resolution (http://due.esrin.esa.int/page_globcover.php). This LiDAR product provides independent estimates of canopy heights without involving tree cover or climatic variables, allowing for inference of relationships between height and these variables. Tree cover data were extracted from the MODIS Vegetation Continuous Field Collection 5 dataset for the year 2006 (Townshend et al. 2011). Mean annual precipitation (MAP) data at 1 km resolution were downloaded from the WorldClim website (Hijmans et al. 2005). Prior to the analyses, all spatial data were resampled to a consistent resolution of 0.5° (using the mean value for MAP and the majority value for tree cover and Globcover data).

As a first step, we examine the frequency distribution of canopy height (log-transformed) and tree cover (arcsine-square-root-transformed, following Hirota et al. 2011), and the relationship between these two variables (Fig. 1a). Also, using the potential analysis technique (Livina et al. 2010), we reconstruct stability landscapes of tree cover and canopy height as a function of mean annual precipitation (Fig. 1b). This approach makes it possible to estimate the position of stable and unstable equilibria directly from the data, and to delineate the basins of attraction for the alternative states.

Results and Discussion

The results reveal a clear relationship between canopy height and tree cover, with corresponding multimodal distributions of both variables (Fig. 1a). Closed tropical forest has a mode of maximum height around 40 m, whereas the savanna characterized by lower tree cover varies in maximum height, with a mode around 12 m. The rainfall constraint on high canopies suggested by our analysis is remarkably sharp (Fig. 1b, c). Below a mean annual precipitation (MAP) of 1,500-mm high canopies (>~25 m) are almost absent. Importantly, the correspondence between tree cover and canopy height is far from perfect. For instance, there are areas with a high canopy (~40 m) but sparse tree cover, but also with dense tree cover but a low canopy. If one assumes that canopy height is in part determined by the presence of savanna vs. forest species, those deviant situations could be interpreted as open forest and dense savanna, respectively. Specifically, places with sparse tree cover that have a forest-like high canopy could be thinned relics of forest. This possibility is supported by the observation (results not shown) that such sparse-high canopies are found almost exclusively in places where a 2000–2012 comparison (Hansen et al. 2013) revealed high forest loss. Clearly, combining canopy height and tree cover gives more information than tree cover alone.

It is interesting to note that in addition to the much discussed savanna and forest states, the frequency distributions of both tree cover and canopy height indicate a third state with hardly any tree cover and a distinctly lower maximum height. Following Hirota et al. (2011), we refer to this state simply as "treeless" (even though there will likely be some isolated trees). This "treeless" state may be dominated by shrubs and grasses, but could also contain very low savanna trees, as observed in parts of Africa and South America (Dantas and Pausas 2013). If one plots the modes of the distributions against MAP, it becomes obvious that the treeless mode occurs quite distinctly below 600 mm rainfall (Fig. 1b). Here the mode of the maximum canopy height drops sharply from 12 to 2 m, coinciding with a decline of tree cover.

The correspondence in patterns found for the independently estimated tree cover and canopy height suggests that the combination of these indicators may give a more comprehensive image of vegetation structure than any of those indicators alone. The emerging image is that the response of tropical vegetation to changes in rainfall is indeed discontinuous. As rainfall decreases, forest is lost sharply at 1,500 mm MAP, whereas below 600 mm, trees disappear as a structuring element from the landscape. For the forest-savanna dichotomy, our results are consistent with the bistability suggested by other studies (Hirota et al. 2011, Staver et al. 2011). There is a range of rainfall conditions (roughly 1,500–2,000 mm) where both states are common, whereas intermediate states—in

