RESEARCH ARTICLE

The influence of topographic variation on forest structure in two woody plant communities: A Remote Sensing approach

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Abstract

Aim of study: The study aimed to characterise variation in structural attributes of vegetation in relation to variations in topographic position using LIDAR data over landscapes.

Area of study: The study was conducted in open canopy eucalypt-dominated forest (Richmond Range National Park-RRNP) and closed canopy subtropical rainforest (Border Ranges National Park-BRNP) in north-eastern New South Wales, Australia.

Material and Methods: one metre resolution digital canopy height model (CHM) was extracted from the LIDAR data and used to estimate maximum overstorey height and crown area. LIDAR fractional cover representing the photosynthetic and non-photosynthetic component of canopy was calculated using LIDAR points aggregated into 50 m spatial bins. Potential solar insolation, Topographic Wetness Index (TWI), slope and the elevation were processed using LIDAR derived digital elevation models.

Main results: No relationship was found between maximum overstorey height and insolation gradient in the BRNP. Maximum overstorey height decreased with increasing insolation in the RRNP (R^2 0.45). Maximum overstorey height increased with increasing TWI in the RRNP. Average crown area decreased with increasing insolation in both study areas. LIDAR fractional cover decreased with increasing insolation (R^2 0.54), and increased with increasing TWI (R^2 0.57) in the RRNP.

Research highlights: The characterization of structural parameters of vegetation in relation to the variation of the topography was possible in eucalyptus dominated open canopy forest. No reportable difference in variation of structural elements of vegetation was detected with topographic variation of subtropical rainforest.

Keywords: forest structure; remotely sensed data; LIDAR; topography; microclimate.

Conflicts of Interest: The authors declare no conflict of interest.

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Introduction

Topography has important influence on forest structure and composition. Variation in topography (slope angle, aspect, or elevation) creates resources heterogeneity across the landscape. Topography generally influences changes in soil depth and soil composition, in water content and soil drainage, and in light availability (Bale & Charley, 1994; Chen *et al.*, 1997; Bale *et al.*, 1998, Olivero & Hix, 1998; Galicia *et al.*, 1999; Tokuchi *et al.*, 1999). This patchy distribution of environmental resources often leads to complexity of forest structure and composition across a landscape. Understanding of forest structure over a landscape is required for sustainable management of forest landscapes for multiple purposes including the provision of wildlife habitats, timber production, and fire hazard reduction. Measurements of structural attributes of vegetation could be used to understand vegetation structure and as key indicators in monitoring long-term vegetation changes in an ecosystem. However, field based vegetation studies over large areas are rare due to limited resources and other difficulties inherent in collecting information on these scales. Therefore, traditional field sampling inevitably encompasses a very small fraction of the landscape, raising the question of how represen-

tative the resulting relationships are for the area not sampled. For example access may be challenging, especially in extensive rugged terrain, resulting in important areas of targeted vegetation being inadequately sampled. These factors are inherent in traditional field surveys, and contribute to the uncertainty of vegetation structure, species composition and richness estimates. Remote sensing technology has produced alternatives for investigating variation in forest structure beyond traditional field surveys of landscape. Remotely sensed data is commonly used to obtain quantitative information on biophysical characteristics of vegetation (Wu & Strahler, 1994). This technology may be used to generate a wide range of estimates that are valuable to ecologists including information on landcover, forest structure, habitat, and forest function (Kerr & Ostrovsky, 2003).

Among the remote sensing sensors, LIDAR has emerged as a robust means to collect and subsequently characterize vertically distributed objects (Wulder *et al.*, 2012). This has been shown to have potential for generating information that is equivalent to the field measurements for instance of tree height (Nilsson, 1996; Magnussen & Boudewyn, 1998; Popescu *et al.*, 2002; Holmgren *et al.*, 2003), foliage cover (Weller *et al.*, 2003; Armston *et al.*, 2009), and area of tree crowns (Popescu *et al.*, 2003) over much larger geographical areas that can be surveyed on the ground. Continuous technological advancements and intense competition among vendors has resulted in substantial reduction in the cost of acquiring LIDAR data (Gatziolis *et al.*, 2010), which provides an opportunity to actively integrate this technology in forestry (i.e. forest inventory, estimation of biophysical parameters of forest) and ecological studies (i.e. habitat mapping, characterization of plant communities and structure).

In regard to changing conditions of environmental gradients with topography in complex terrains, it can be assumed that such changes in vegetation structure caused by variation of topography could be discernible using remotely sensed data. The objective of our study was to characterise variation in structural attributes of forest including maximum overstorey height, average crown area, and density of photosynthetic and non-photosynthetic components of the canopy (LIDAR fractional cover) in relation to variations in topographic position using airborne discrete return LIDAR data over landscapes. The chosen forest structural parameters of present study represent vertical (maximum overstorey height), and horizontal (average crown area) as well as species richness (LIDAR fractional cover) of distributed vegetation over the landscape. Characterization of vegetation structure by potential insolation, topographic wetness index, and the slope and

elevation of terrain were used as proxies for energy, soil water distribution, and topographic variations respectively.

