



Seeing the forest from drones: Testing the potential of lightweight drones as a tool for long-term forest monitoring

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ABSTRACT

Long-term ecological monitoring has contributed substantially towards advancements in theoretical and applied ecology. However, the costs to maintain a long-term monitoring site are enormous. Lightweight unmanned aerial vehicles (UAVs or drones) have been rapidly emerging as a new tool for local-scale monitoring. To evaluate the value of drone applications in long-term ecological studies, we combined drone-derived canopy variables, detailed ground-based stem-mapping data and topographic and edaphic variables from a 20-ha forest dynamics plot in a species-rich subtropical forest. Specifically, we evaluated the relative importance of these variables in explaining local-scale variation in forest stand and species measures. We found that drone-derived canopy variables contributed substantially towards explaining local patterns of biodiversity and more specifically in supporting a gap dynamics hypothesis in structuring observed forest biodiversity. Stand basal area was positively related with canopy closure, indicating the importance of protecting old-growth forests as carbon sinks. The importance of topographic and edaphic variables was also demonstrated, supporting a niche differentiation hypothesis in structuring patterns in biodiversity. Species-level analyses illustrated that light-demanding species were more strongly correlated with canopy variables than shade-tolerant species. We provide convincing evidence that drones can add substantial value to long-term ecological monitoring by providing low cost, high resolution data. Drones should be included in the ecologist's toolbox to complement traditional field surveys.

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1. Introduction

High-quality biodiversity data on species' distributions and its integration with environmental variables are critical for addressing basic research questions in ecology, tracking biodiversity changes, and developing effective conservation actions. Although we gain a wealth of knowledge by spending an enormous amount of time and energy in the field, traditional field surveys can be exhausting and costly (Lawton et al., 1998; Gardner et al., 2008). For example, a field team of 12 to 14 individuals took ~3 years to complete the first tree census for a 50 ha forest dynamics plot in Barro Colorado Island, Panama. Costs to establish similar plots are estimated at about US\$100,000 to US\$500,000 (Condit, 1998). Additional measurements and monitoring of tree height, canopy openness, forest disturbance and other forest parameters are limited by available human labor and financial resources. Due to these limitations, ground-based surveys are not as

frequent as required for analysis and monitoring of short-term change. Therefore, a key challenge remains on how to collect forest attribute data in a timely and cost effective manner.

Remote sensing techniques are increasingly being used to assess changes in forest cover (Hansen et al., 2013; Nijland et al., 2015), tree density (Crowther et al., 2015), species distributions (Cord et al., 2013), canopy height (Simard et al., 2011; Nijland et al., 2015; Zhang et al., 2016), and carbon stocks (Saatchi et al., 2011; Zhang et al., 2014). However, satellite and airborne sensors can be expensive and inaccessible for most researchers, requiring trade-offs between resolution, scale, and frequency (Anderson and Gaston, 2013). For ecological studies at local and regional scales, satellite and airborne data are not often well-suited to the scale of the study (Wulder et al., 2004). Small unmanned aircraft systems, also known as lightweight unmanned aerial vehicles (UAVs) or drones, provide "a promising route to responsive, timely, and cost-effective monitoring of environmental phenomena" (Anderson and Gaston, 2013). Although drones in military applications have a relatively long history, civilian applications have only recently emerged (Koh and Wich, 2012; Anderson and Gaston, 2013). Pioneering ecologists and conservation biologists have recently been using drones to monitor wildlife and plant populations (Jones et al., 2006; Chabot and

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Bird, 2012; Vermeulen et al., 2013), wildlife poachers (Schiffman, 2014), vegetation structure (Getzin et al., 2012; Dandois and Ellis, 2013; Puliti et al., 2015), and mapping of land cover change (Rango et al., 2009). Compared with satellite and airborne remote sensing techniques, drones can fly at low altitudes and at slow speeds, allowing them to take ultra-high spatial resolution (1–20 cm) imagery and thereby collect near-earth data of plant and wildlife populations and biophysical variables (Rango et al., 2009; Koh and Wich, 2012; Whitehead and Hugenholtz, 2014). Using drones also avoids many limitations associated with satellite data, including the lack of sufficient spatial resolution to detect and measure certain critical biophysical properties (e.g., forest canopy gaps and single-tree identification), the lack of sufficient temporal resolution data to detect changes in phenology and stand structure by disturbance events, and long-duration cloud contamination over many types of tropical and subtropical forests (Paneque-Gálvez et al., 2014; Whitehead et al., 2014). Additionally, the cost of one camera-equipped drone is relatively low (Koh and Wich, 2012). Despite these advantages, current cost-effective drones have relatively limited spatial extent per flight, small payloads and low spectral resolution (Paneque-Gálvez et al., 2014; Whitehead et al., 2014), and therefore this technology has yet to receive much attention by field ecologists, especially for long-term ecological studies.

Long-term ecosystem monitoring is the keystone of ecological research and management (Callahan, 1984; Likens, 1989; Condit, 1995; Lindenmayer et al., 2012) because these data provide important insights to complex ecological systems. There are a number of well-known long-term ground-based monitoring programs, such as International Long Term Ecological Research Network (ILTER, <http://www.ilternet.edu>), North American Breeding Bird Survey (BBS, <https://www.pwrc.usgs.gov/bbs>), United States Forest Inventory and Analysis National Program (FIA, <http://www.fia.fs.fed.us>), Amazon Forest Inventory Network (RAINFOR, <http://www.rainfor.org>), and the Center for Tropical Forest Science and Forest Global Earth Observatory (CTFS-ForestGEO, <http://www.forestgeo.si.edu>). Using the CTFS-ForestGEO network as an example, this network comprises over 60 plots from 24 countries across the Americas, Africa, Asia, and Europe, on over 10,000 woody plant species, and more than 6 million living individuals (Anderson-Teixeira et al., 2015). Since the first 50-ha forest dynamics plot was established at Barro Colorado Island in Panama in 1980, over 200 researchers have published over 1000 scientific articles using CTFS-ForestGEO data. These publications have had a substantial impact across a large variety of science and policy issues (e.g., Hubbell et al., 1999; Harms et al., 2000; Hubbell, 2001; Condit et al., 2006; John et al., 2007; He and Hubbell, 2011; Stephenson et al., 2014). Likewise, remote-sensing-based long-term monitoring, such as the National Ecological Observatory Network (NEON, <http://www.neoninc.org>) and NASA's Moderate Resolution Imaging Spectroradiometer (MODIS) platform, have contributed substantially to our understanding of a variety of ecosystems at regional and global scales (Kerr and Ostrovsky, 2003).