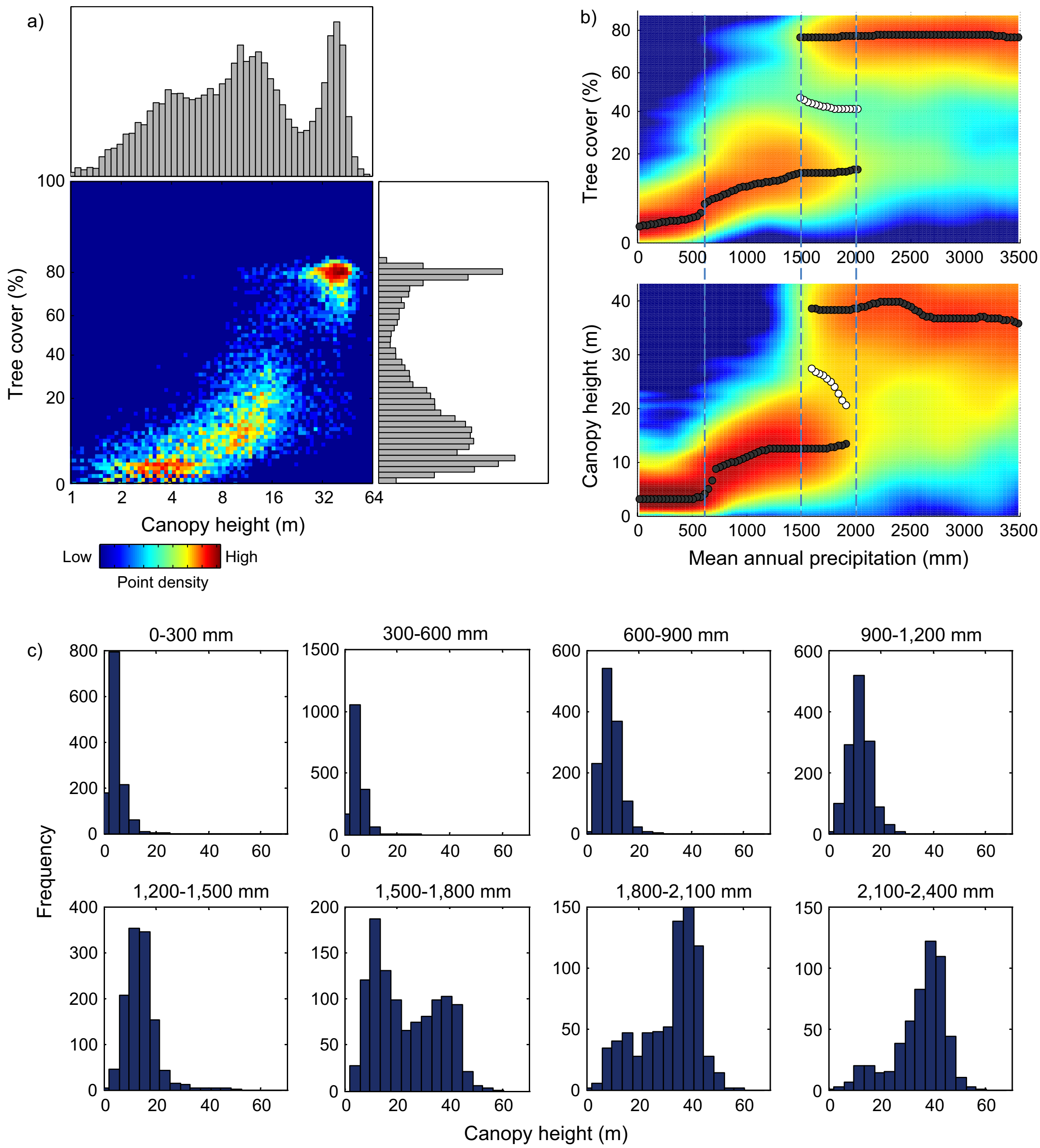

Fig. 1. Alternative states of tropical vegetation structure as revealed by remotely sensed canopy height and tree cover. (a) Relationship between multimodal distributions of maximum canopy height and tree cover. (b) Stability landscapes of canopy height and tree cover as a function of mean annual precipitation computed directly from the data using potential analysis (Livina et al. 2010). The color gradient of blue-yellow-red represents probability densities from low to high. The red areas approximately represent basins of attraction of the vegetation states. Maxima (solid dots) and minima (open dots) in the probability density approximate stable and unstable equilibria, respectively. (c) Frequency distributions of canopy height based on 0.5° grid cells for different ranges of mean annual precipitation.

terms of canopy height or tree cover—are rare. Such a bimodality is consistent with the existence of alternative attractors (Scheffer and Carpenter 2003, Livina et al. 2010) and thus implies tipping points and hysteresis in the response to climate change (Hirota et al. 2011). By contrast, for the shift from savanna to the treeless state centered around 600 mm MAP, there is little evidence for the co-occurrence of alternative states over a range of rainfall conditions. Nonetheless, the sharpness of the transition in canopy height suggests a marked nonlinear change around this climatic condition, which raises the fascinating question of the possible explanation for this apparent pantropical threshold.

Only through thoughtful field experiments will we be able to unravel the mechanisms that drive these surprisingly universal patterns. On the other hand, we are clearly at the onset of an era where ongoing improvement of remote sensing algorithms and sensors produces novel indicators ranging from chlorophyll fluorescence-based estimates of primary productivity to Radar-inferred vegetation optical depth. Such complementary sets of remotely sensed indicators provide increasingly sophisticated ways to study ecological phenomena at a global scale.

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