Material and methods

Study area

Two study areas were selected in north-eastern New South Wales (NSW), Australia (Figure 1) including the Richmond Range National Park (RRNP) (28.69º S, 152.72º E) and the Border Ranges National Park (BRNP) (28.36ºS, 152.86º E). The RRNP lies predominantly along the Cambridge Plateau which is north-south orientated along part of the Richmond Range. The elevation of RRNP study area ranges from approximately 150 to 750 m above mean sea level with an average slope of 27º. Annual rainfall is approximately 1200 mm and the average temperature ranges in the winter and summer are 12–21 and 25–31 ºC respectively (Bureau of Meteorology, 2010). The soils are fertile, being classified as Ferrosols and chocolate (Isbell, 1998) derived mainly from basalt. Other un-
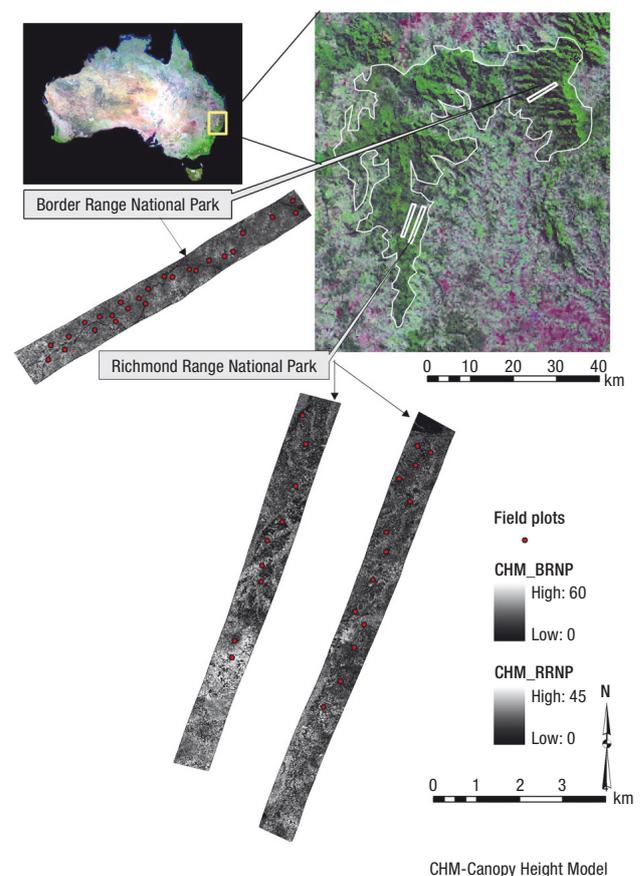

Figure 1. The Border Range National Park, the Richmond Range National Park study sites and LIDAR acquisition areas.

derlying major rock type in the RRNP region is Triassic sedimentary rocks (Stevens, 1977) and typically comprise sandstones, claystones, mudstones, and conglomerate which erode to form low-nutrient, free-draining soils. The RRNP is an open canopy eucalypt-dominated forest with 30–70% foliage projective cover (vertically projected percentage cover of photosynthetic foliage of all strata) (Specht & Specht, 1999). The most common species based on basal area dominance are found in the overstorey of the RRNP include *Corymbia maculata*, *Eucalyptus propinqua*, *Eucalyptus siderophloia,* and *Lophostemon confertus*. The understorey is mainly covered by native grass and shrub species.

The elevation of the BRNP study area ranges from approximately 600 to 1200 m above mean sea level with an average slope of 36º. Annual rainfall is approximately 3000 mm, and the average temperature ranges 3–19 ºC in the winter and 15–31ºC in the summer (Bureau of Meteorology, 2010). The topography of the BRNP varies from coastal floodplains to hilly ranges. The soils are fertile, being classified as kraznozems or Ferrosols (Isbell, 1998) derived mainly from tertiary basalt flows. The BRNP is a tall closed canopy subtropical rainforest with 70–100% foliage projective cover (Specht & Specht, 1999). The most common species based on proportional basal area are *Planchonella australis*, *Heritiera actinophylla*, *Sloanea woollsii, Geissois benthamiana* and *Syzygium crebrinerve* (Smith *et al.*, 2005). Both study areas are managed by the NSW Office of Environment and Heritage.