Despite the tremendous value of these long-term data sets, many data gaps remain. First, ground-based monitoring sites only cover a small fraction of the Earth's surface and are not representative with several geographic biases. Martin et al. (2012) analysed the distributions of 2573 terrestrial ecological sites, and found that these sites overrepresented protected areas and wealthy countries, and were rarely distributed in the 75% of the terrestrial world where humans live. One main reason for the paucity of these ground-based sites is their high monitoring and maintenance costs. Second, challenges remain between linking broad-scale remote sensing data with local-scale ground data (Kerr and Ostrovsky, 2003; Wulder et al., 2004). The problem of mismatch of spatial scales results in limitations to monitoring and predictions of species distributions and dynamics (e.g., Saveraid et al., 2001). Likewise, mismatches in temporal scales also occur. Broad-scale remote sensing data are not generally as frequent as required to address a number of pressing ecological questions. For instance, human and natural disturbance events at local and/or regional scales, such as forest harvesting,

windfall and drought, may not be captured by satellite remote sensors (Wulder et al., 2004). Therefore, drone-based ecosystem monitoring that can be applied at the temporal and spatial scales relevant to ground measures will greatly benefit long-term studies of ecological properties, potentially "revolutionizing spatial ecology" (Anderson and Gaston, 2013).

In this study, we explore the utility of using lightweight drones as a flexible, cost-effective, and accurate method for mapping forest stand characteristics in a 20-ha CTFS-ForestGEO subtropical forest plot in China. By combining aerial photographs collected by the drone with photogrammetry and using detailed ground survey data on species distribution, topography and edaphic variables, we mapped forest canopy structure, and analysed the relative contribution of drone-derived canopy attributes, topography and edaphic variables to observed patterns of biodiversity and tree regeneration. Specially, we assess: (1) the feasibility of using drone technology to collect high resolution aerial photographs for mapping three-dimensional (3D) forest canopy structure; (2) to what extent drone-derived canopy attributes contribute to our understanding of local-scale patterns in biodiversity and biomass storage; and (3) how species with different life history strategies (i.e., light-demanding vs. shade-tolerant species) respond to drone-derived canopy attributes and other environmental variables.

2. Materials and methods

2.1. Ground inventory data

This study was conducted in a 20-ha (500 m × 400 m) forest dynamic plot in the Dinghushan (DHS) National Nature Reserve (23°09'–23°11'N, 112°30'–112°33'E) in Southern China (Fig. 1). The DHS reserve, which was established in 1956 as China's first nature reserve, encompasses approximately 1155 ha of forests with elevations ranging from 14.1 m to 1000.3 m above sea level. This reserve joined the International Man and Biosphere Reserve Network (MAB) as a global conservation hotspot in 1979. The region is characterized by a south subtropical monsoon climate, with mean annual temperature of 20.8 °C, and monthly mean temperatures varying between 12.6 °C in January to 28 °C in July (Huang et al., 1998). Mean annual precipitation is 1929 mm, with most precipitation occurring between April and September. Mean annual evaporation is 1115 mm with relative humidity averaging 80% (Huang et al., 1998). The vegetation is mainly covered by well-protected monsoon evergreen broadleaved forest. In contrast to the surrounding disturbed forests, the reserve contains rare primary forests of at least 400 years of age that were conserved by monks at the Buddhist temple near the plot (Fig. 1c).

The 20 ha DHS plot was established in 2004–2005 (Fig. 1). Following the protocols from the CTFS-ForestGEO network (Condit, 1998), all stems with ≥ 1 cm diameter at breast height (DBH) were tagged, georeferenced, and identified to species. The first inventory of this plot was completed in 2005, and has been re-censused at five-year intervals ever since. Data for the 2010 census were used for the current analysis which includes 60,015 living individual stems with ≥ 1 cm DBH representing 177 woody plant species. Among these species, 47% (84 species) are considered rare as defined as being less than one individual per hectare (Ye et al., 2008). Based on importance values, Chinese chestnut (*Castanopsis chinensis*, Fagaceae), Chinese guger tree (*Schima superba*, Theaceae), and yellow basket-willow (*Engelhardtia roxburghiana*, Juglandaceae) are the three most dominant species.

2.2. Topographic and edaphic variables

Topography of the study plot was measured by four variables: elevation, slope, aspect, and convexity. Elevation was surveyed on a 20 m × 20 m grid within the 20-ha plot using an Electronic Total Station with elevation values averaged from the four corner of each 20 m × 20 m quadrat (Ye et al., 2008). Slope was defined as