LIDAR data

LIDAR data were collected in July and August 2010 using a Leica ALS50-II LIDAR system at a flying height of 2000 m. The laser pulse repetition frequency was 109 kHz. The laser scanner was configured to record up to four returns per laser pulse. The average point spacing and point density were 1 m and 1.3 points per square meter respectively and the footprint diameter was 0.5 m. Average range varied between 524 m and 1018 m (mean 800 m) for the BRNP and 157 m and 460 m (mean 256 m) for the RRNP. Mean rates of penetration through the vegetation varied from 4.3% in the closed canopy of BRNP and 19% open canopy of RRNP. The LIDAR data were documented as 0.07 m for vertical accuracy and 0.17 m for horizontal accuracy by the data provider. The LIDAR data were classified into ground and non-ground points using Leica Xpro software by NSW Land and Property Information and were delivered in LAS 1.2 file format.

Data processing

All returns were considered for subsequent analysis for both study areas. Ground and non-ground returns were separated and a 1 m digital elevation model (DEM) was produced using ground returns via Kriging interpolation to the nearest 6 data points. For the LIDAR data analysis, non-commercial LIDAR processing code developed by Armston *et al.* (2009) in IDL 8.0 and ESRI Inc. ArcGIS 9.3 were employed.

Terrain Analysis and Remote Sensing Sampling Design

All LIDAR derived DEMs were Bicubic Spline resampled into 10 m x 10 m pixels resolution. LIDAR derived 10 m resolution DEMs were used as input for the area solar radiation analysis tool (ArcGIS Spatial Analyst Extension: ESRI Inc) to calculate total insolation (direct and diffuse) at monthly intervals for the whole year 2011 and were then averaged for a month period.

Topographic wetness index (TWI) is designed to model soil moisture determined by topography and its performance is related to the relief of study site. The TWI is defined as ln (a / tan β), where a is specific catchment area (the cumulative upslope area draining through a cell divided by contour width) and β is the local slope (Beven & Kirkby, 1979). The specific catchment area is a parameter describing the tendency of the site to receive water from upslope area and local slope is parameter describing the tendency to evacuate water. In order to calculate TWI, the multiple flow routing algorithm (Quinn *et al.*, 1991) was used as recommended by (Kopecky & Cizkova, 2010). Spatial Analyst: ESRI Inc was employed for TWI calculation of both study areas.

The insolation and TWI surfaces were stratified into low and high solar insolation, and two classes of TWI (low and high) were identified. A total of 150 sampling plots representing 75 plots for each study site were randomly and remotely selected using Hawth's Analysis Tools (version 3.27). In order to maintain the homogeneity of the topography (i.e. to select uniform slope angle and aspect) the area of a sample plot was restricted to 50 m x 50 m. Selected plots were located in two classes of solar insolation (low and high) and two classes of TWI (low and high). The insolation and TWI classification thresholds for BRNP and RRNP are summarised in Table 1. During the remote sensing based sampling plot selection, field knowledge and existing topographic maps were used to exclude plots which were located near roads, camping areas or other anthropogenic disturbance areas.

Derivation of Structural Variables of Forests using LIDAR

(a) Plot scale maximum overstorey height

The separated non-ground LIDAR point clouds were used to construct Canopy Surface Models (CSM) using natural neighbour interpolation at 1 m resolution. Potential CSM interpolation artefacts-a consequence of data gaps in the open-canopy RRNP study area were reduced by incorporating spatially selected ground points that fell closer to non-ground points than the nominal point spacing (1 m) to fill the gaps. Canopy Height Models (CHMs) were derived by subtracting the DEM from CSM. A 3 x 3 median filter was applied to the CHM to preserve edges while reducing the effect of inter-canopy variation (Popescu *et al*., 2003), which should enhance canopy-open-canopy discrimination. Maximum overstorey height was derived by subtracting of DEM height from the discrete non-ground data points. Two classes of solar insolation and two classes of TWI representing 50 m x 50 m sample plots were separated from CHMs.

(b) Plot scale average crown diameter

Tree crown diameter was measured on the LIDAR derived 1 m resolution CHM by automated processing using non-commercial TreeVaw 1.1 software (Popescu et al., 2003), with the algorithm described in (Popescu et al., 2003; Popescu, 2007). TreeVaw computes crown area based on a local maximum technique, which assumes that high laser values in a spatial neighbourhood represent the top of a tree crown. The derivation of the appropriate window size to search for tree tops is based on the developed relationship between the height of the trees and their crown area.   For each study area, measured height and crown data were used to derive an allometric relationship between tree height and crown areas. A 100 x 100 m plot demarcated in each study area and 85 and 70 trees per RRNP and BRNP were measured respectively. The developed allometric relationships showed excellent agreement between ground measured tree height and crown diameters (R2 values for the RRNP and the BRNP were 0.82 and 0.74 respectively) for both study areas.