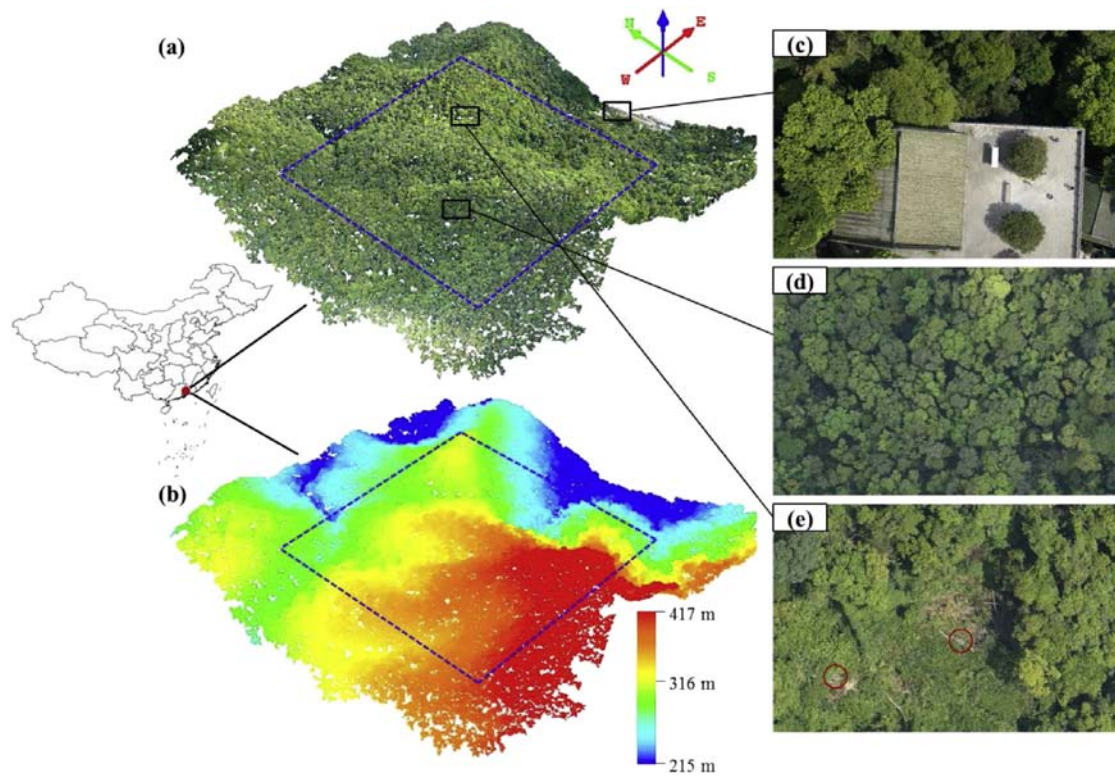


Fig. 1. Geographic location of the study area in Dinghushan National Nature Reserve, Southern China. (a) Aerial photography of our study area. The dotted blue lines represent the boundary of the 20-ha ($400 \text{ m} \times 500 \text{ m}$) forest dynamics plot. (b) Point cloud map for DSM of the region covered by the aerial survey using the drone. (c) This image shows the Buddhist temple used for takeoff and landing. (d) This image illustrates a small area with close canopy occupied by multiple species, while (e) illustrates an area with open canopy. The two red circles in (e) highlight the locations of two ground-level seed traps.

the mean angular deviation from the horizontal of each of the four triangular planes formed by connecting three of the corners of each $20 \text{ m} \times 20 \text{ m}$ quadrat. Aspect was defined as the compass direction in which a slope faces. Convexity of each $20 \text{ m} \times 20 \text{ m}$ quadrat was calculated as the elevation of the focal quadrat minus the mean elevation of eight surrounding quadrats. For the edge quadrat, convexity was the elevation of the center point minus the mean of its four corners (Harms et al., 2001; Wang et al., 2009). The landform of this plot is complex, with a 230 m range in elevation (240–470 m), resulting in numerous extremely steep slopes ranging from 30° to 50° (Wang et al., 2009). The elevation of each $1 \times 1 \text{ m}^2$ point was interpolated by ordinary kriging from the $20 \text{ m} \times 20 \text{ m}$ base grid. The ordinary kriging interpolation technique has been used in many CTFS-ForestGEO plots (e.g., Harms et al., 2001; John et al., 2007) and recent drone study by Dandois and Ellis (2013). The accuracy of this technique was judged by the mean error (ME) and the root mean square error (RMSE) between estimations and observations. The values of ME and RMSE were 0.04 m and 4.28 m respectively.

Edaphic variables were collected using a standard protocol developed by the CTFS-ForestGEO (John et al., 2007). Specifically, we collected topsoil samples (0–10 cm depth) by using a regular grid of points at each 30 m interval within the 20-ha plot. Each sampling point was paired with two additional sampling locations at 2, 5, or 15 m in a random compass bearing from the point to capture fine-scale variation in soil properties (John et al., 2007). In total, 710 samples were collected with eight edaphic variables measured for each sample. These variables included soil organic carbon (SOC), available potassium (AK), total potassium (TK), available phosphorus (AP), total phosphorus (TP), available nitrogen (AN), total nitrogen (TN), and soil pH (Lin et al., 2013). Soil values for each $20 \text{ m} \times 20 \text{ m}$ quadrat were calculated using ordinary kriging, and the accuracy of these estimations was reported in Lin et al. (2013).

2.3. Aerial drone survey

The Microdrones MD4-1000 small drone (<https://www.microdrones.com>) was used for aerial survey of the 20-ha plot (Appendix A). This UAV weighed 2.65 kg, had a cruising speed of 12 m/s, maximum flight duration of 88 min without payload under optimal weather conditions, and maximum payload mass of 1.2 kg. This quadcopter (four brushless battery powered motors) drone can fly by remote control or autonomously with the aid of its GPS receiver and its waypoint navigation system. A Sony NEX-5 still-photograph camera was mounted to the bottom of the drone to acquire aerial imagery. Our team member (J.H.) has used this system for over 200 successful missions investigating land cover changes and vegetation dynamics.

The flight mission was planned with the mdCockpit software that came with the drone. The flight route was planned using orthoimages and a digital elevation model (DEM) of the flight area (Appendix A). To keep the pixel size of the orthoimages relatively constant, the flight could not be horizontal (as with traditional fixed-wing planes) because of the large elevational difference (230 m) in this study site. The vertical distance between the drone and the ground surface was kept at about 240 m. Total flight time was nearly 28 min with the speed of 5 m per second to cover the whole study plot (Fig. 1 & Appendix A). In total, we collected 312 images with about 70% average overlap and the average pixel size was 4.3 cm.

Aerial photographs were processed into georeferenced orthoimages, a digital surface model (DSM), and point clouds using the photogrammetric software “Pix4dmapper” (<http://pix4d.com>), which has been widely used for UAV photogrammetry. Based on the aerial images collected from the drone, we selected 9 ground control points (GCPs) to geocorrect the point cloud. The XYZ locations of each GCP were measured using a Trimble RTK (Real-Time Kinematic) GPS within 1 m accuracy (UTM Zone 49 N, WGS84 horizontal datum). We followed a

standard workflow in photogrammetry to extract the DSM and orthomosaic from images (McGlone, 2013). Then we evaluated the spatial accuracy using the RMSE by comparing digitized and known coordinates from ground. Finally, we generated the DSM with a resolution of 5 cm. The RMSEs were 32 cm in X (east), 44 cm in Y (north), and 69 cm in Z.

2.4. Canopy height model (CHM) generation and canopy height metrics

We generated a canopy height model (CHM) with a pixel size of 1 m by subtracting the DEM from the DSM. We then developed a suite of forest canopy metrics across the 20-ha plot at three spatial scales (5 m, 10 m, and 20 m) by aggregating the CHM data with 1 m resolution to three raster grids consisting of cells of 5 m × 5 m, 10 m × 10 m and 20 m × 20 m, respectively. In total, there were 8000, 2000 and 500 cells at the scales of 5 m, 10 m and 20 m, respectively. These metrics included canopy height (the average of three highest values), mean height, skewness of the heights, standard deviation of heights, vertical distribution ratio (VDR; Goetz et al. (2007)), and canopy closure. We calculated VDR using the equation: $VDR = \frac{HT_{max} - HT_{med}}{HT_{max}}$, where HT_{max} and HT_{med} were maximum and median values of canopy height at each grid cell. We quantified canopy closure by the percentage of 1 × 1 m pixels with > 10 m height. Values of canopy closure ranged from 0 to 100 with higher values indicating close canopy and lower values indicating open canopy.

2.5. Variables generated from ground inventory data

Since we had the detailed georeferenced locations of each individual tree with ≥ 1 cm DBH in the entire 20-ha plot from the ground inventory, we assigned each of individuals to three raster grids (5 m × 5 m, 10 m × 10 m, and 20 m × 20 m) to match with drone-driven variables. Both community- and species-level biodiversity metrics were calculated at these three spatial scales.

2.5.1. Community-level metrics

At each of three spatial scales, we calculated species richness (S), Shannon diversity index (H), species evenness, and stand basal area for each subplot for two tree size groups: all stems (≥ 1 cm DBH) and saplings (1 cm ≤ DBH < 5 cm). Shannon diversity index (H) accounts for both abundance and evenness of the species present, and is calculated as follows: $H = -\sum_{i=1}^S (p_i) \ln(p_i)$, where p_i is the proportion of total individuals represented by species i . Species evenness was calculated as the Shannon diversity index divided by the natural logarithm of species richness (Pielou, 1975).

2.5.2. Species-level metrics

Considering possible species-specific requirements for growth and reproduction, we selected two light-demanding species and two shade-tolerant species to compare how these species respond to their environment measured by the drone-derived canopy metrics, topography, and soils. The two light-demanding species were fissure chestnut (*Castanopsis fissa*; Fagaceae; CAFI) and panicle Mallotus (*Mallotus paniculatus*; Euphorbiaceae; MAPA), and two shade-tolerant species were willow-leaf Acmena (*Acmena acuminatissima*; Myrtaceae; ACAC) and fleshy nut tree (*Sarcosperma laurinum*; Sapotaceae; SALA). For each species, the abundance for each subplot and for different tree size groups was calculated.

2.6. Statistical analysis

We first used Pearson correlations to analyse pair-wise relationships among different variables to identify multicollinearity and we used Dutilleul's (1993) modified t -test to calculate statistical significance accounting for spatial autocorrelation. To avoid multicollinearity problems (Dormann et al., 2013), we excluded variables with high

correlations (coefficient > 0.7). After collinearity assessments, we kept four drone-derived canopy variables (canopy height, mean height, standard deviation of heights, and canopy closure), three topographic variables (elevation, convexity and slope), and four edaphic variables (soil organic carbon, available potassium, total potassium, and total phosphorus). Considering the spatial accuracy of topographic and edaphic predictor variables, we primarily limited our statistical analysis to the 20-m scale (grain resolution). This spatial scale is also widely used for field sampling in forest communities. It is worth mentioning that the further analyses at finer scales can shed light on many important ecological questions, such as forest regeneration and phenology, and therefore should explore deeply depending on research questions and overall data quality of available attributes.

Spatial simultaneous autoregressive error models (SARs), which allow the inclusion of residual spatial autocorrelation in data (Kissling et al., 2008), were used to evaluate the relative importance of each variable to forest stand and species patterns. For each analysis, all possible combinations of 11 predictor variables were used to fit the models. Among all the 2047 ($2^{11}-1$) combinations, the best combination of variables was selected by comparing all model subsets using Akaike's Information Criterion (AIC) (Burnham and Anderson, 2002). Then, for the 'best' model, we calculated the relative importance of predictor variables by using the standardized partial regression coefficients of all predictor variables (cf. Kissling et al., 2008; Zhang et al., 2013). The Akaike weight (w) for each variable based on all possible combinations of predictor variables was also calculated.

All statistical analyses were carried out using R 3.1.2 software (R Core Team, 2014). Pearson correlation coefficients after accounting for spatial autocorrelation were calculated with the R package 'SpatialPack 0.2-3' (Osorio and Vallejos, 2014), and SARs were calculated using the R package 'spdep 0.5-88' (Bivand et al., 2015). The spatial weight matrices of the SARs were calculated with the nearest neighbour and a row-standardized coding style (Kissling and Carl, 2008).

3. Results

3.1. Stand-level analysis

Drone-derived canopy variables, stand-level attributes, and topographic and edaphic variables varied greatly at the three spatial scales (Fig. 2). At the 20-m scale, species richness ranged from 12 to 49 species with stand basal area varying from 5.5 m² ha⁻¹ to 64.9 m² ha⁻¹ (Table 1). For the drone-derived canopy variables, canopy height ranged from 7.0 m to 44.3 m with canopy closure varying from open canopy (0%) to completely close canopy (100%) and averaging overall 73.5%. Comparing spatial patterns of these variables at three spatial scales (Fig. 2), we detected similar patterns between canopy height and canopy closure: tall and close canopies were found in the northwest corner of the plot, while low and open canopies occurred in the southeast corner. Patterns in abundance and species richness differed (Fig. 2) with higher abundance and species richness in low to open canopies with abundance and richness lower in tall and close canopies.

After accounting for spatial autocorrelation, negative correlations with canopy closure and skewness of the height ($ht_skewness$) were found for all stems and only the saplings, species richness, Shannon index and evenness, while weak correlations with ground measures were found for canopy height (ht_canopy) and standard deviation of the heights (ht_sd) (Tables 2 and 3). Among three topographic variables, slope and convexity were significantly related with species richness and the Shannon index, but not for evenness. Among four selected edaphic variables, soil organic carbon (SOC) was positively correlated with species richness for all stems and the saplings and Shannon index for the saplings, while total potassium (TK) was negatively correlated with species richness for all stems and the saplings and positively related with the evenness for the saplings. For stand basal area (BA), canopy closure was the most important explanatory variable at the