(c) Plot scale LIDAR fractional cover

LIDAR fractional cover equals to the density of photosynthetic and non-photosynthetic component of canopy. LIDAR fractional cover is defined one minus the gap fraction probability at a zenith of zero (Lovell

et al., 2003) which corresponds to the photosynthetic and non-photosynthetic components of canopy. LIDAR fractional cover was calculated by aggregating all points into 50 m spatial bins using equation 1

$$1 - P_{gap} = \frac{C_v(z)}{C_v(0) + C_G} \qquad (1)$$

where $C_v(z)$ is the number of first returns counts above Z meters, $C_v(0)$ is the number of first returns above the ground and C_G was the number of first return points from the ground level. Z was set to 0.5 m for both study areas with the objective of reducing the impact of understorey and other ground objects.

Data analysis

Figure 2 shows a flowchart of the processing steps carried out in this study. The data of BRNP and RRNP study area were analysed separately within the General Linear Models (GLM). SPSS software (IBM SPSS Statistic version 20) was employed to establish how plot scale maximum overstorey height, crown diameter, and density of photosynthetic and non-photosynthetic component of canopy vary with TWI, potential insolation,
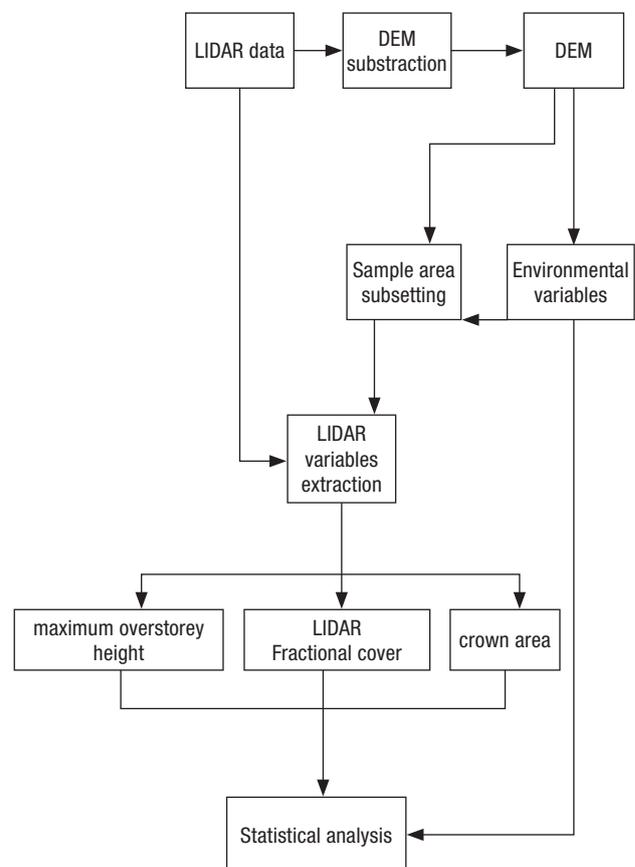

Figure 2. Flowchart of data processing and analysis.

Table 1. Classification of insolation and TWI classes in the BRNP and RRNP study areas

Study area	Insolation (MJ/m2/hour)	TWI	Plot type	Plot location
BRNP	3813-5283 (low)	> 5.5 (high)	BRNP-A	valley
	5283-5950 (high)	4.5-5.5 (low)	BRNP -B	upper slope
RRNP	4041-5283 (low)	> 5 (high)	RRNP-A	valley
	5283-6211 (high)	3-5 (low)	RRNP -B	upper slope

Note that, BRNP low insolation and high TWI (herein BRNP-A), BRNP high insolation and low TWI (herein BRNP-B), RRNP low insolation and high TWI (herein RRNP-A), RRNP high insolation and low TWI (herein RRNP-B), are used in the results and discussion.

Table 2. Results of GLM analysis on maximum overstorey height (m), Average crown area (m^2), and LIDAR fractional cover with abiotic factors (insolation, TWI, elevation, and slope of the terrain) of the BRNP subtropical rainforest. Degree of significance: **** $P<0.0001$, ***$P<0.001$, **$P<0.01$, *$P<0.05$

	Maximum overstorey height (m)			Average crown area (m^2)			LIDAR fractional cover		
	df	F	P	df	F	P	df	F	P
Elevation	1	26.36	****	1	0.35	ns	1	2.9	ns
TWI	1	1.80	ns	1	0.15	ns	1	2.2	ns
Insolation	1	0.14	ns	1	9.42	***	1	1.7	ns
Slope	1	2.22	ns	1	1.78	ns	1	0.9	ns

slope of the terrain, and elevation in different topographic locations. In this study TWI, potential insolation and others (i.e. slope of the terrain, and elevation) are being used as continuous covariates. Mean comparison of potential insolation, TWI, elevation, and slope of the terrain effect on maximum overstorey height, crown diameter, and LIDAR fractional cover were performed using Analysis of Variance (ANOVA) and type-I sums of squares where results were considered significant at P <0.05. In each case, residual plots were assessed to ensure that the models satisfied the standard GLM assumptions.