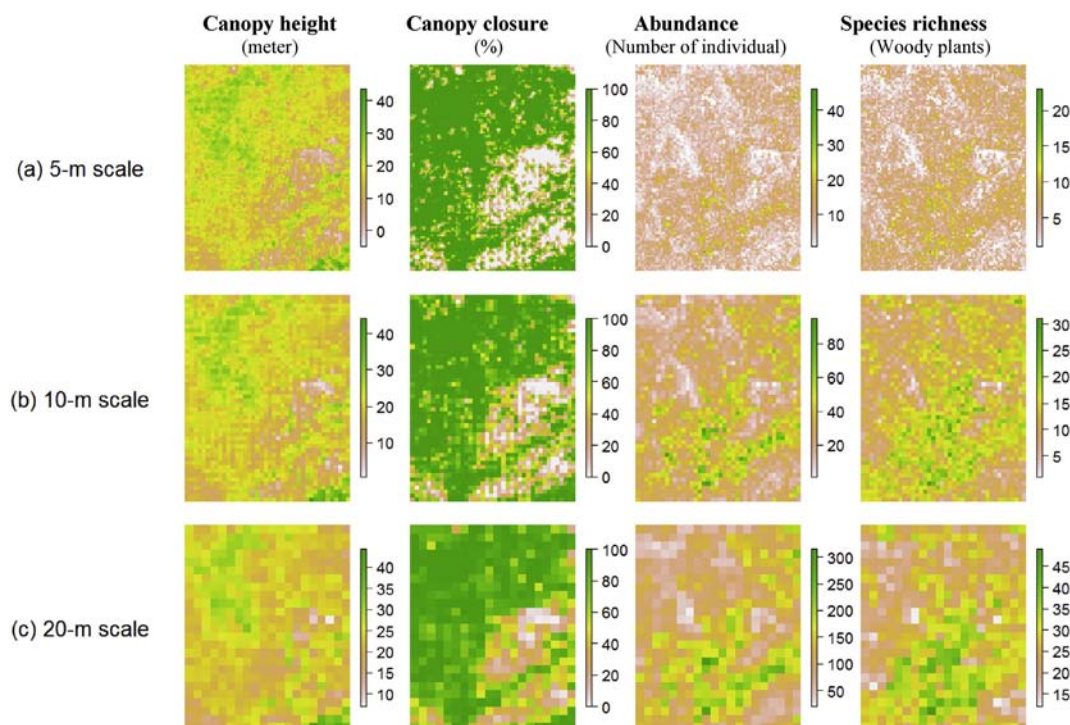


Fig. 2. Maps for drone-derived canopy height and closure, and woody plant abundance and species richness generated from ground inventory data at three spatial scales, 5 m, 10 m, and 20 m, respectively. Canopy height at each scale was calculated by averaging the three tallest canopies of $1 \text{ m} \times 1 \text{ m}$ pixels. Canopy closure was measured by the percentage of $1 \text{ m} \times 1 \text{ m}$ pixels with heights $> 10 \text{ m}$ as estimated by the drone. Canopy closure values range from 0 to 100; higher values indicate more close canopy, while lower values indicate more open canopy. Note that the maps at 5-m and 10-m scales are presented to show the potential applications of drones as a tool for forest monitoring but were not used for analyses in this study.

20-m scale, following by convexity, total potassium (TK) and total phosphorus (TP) (Table 3).

3.2. Species-level analysis

Species abundance distributions for the four selected species showed individual patterns, while similar patterns were detected for all stems and only the saplings of the same species (Fig. 3). For all living stems of each species, the abundance of CAFI, one light-demanding species, was positively related to elevation and convexity, and negatively related to canopy closure (Tables 4 and 5). For CAFI saplings, abundance was only related to elevation and convexity. However, for another light-

demanding species, MAPA, the abundance had significantly negative relationships with canopy closure, ht_sd, and ht_skewness, and positive relationships with canopy height, but weak relationships with all selected topographic and edaphic variables. Abundance of MAPA saplings also showed a negative relationship to canopy closure and a positive relationship to canopy height.

For two shade-tolerance species, ACAC and SALA, the correlations between abundance of all stems and drone-derived canopy variables were quite weak (Table 4). In contrast, elevation and several edaphic variables showed relatively strong relationships with abundance. Similar trends were observed when analyzing only saplings of these two species (Table 4).

Table 1

Descriptive statistics of drone-derived canopy variables, stand-level attributes, and topographic and edaphic variables at the 20-m scale.

Variables		Abbreviation	Mean $\pm$ SD	Min	Max
Stand-level attributes	Species richness	Richness	26.41 $\pm$ 6.45	12	49
	Shannon diversity index	Shannon	2.66 $\pm$ 0.29	1.38	3.23
	Species evenness	Evenness	0.82 $\pm$ 0.06	0.50	0.94
	Stand basal area ($\text{m}^2 \text{ ha}^{-1}$)	BA	26.98 $\pm$ 0.35	5.50	64.87
	Species richness for saplings	Richness_S	19.12 $\pm$ 5.91	5	40
	Shannon diversity index for saplings	Shannon_S	2.32 $\pm$ 0.38	0.80	3.09
	Species evenness for saplings	Evenness_S	0.80 $\pm$ 0.09	0.38	0.97
Drone-derived canopy variables	Canopy height (m)	ht_canopy	23.56 $\pm$ 4.21	7.02	44.26
	Mean height (m)	ht_mean	13.90 $\pm$ 5.01	0	25.97
	Standard deviation of heights (m)	ht_sd	4.60 $\pm$ 1.60	1.61	10.62
	Canopy closure (%)	Closure	73.45 $\pm$ 28.02	0	100
Topographic variables	Elevation (m)	elev	339.23 $\pm$ 50.83	237.12	466.16
	Slope ($^{\circ}\text{C}$)	slope	32.59 $\pm$ 7.96	8.54	57.91
	Convexity (m)	Conv	0.47 $\pm$ 6.51	−13.98	17.67
Edaphic variables	Soil organic carbon (g kg^{-1})	SOC	60.98 $\pm$ 11.21	42.61	98.05
	Available potassium (g kg^{-1})	AK	18.15 $\pm$ 3.41	8.45	31.22
	Total potassium (g kg^{-1})	TK	54.99 $\pm$ 19.58	30.11	121.18
	Total phosphorus (g kg^{-1})	TP	1.80 $\pm$ 1.43	0.41	4.87

Table 2

Pearson correlation coefficients between stand plant measures (species richness, Shannon diversity index, species evenness, and stand basal area) and drone-derived canopy measures, terrain variables, and edaphic variables. *p* values were calculated after accounting for spatial autocorrelation using Dutilleul's (1993) method: *** *p* < 0.001; ** *p* < 0.01; * *p* < 0.05. The correlation coefficients with *p* < 0.05 are marked in bold. Abbreviations of predictors are explained in Table 1.