Results

Effect of Insolation, TWI and Topography on Forest Structure

A General Linear Model was employed to examine the forest structure-environment relationship by comparing structural attributes of vegetation; maximum overstorey height, average crown area, and LIDAR fractional cover in sample plots of both study areas. Low insolation and high TWI (BRNP-A and RRNP-A plot type) was observed in the selected sample plots of the valley area, whereas high insolation and low TWI (BRNP-B and RRNP-B plot type) were observed in the upper slopes in the BRNP and the RRNP study areas. Tables 2 and 3 show a statistical summary for the effect of insolation, TWI and other topographic variables on maximum overstorey height, average crown area, and LIDAR fractional cover in both study areas.

Maximum overstorey height reflects the influence of potential insolation and TWI along topographic gradients. The maximum overstorey height of both study areas was found to be the greatest in the sample plots with high TWI and low insolation. The maximum overstorey height decreased from plot type BRNP-A to BRNP-B, and varied between 50.8 m in BRNP-A plot type to 48.1 m on BRNP-B plot type in the BRNP while height ranged from 47.1 m in RRNP-A plot type to 42.4 m on RRNP-A plot type in the RRNP (Table 4). However, no relationship was found between maximum overstorey height and insolation gradient in the BRNP. In contrast, a negative trend (R^2 0.45) was shown between maximum overstorey height and insolation in the RRNP (Figure 3A). As would be expected in the BRNP, maximum overstorey height showed significant change with elevation. Regressions for this variable depicted a decreasing trend with increases in elevation from 400 m to 1200 m amsl (Figure 4A). In addition Table 2 and Figure 3B show that maximum overstorey height increased with increasing TWI in the RRNP study area.

In general, it is expected that taller trees have a larger crown area, thus, average crown area can vary with the average height of trees. The greatest average crown areas were recorded in   BRNP- A (44.8 m^2) and RRNP-A (36.3 m^2) sampling plots. In this study, average crown area decreased with an increase in insolation in both study areas (see Figures 3 C and 4 B). How-
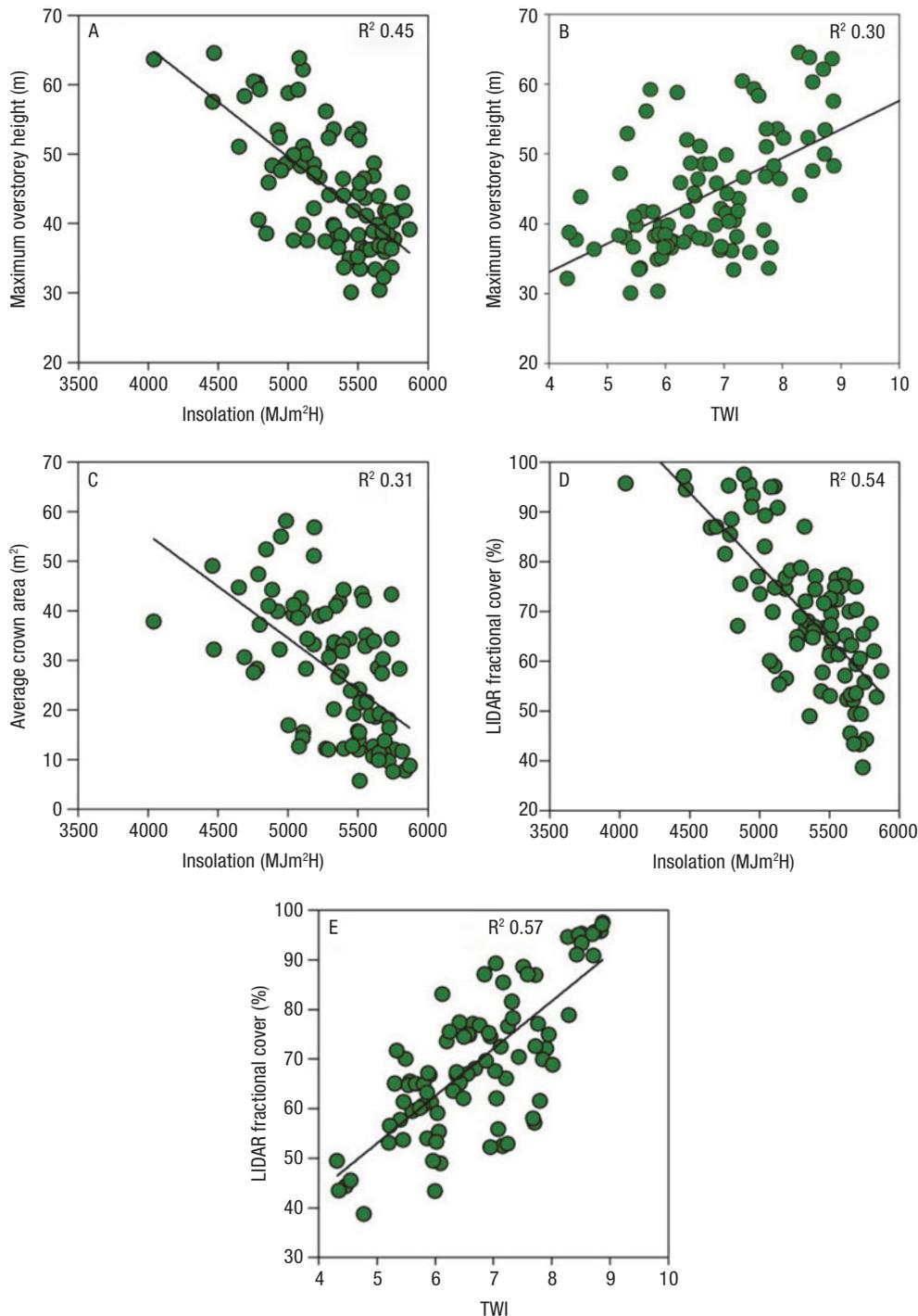
Figure 3. Open-canopy forest RRNP study area regressions depicting (A) maximum overstorey height vs insolation (B) maximum overstorey height vs TWI (C) average crown area vs insolation; (D) LIDAR fractional cover vs insolation and (E) LIDAR fractional cover vs TWI.