	All stems				Saplings		
	Richness	Shannon	Evenness	BA	Richness	Shannon	Evenness
ht_canopy	−0.154	−0.134	−0.027	0.133	−0.154	−0.189	−0.102
ht_sd	0.152	0.086	−0.032	−0.231**	0.168	0.170	0.085
ht_skewness	0.151	0.125	0.045	−0.230***	0.162	0.244*	0.220*
Closure	−0.248	−0.191	−0.029	0.409***	−0.263	−0.338*	−0.238
elev	0.364	0.193	−0.075	0.131	0.357	0.143	−0.153
conv	0.268***	0.166*	−0.036	0.315***	0.261***	0.161*	−0.042
slope	0.450**	0.289**	−0.027	−0.145	0.422**	0.377**	0.120
SOC	0.397	0.204	−0.094	−0.165	0.441	0.420*	0.170
AK	0.099	0.079	0.004	−0.145	0.138	0.230	0.197
TK	0.019	−0.017	−0.045	−0.362***	0.086	0.226	0.235
TP	−0.317	−0.159	0.077	0.15	−0.371	−0.316	−0.097

4. Discussion

4.1. Effects of drone-derived canopy variables on stand attributes

By combining data from lightweight drones and ground-based surveys on species distribution, topography and edaphic variables, we found that drone-derived canopy variables contributed substantially to explaining patterns of biodiversity in this species-rich subtropical forest plot. For both all living stems and saplings, forest canopy closure and skewness of canopy heights, which are directly related to canopy light heterogeneity, had much stronger relationships (negative) with species richness and Shannon diversity than the average and standard deviation of canopy heights. This suggests that local light availability plays a critical role on determining biodiversity patterns (Grubb, 1977; Denslow, 1987). Local disturbances, such as gaps formed by treefall and standing dead alders, increase heterogeneity in light conditions and may promote the coexistence of species by providing opportunities for niche differentiation (Denslow, 1987). Rüger et al. (2009) evaluated the influence of light gap disturbances on tree recruitment in a 50-ha tropical forest plot in Barro Colorado Island, which was the first established plot of the CIFS-ForestGEO network, concluding that nearly all species increased in recruitment with increasing light. These findings by Rüger et al. (2009) were contrary to the early work by Hubbell et al. (1999). Due to the practical difficulties in measuring canopy structure directly, both of the studies were based on a rough estimation of the light environment in the forest, which may affect their results (Rüger et al., 2009). Compared with traditional ground-based surveys, lightweight drones provide a high-quality measure of forest vertical structure, and could serve as a cost-effective and time-saving tool for monitoring canopy dynamics.

Table 3

Spatial simultaneous autoregressive models of response variables (species richness, Shannon diversity index, species evenness, and stand basal area) against combinations of predictor variables. Standardized coefficients (Coef) for the model with the highest Akaike weight (*w*) for a given variable group are given, as well as the Akaike weight (*w*) for each variable based on all possible combinations of predictor variables. Pseudo *r*² of each model was in bold. *** *p* < 0.001; ** *p* < 0.01; * *p* < 0.05. Abbreviations of predictors are explained in Table 1.

	All stems								Saplings (1 cm ≤ DBH < 5 cm)							
	Richness		Shannon		Evenness		BA		Richness		Shannon		Evenness			
	Coef	<i>w</i>	Coef	<i>w</i>	Coef	<i>w</i>	Coef	<i>w</i>	Coef	<i>w</i>	Coef	<i>w</i>	Coef	<i>w</i>	Coef	<i>w</i>
ht_canopy		0.319		0.477		0.374		0.285		0.341		0.498		0.502		
ht_sd		0.293		0.419		0.362		0.276		0.328		0.391		0.351		
ht_skewness	−0.110**	0.911	−0.065	0.422		0.365		0.270	−0.108**	0.959	−0.074	0.464		0.422		
Closure	−0.111*	0.619	−0.144*	0.579	−0.097	0.495	0.421***	1.000		0.431	−0.121*	0.509	−0.117	0.550		
elev	0.202*	0.777	0.183	0.526		0.347		0.351	0.192	0.795		0.353		0.469		
conv	0.090*	0.789	0.120**	0.879		0.441	0.135**	0.953	0.087*	0.806	0.106*	0.830		0.401		
slope	0.273***	1.000	0.192***	0.995		0.317		0.277	0.230***	1.000	0.178***	0.992		0.316		
SOC	0.336**	0.935		0.506		0.294		0.384	0.338**	0.952	0.294***	0.947		0.381		
AK		0.369		0.350		0.288		0.285		0.310		0.443		0.413		
TK	−0.265*	0.887		0.490		0.289	−0.173*	0.688	−0.219	0.764		0.328	0.217*	0.635		
TP		0.439		0.286		0.307	−0.159*	0.592	−0.154	0.503		0.336		0.286		
Pseudo <i>r</i>²	0.537		0.430		0.357		0.334		0.538		0.435		0.401			

Stand basal area, which has frequently been used as a surrogate for forest biomass and carbon stocks (Houghton et al., 2009), was significantly related to canopy closure in our study forest. This positive relationship indicates that forests with undisturbed close canopy store higher aboveground biomass and carbon than disturbed open forests, supported by Liu et al.'s (2007) finding on biomass allocation in five forest types in Dinghushan Nature Reserve. It also highlights the importance of protecting old-growth forests as carbon sinks (Luyssaert et al., 2008), especially in this highly fragmented region packed with intense human activities.

4.2. Effects of topographic and edaphic variables on stand attributes

After accounting for the effects of edaphic variables and drone-derived canopy variables, topographic variations in this plot were among the most important factors relating to biodiversity patterns for both all living stems and saplings. With a 230-m elevation range in this 20-ha plot, the DHS plot has high microhabitat heterogeneity leading to topographic niche differentiation among species (Brown et al., 2013). The importance of habitat heterogeneity is supported by previous studies in DHS where habitat conditions affected species abundance distributions for 83% of all woody species (Wang et al., 2009) and significantly influencing on intraspecific variation of one common species *C. chinensis* (Wang et al., 2012). In contrast, there was little evidence for habitat heterogeneity affecting species in a 50-ha tropical forest plot in Barro Colorado Island with only 40 m in elevation range (Harms et al., 2001). Our finding confirms the niche differentiation hypothesis in this species-rich forest (Brown et al., 2013).