ever, the average crown area of both plant communities did not show a clear relationship with TWI, which is a surrogate for variation in soil water accumulation.

Estimates of LIDAR fractional cover of sample plots characterized vertical and horizontal distribution of density of photosynthetic and non-photosynthetic overstorey components across the landscape. No significant trends were shown for LIDAR fractional cover with insolation or TWI in the BRNP (Table 2). Significant trends were shown (Table 3) with insolation and TWI for LIDAR fractional cover in the RRNP. Interestingly, LIDAR fractional cover decreased with increased insolation, and increased with increasing TWI (Figure 3 D and E). The differences in LIDAR fractional cover

Table 3. Results of GLM analysis on maximum overstorey height (m), Average crown area (m²), and LIDAR fractional cover with abiotic factors (insolation, TWI, elevation, and slope of the terrain) of eucalypt dominated open-canopy RRNP. Degree of significance: **** P<0.0001, ***P<0.001, **P<0.01, *P<0.05

	Maximum overstorey height (m)			Average crown area (m²)			LIDAR fractional cover		
	df	F	P	df	F	P	df	F	P
Elevation	1	1.73	ns	1	1.66	ns	1	3.4	ns
TWI	1	9.79	****	1	1.40	ns	1	44	****
Insolation	1	78.75	****	1	39.9	****	1	46.6	****
Slope	1	0.69	ns	1	1.36	ns	1	0.02	ns

Table 4. Comparisons of the various measures of DEM derived potential insolation and TWI in sample plots across topographic positions. Plot means, standard error and for a given mean sharing the same letter are not significantly different at (P<0.05)

Plot type	Average maximum overstorey height (m)	Average crown area (m2)	LIDAR fractional cover
BRNP			
BRNP-A	50.8±1.2a	44.8±2a	96.5±0.4a
BRNP-B	48.1± 0.8a	38.8±0.9b	95.3±0.6a
RRNP			
RRNP-A	47.1±1.2a	36.3±1.5a	75.1±1.9a
RRNP-B	42.4±1.3b	18.5±1.6b	69.4±1.5b

which were shown across TWI gradient could be related to changes in underlying soil water content.

In conclusion, the maximum overstorey height estimated from LIDAR for the RRNP study showed significant trends with variation in DEM derived potential insolation and with TWI (Table 2). The greatest maximum overstorey heights were observed in low sunlight and wet (i.e. high TWI), compared to high sunlight and dry (low TWI). In contrast, maximum overstorey heights of the BRNP did not show significant trends with changing insolation and TWI, however, maximum overstorey heights of the BRNP varied with elevation. Average crown areas varied with intensity of insolation and no trends were observed with TWI in both plant communities. Variation of LIDAR fractional cover showed good correlations with insolation and TWI in the RRNP, however, there was no significant trend observed for LIDAR fractional cover in relation to insolation and TWI in the BRNP.

Discussion

Studying relationships between vegetation structure-environment

This study investigated the variation in structural attributes of forest: maximum overstorey height, average crown area, and density of photosynthetic and non-photosynthetic components of the canopy in relation to variations in topographic position using airborne discrete return LIDAR data over landscapes. Low insolation and high TWI (both BRNP-A and RRNP-A plot types) was observed in the selected sample plots of the valley area, whereas high insolation and low TWI (both BRNP-B and RRNP-B plot types) were observed in the upper slopes in the BRNP and the RRNP study areas.

The maximum overstorey height of canopy trees at plot scale trended downward with an increase in insolation in the open-canopy eucalypts forest in the RRNP study area. This is likely to be the variation of incoming surface solar radiation which in turn determines the dynamics of many landscape processes, such as surface heating, moistening evapotranspiration, and photosynthesis (Specht & Specht, 1999; Chen *et al.*, 2006), which in turn indirectly determines plant growth in forest structure across radiation gradient (Tanner, 1980a; Tanner, 1980b; Takyu *et al.*, 2002). The maximum overstorey height of the RRNP study area was found to be the greatest in the valley sample plots with high TWI. This finding is consistent with Ashton & Hall (1992) and Aiba & Kitayama (1999), who demonstrated changes in canopy height in response to water availability; in general, the forest canopy height is lower in dry than in wet environments. The maximum
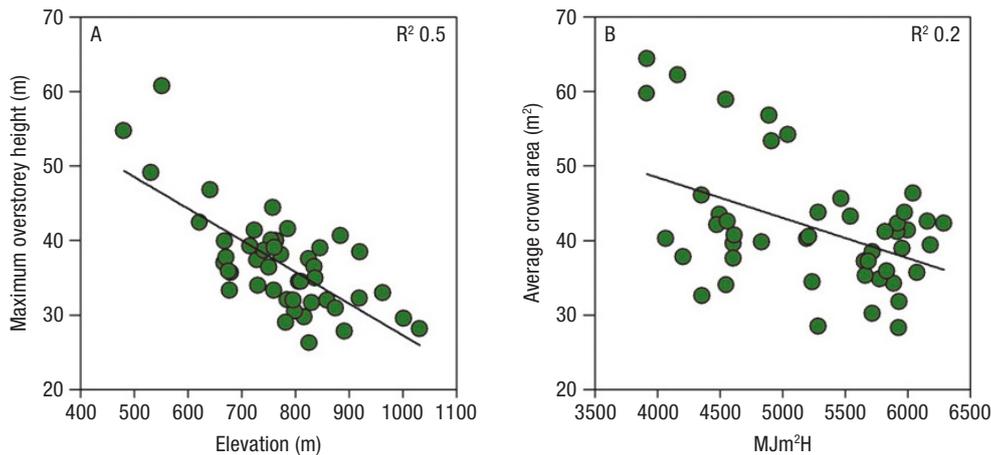
Figure 4. Closed-canopy BRNP study area regressions depicting (A) maximum overstorey height against elevation and (B) average crown area against insolation.

overstorey height decreased with increased elevation in the BRNP as is reported by many studies that have measured forest structure across elevation gradients elsewhere (Weaver & Murphy, 1990; Singh *et al.*, 1994; Kitayama & Aiba, 2002; Ediriweera *et al.*, 2008). Due to dramatic changes in the processes causing hillslope erosion especially in areas such as the BRNP (high rainfall compared to the RRNP), soil and soil nutrients tend to accumulate to considerable depths in valleys, which have contributed to the spatial distribution of the nutrient pool and subsequently changes in vegetation structure. Additionally, slow growth of high elevation forests may be influenced by cool temperatures, with persistent cloud cover and fog, and exposure to wind (Bruijnzeel & Veneklaas 1998; Bellingham & Tanner 2000) and shallow soil. No difference in variation of maximum overstorey height was detected with potential insolation in the BRNP. This indicates the variation in insolation in relation to the topography probably does not have a marked influence on tree height of subtropical rainforest compared to the eucalypt dominated open- canopy.

LIDAR fractional cover corresponds to the foliage and non-foliage components of the canopy, which decreased with increased insolation in the RRNP. The greatest LIDAR fractional cover was recorded in valleys and was approximately 75%. This suggests that as potential insolation increases across the landscape, evapotranspiration will increase, thus it can be expected the density of the foliage of the overstorey will decrease (Specht & Specht, 1999; Ackerly *et al.*, 2002). Similarly, in the present study, TWI increased at lower topography where there is a high potential for water accumulation, in turn the greatest value of LIDAR fractional cover was observed in sample plots in gullies in the RRNP. This suggests that the variation in density of foliage and other non-photosynthetic compo-

nents as captured by LIDAR fractional cover in the open-canopy RRNP study area was caused by insolation and soil water gradients. Since solar radiation and the slope are directly related to water availability in plant communities and soil properties, there may consequently be a noticeable variation of structure and composition among plant communities (Specht, 1988). However, neither insolation nor TWI showed a significant trend with LIDAR fractional cover in the closed-canopy BRNP study area.