Among the four selected edaphic variables, soil organic carbon explained additional variation in species richness and Shannon diversity

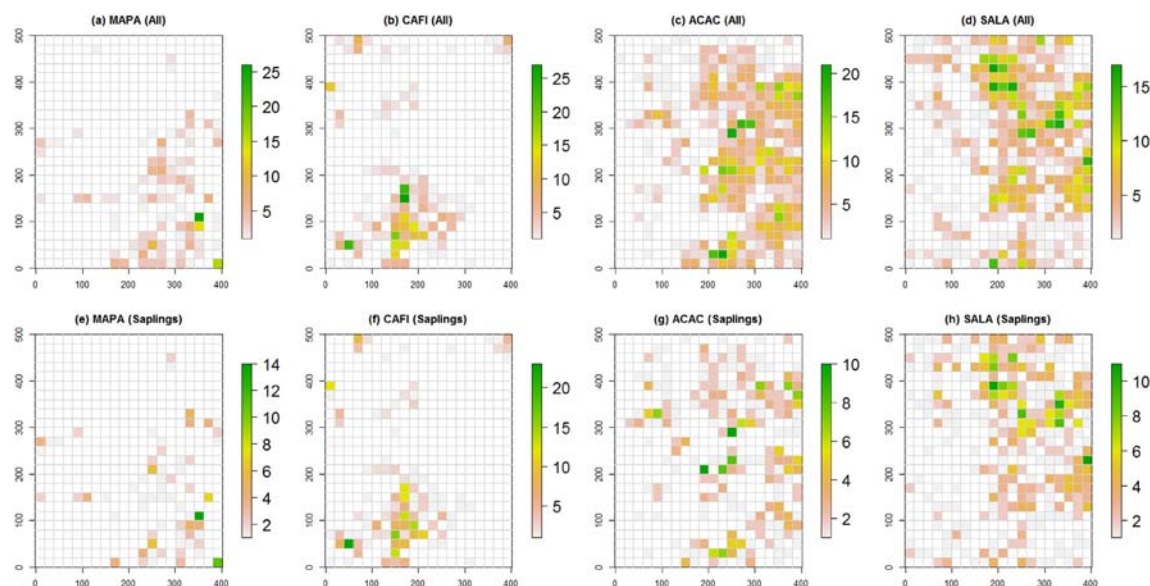


Fig. 3. Spatial distribution at the 20-m scale of species abundance for two light-demanding species (*Mallotus paniculatus* (MAPA) and *Castanopsis fissa* (CAFI)) and two shade-tolerant species (*Acmena acuminatissima* (ACAC) and *Sarcosperma laurinum* (SALA)). Patterns for all individuals (a–d) and saplings (e–h) are shown here.

for both all living stems and saplings, but explained less for the evenness and stand basal area. Zhou et al. (2006) analyzed soil carbon dynamics from 1979 to 2003 in the same forest and found that old-growth forests accumulated atmospheric carbon at an unexpectedly high rate, but they did not give a clear explanation for the potential mechanisms and possible consequences for biodiversity and ecosystem functioning. The relationships we found between soil organic carbon and biodiversity and stand basal area give some insight to this question.

4.3. Species-specific responses to their environment

The results of the species-specific analyses of abundance distributions support the hypothesis that different habitat requirements among species result in the coexistence of diverse species in one community (Levine and HilleRisLambers, 2009). The abundance distribution of the light-demanding species *M. paniculatus* (MAPA) was markedly affected by canopy closure when considering all stems and only saplings, supporting traditional gap dynamics theory (Oliver and Larson, 1996). In contrast, shade-tolerant species had only weak relationships with canopy variables. Species-specific responses to topography and edaphic variables found in this study have been documented previously (e.g., Li et al., 2009; Lin et al., 2013; Wang et al., 2009). By combining drone-derived variables with other biotic and abiotic variables, future studies

of all species across different tree life stages will provide important evidence for how and why species respond to their environment in different ways.

4.4. Drone ecology and long-term ecosystem monitoring

We demonstrate an example of how drone-derived variables can contribute to our understanding of biodiversity maintenance and species coexistence for a diverse subtropical forest plot. Clearly, drones hold great potential for providing advancements in mapping and monitoring of forest dynamics. Compared with satellite and airborne remote sensing techniques, drones collect the data with ultra-high spatial resolution (e.g., nearly 5 cm in our study) in a cost-effective manner, which can be used to measure some key stand attributes that have been demonstrated by a few recent drone studies in forest ecosystems (Getzin et al., 2012; Dandois and Ellis, 2013; Puliti et al., 2015; Zahawi et al., 2015; this study). Our analyses also showed that the drone imagery of our study plot matched very well with ground reference points, with the precision of 32–44 cm horizontal RMSE and 69 cm vertical RMSE. High accuracy between drone imagery and ground data was also reported in boreal (Puliti et al., 2015) and temperate forests (Getzin et al., 2012; Dandois and Ellis, 2013). The mismatch between most remote sensing data sources and ground inventory data has

Table 4
Pearson correlation coefficients of four selected species' abundances and drone-derived canopy measures, terrain variables, and edaphic variables, after accounting for spatial autocorrelation. CAFI (*Castanopsis fissa*; Fagaceae) and MAPA (*Mallotus paniculatus*; Euphorbiaceae) are light-demanding species, while ACAC (*Acmena acuminatissima*; Myrtaceae) and SALA (*Sarcosperma laurinum*; Sapotaceae) are shade-tolerant species. The results that are statistically significant are typed in bold. *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$. Other symbols and explanations are as in Table 1.

	All stems				Saplings			
	CAFI	MAPA	ACAC	SALA	CAFI	MAPA	ACAC	SALA
ht_canopy	−0.105	−0.077	−0.138	−0.110	−0.086	0.009	−0.026	−0.021
ht_sd	−0.047	0.187	0.270	0.098	−0.048	0.192*	0.127	0.041
ht_skewness	0.063	0.241*	0.244	0.043	0.045	0.152	0.088	−0.013
Closure	−0.065	−0.358**	−0.399*	−0.151	−0.033	−0.225*	−0.153	−0.016
elev	0.387*	−0.060	−0.296	−0.310	0.394*	−0.062	−0.184	−0.293
conv	0.226**	−0.095	−0.162*	−0.055	0.203**	−0.071	−0.084	0.005
slope	0.193	0.206	0.286	0.084	0.169	0.114	0.157	0.012
SOC	0.206	0.268	0.329	0.113	0.171	0.168	0.169	0.029
AK	−0.099	0.183	0.277	0.246	−0.096	0.138	0.135	0.205
TK	−0.091	0.408**	0.474*	0.167	−0.105	0.304**	0.222	0.069
TP	−0.104	−0.237	−0.362	−0.121	−0.086	−0.179	−0.186	−0.042

Table 5

Spatial simultaneous autoregressive models of response variables (the abundance of each of four selected species) against combinations of predictor variables. *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$. Other symbols and explanations are in Tables 3 and 4.