In this study, eucalypt trees with the largest crowns were found in gullies, as opposed to the upper slopes or ridges of the RRNP and BRNP. The spatial variation in LIDAR estimated crown area is influenced by the local landscape topography, hydrology, soil type and potential insolation. Additionally a weak relationship was observed between average crown area with insolation in the closed-canopy BRNP study area. A similar trend for the variation in tree crowns has been reported through field investigation in dipterocarp dominated tropical rainforest in Sri Lanka (Ashton, 1992; Ediriweera *et al.*, 2008). In this study the greatest maximum overstorey height was observed on lower slopes in both study areas and thus the variation of crown area appear be related to decrease in tree stature. The weak correlation for crown area with insolation in BRNP is likely a failure to accurately delineate the tree crowns due to the complexity of the irregular shaped overlapped tree crowns, and the spatial organization of tree crowns within the canopy.

Overall, the subtropical rainforest of the BRNP study area did not display strong regional gradients, and these were not affected by TWI and mean insolation. Presumably, potential insolation or TWI was not able to describe the variation in forest structure in the hilly subtropical rainforests compared to the open-canopy eucalypt forests. This indicates that forest structure of subtropical rainforest of the BRNP can be expected to

vary with other environmental variable perhaps geology. Conversely, due to the density and complexity of the spatial organization of the canopy of the BRNP which could be affected the accuracy of structural elements of vegetation derived from small footprint LIDAR. This may have a significant impact on the derived relationships between vegetation structure and environmental, topographic variables of the BRNP. Other most striking outcomes of the study are the greater variations of vegetation structure in relation to the environmental (TWI and insolation) and topographic variables which were discerned in the open-canopy eucalypt plant community. This suggests the characterisation of forest structure in relation to topography using remotely sensed data is determined by the strength of the correlation of vegetation with topographic and environmental variations.

A long history of intensive silvicultural practice (i.e. site preparation, brush control and fertilization treatments) impacts on vegetation structure and composition (Fu et al., 2007). Both our study sites are located in two National Parks thus no significant management practices are carried out. Webb et al. (1972) described that BRNP was true "virgin" forest, in that aboriginal people in the area did not practice agriculture perse or systematic tree felling. They also believed that fires had not taken place in these rainforests, so that the main disturbances would come from individual tree falls, wind and cyclones.

Overall Assessment of the Methodology

This study using remote sensing technology assessed how complex terrain, soil water availability, solar insolation, and topographic variables influence the relationship with vegetation structure of two structurally different plant communities. Finding of this study confirms the potential to discern, to some extent, the vegetation structure-environmental relationship at a landscape scale. However, the method indicates important practical and technical consequences related to the assessment of forest structure with environmental and topographic variables over extensive areas.

Firstly, identifying a suitable resolution for the DEM was challenging as it can affect the accuracy of the computed topographic indices. This issue has explained other several studies (Zhang & Montgomery 1994; Hancock 2005; Sørensen & Seibert 2007). Secondly, this investigation was an extreme application of LiDAR technology on structurally complex subtropical rainforest in highly topographically complex environments with steep slopes and gullies, compared to applications in open canopy vegetation in similar topography. For instance

Ediriweera (2013); Ediriweera et al. (2014) showed a low level of accuracy in estimation of mean and dominant canopy height (i.e. Adj. R^2 0.40 and 0.61 for mean and dominant height respectively) using LIDAR metrics in the same study area. In contrast, the estimation of dominant and mean canopy height from LIDAR data achieved a high level of accuracy (error <3%) and explained over 80% of total variation in dominant height for open canopy eucalypts forest of the RRNP. As the complexity of a canopy structure increases, the probability that LIDAR pulse penetrates below the canopy decreases and leads to occlusion of middle and understorey strata. Furthermore, with increased topographic variation, the variability in laser pulse ranges tends to increase. This may be due to the relatively large footprint differing from one plot to another (Nilsson, 1996).

Conclusions

The key finding of this study revealed that if environmental variables show higher level of gradients with variation of topography in the landscape, such variations could be discernible through structural and compositional variation of the plant community. The potential applications for this adopted method include interpretation of ecological variation and gradients within a landscape based context, understanding responses to climate change, monitoring the vigour of vegetation using quantitative assessment, and incorporation of structural assessment for biodiversity related studies. Pattern analysis in landscape ecology is one of the fundamental requirements of landscape ecology, and the methods described here offer statistically significant, quantifiable and repeatable means to realise that goal at a fine spatial scale.

Acknowledgements

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