Groups	Variables	CAFI		MAPA		ACAC		SALA	
		Coef	w	Coef	w	Coef	w	Coef	w
All stems	ht_canopy		0.304	0.260***	0.950		0.381		0.425
	ht_sd		0.281	−0.233**	0.950		0.334		0.296
	ht_skewness		0.282	−0.094	0.592		0.275	−0.074	0.642
	Closure	−0.098	0.550	−0.475***	0.999		0.337		0.301
	elev	0.390***	0.988		0.412	−0.274**	0.937	−0.348**	0.954
	conv	0.106*	0.760		0.386		0.480		0.284
	slope		0.321		0.296	0.096*	0.744		0.316
	SOC		0.554		0.326		0.382	0.193	0.566
	AK		0.438		0.287		0.338	0.136	0.656
	TK		0.430	0.305***	1.000	0.273**	0.871		0.348
	TP		0.282		0.308	−0.185*	0.693		0.435
	Pseudo r^2	0.334		0.192		0.490		0.493	
Saplings (1 cm ≤ DBH < 5 cm)	ht_canopy		0.299	0.119*	0.691		0.287		0.284
	ht_sd		0.310		0.362		0.296		0.301
	ht_skewness		0.274		0.321		0.298	−0.070	0.565
	Closure		0.367	−0.152*	0.703		0.293		0.349
	elev	0.384***	0.995		0.363	−0.211**	0.857	−0.383***	0.952
	conv	0.075	0.570		0.300	−0.069	0.527		0.286
	slope		0.298		0.295		0.447		0.311
	SOC		0.437		0.375		0.443	0.251*	0.548
	AK		0.338		0.271		0.298	0.152	0.648
	TK		0.362	0.229***	0.998		0.365	−0.234	0.532
	TP		0.277		0.284	−0.196*	0.580		0.395
	Pseudo r^2	0.315		0.109		0.225		0.384	

been documented and much debated in recent years (Kerr and Ostrovsky, 2003; Turner et al., 2003). For example, the debates on the accuracy of biomass estimation in Amazon forests (Mitchard et al., 2014; Saatchi et al., 2015) and the quality of global forest cover change maps (Hansen et al., 2013; Tropek et al., 2014). Considering their high accuracy, drone surveys provide an effective solution for this issue at local or regional scales.

Although our research has shown several applications of drone technology, there are an increasing number of potential ecological applications that we have not discussed (Koh and Wich, 2012; Floreano and Wood, 2015). Here we list several potential applications, especially for use in long-term monitoring networks. First, drones can be used to monitor long-term ecosystem dynamics. Long-term ecological studies are critical for understanding how biodiversity and ecosystem function responds to natural and anthropogenic disturbances (e.g., Condit et al., 2006; Hubbell et al., 1999; Zhang et al., 2015). Similar with several other pioneering studies (e.g., Getzin et al., 2012; Zahawi et al., 2015), our study had only a one-time snapshot of the forest canopy structure. With increases in time of drone-derived variables, we will be able to quantify how different ecosystems evolve under the changes in climate and land use (Whitehead et al., 2014). Second, using drones to collect multispectral and hyperspectral images will provide a biophysical and biochemical approach for mapping ecosystems. These images can provide detailed information on plant chemical and structural properties, such as canopy water content and leaf nitrogen concentration (Asner et al., 2015; Malenovsky et al., 2015) and Normalized Difference Vegetation Index (NDVI) (Zarco-Tejada et al., 2013). These data can be used for single individual tree detection, phenology monitoring, biomass mapping and so on (Whitehead and Hugenholtz, 2014).

Our use of drones in this study identified several caveats and practical challenges that need to be considered for further studies. First, terrain data collected from the field may not spatially match the digital surface model (DSM) generated from the drone. Following the standard protocols of the CTFS-ForestGEO network (Condit, 1998), nearly all of over 60 plots had topographic variables measured at the 20-m scale. Some errors of this approach exist, especially for the plots with large ranges of topography. Although we selected 9 ground control points to geocorrect the point cloud and the results showed high precision for these control points, the estimation of canopy height data was still

affected by the relatively coarse ground-based DEM data (4.28 m in RMSE when interpolating to 1-m scale). This concern has also been raised by recent drone studies in temperate deciduous forests (Dandois and Ellis, 2013) and tropical forests (Zahawi et al., 2015). Despite this limitation, our analyses at the 20-m scale were still robust to explain local-scale variations in biodiversity and other stand attributes. This spatial scale has been widely used for many studies in community ecology and forest management (e.g., Dandois and Ellis, 2013; Zahawi et al., 2015). We detected some inconsistencies when comparing spatial variations of drone-derived canopy variables at three spatial scales (Fig. 2), suggesting the importance of spatial scale in ecological studies (Levin, 1992). Further analyses at finer scales (even the individual level) could be used to address questions involving forest regeneration, phenology, and others, and therefore it is worthwhile to continue exploring when high-quality data on topographic and edaphic variables are available. To improve the quality of ground-based terrain data, one ongoing development is to mount light detection and ranging (LiDAR) systems onto drones (Lin et al., 2011; Wallace et al., 2012), but the cost of aerial LiDAR sensors for drones is currently very high and specific technical expertise for expensive processing softwares is required.

The second challenge is to accurately identify species and individuals using drones, especially in subtropical and tropical forests with high species richness and dense canopies. The application of hyperspectral remote sensing may provide insight into this problem (Asner et al., 2015). Third, although drones are becoming much easier to operate than other types of remote sensing equipment, training is needed for designing flight paths, operating drones, and image post-processing (Dandois and Ellis, 2013; Paneque-Gálvez et al., 2014). Previous experience on over 200 successful missions by our team members ensured our current achievement. Collaborations between ecologists and experts on remote sensing will advance the application of drones in ecology. Additionally, drones with high performance and flexibility, such as the equipment used here, can be costly, although it is cheaper than the cost of acquiring imagery from very high spatial resolution satellites (e.g., Quickbird, WorldView, IKONOS, and RapidEye) or piloted aircraft missions in most cases. Ongoing efforts to design inexpensive equipment (e.g., <http://conservationdrones.org>) and open-source computer vision software (e.g., <http://ecosynth.org>; <http://ardupilot.com>) will

advance the development of this field (Koh and Wich, 2012; Dandois and Ellis, 2013).

In conclusion, our research provides one of the first tests of how light-weight drones can be used for long-term ecological research programs. We believe that drone technology, as a complementary tool of traditional field surveys, offers the potential to collect a large volume of data with high spatiotemporal resolution and at low costs (Anderson and Gaston, 2013). Further, the combining drone-derived variables and detailed ground inventory data allows us to advance our understanding of key processes in complex ecosystems in a changing world.

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