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RESEARCH ARTICLE

Landscape-scale drivers of liana load across a Southeast Asian forest canopy differ to the Neotropics

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Abstract

1. Lianas (woody vines) are a key component of tropical forests, known to reduce forest carbon storage and sequestration and to be increasing in abundance. Analysing how and why lianas are distributed in forest canopies at landscape scales will help us determine the mechanisms driving changes in lianas over time. This will improve our understanding of liana ecology and projections of tropical forest carbon storage now and into the future. Despite competing hypotheses on the mechanisms driving spatial patterning of lianas, few studies have integrated multiple tree-level biotic and abiotic factors in an analytical framework. None have done so in the Palaeotropics, which are biogeographically and evolutionarily distinct from the Neotropics, where most research on lianas has been conducted.
2. We used an unoccupied aerial system (UAS; drone) to assess liana load in 50-ha of Palaeotropical forest canopy in Southeast Asia. We obtained data on hypothesised drivers of liana spatial distribution in the forest canopy, including disturbance, tree characteristics, soil chemistry and topography, from the UAS, from airborne LiDAR and from ground surveys. We integrated these in a comprehensive analytical framework to extract variables at an individual-tree level and evaluated the relative strengths of the hypothesised drivers and their ability to predict liana distributions through boosted regression tree (BRT) modelling.
3. Tree height and distance to canopy gaps were the two most important predictors of liana load, with relative contribution values in BRT models of 34.60%–45.39% and 7.93%–10.19%, respectively. Our results suggest that taller trees were less often and less heavily infested by lianas than shorter trees, opposite to

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Neotropical findings. Lianas also occurred more often, and to a greater extent, in tree crowns close to canopy gaps and to neighbouring trees with lianas in their crown.

4. *Synthesis*. Despite their known importance and prevalence in tropical forests, lianas are not well understood, particularly in the Palaeotropics. Examining 2428 trees across 50-ha of Palaeotropical forest canopy in Southeast Asia, we find support for the hypothesis that canopy gaps promote liana infestation. However, we also found that liana presence and load declined with tree height, which is opposite to well-established Neotropical findings. This suggests a fundamental difference between Neotropical and Southeast Asian forests. Considering that most liana literature has focused on the Neotropics, this highlights the need for additional studies in other biogeographic regions to clarify potential differences and enable us to better understand liana impacts on tropical forest ecology, carbon storage and sequestration.

KEYWORDS
boosted regression trees, drone, gap ecology, liana ecology, remote sensing, tropical forest canopy science, UAV, unmanned aerial vehicle

1 | INTRODUCTION

One of the central goals in ecology is to determine the mechanisms responsible for the abundance and distribution of organisms (Brown, 1984; Krebs, 1972), but most studies testing ecological theory in tropical forests focus on trees. Lianas (woody vines) are a key component of tropical forests, where they peak in their abundance, biomass, richness and species diversity (Gentry, 1991; Schnitzer & Bongers, 2002). Lianas affect many ecological processes, including carbon cycling and storage in tropical forests (van der Heijden et al., 2015). Lianas are prevalent in the forest canopy, where they are commonly found in ~50% of tree crowns (e.g. Ingwell et al., 2010; Wright et al., 2015), as they use the structural investment of trees to deploy leaves in the forest canopy. By quantifying the distribution of lianas in the forest canopy at a landscape scale and developing our understanding of the mechanisms driving this, we may enhance our knowledge of liana ecology, provide a step towards more comprehensive testing of ecological theory in tropical forests and further our understanding of the impact of lianas on tropical forest carbon cycling.

Lianas can reduce tropical forest net carbon uptake (van der Heijden et al., 2015) via above- and below-ground liana–tree competition for resources such as essential nutrients, water and light, which can be more intense than tree–tree competition (Álvarez-Cansino et al., 2015; Tobin et al., 2012). Lianas can thereby reduce tree growth (Ingwell et al., 2010; Schnitzer et al., 2014; van der Heijden & Phillips, 2009; Venegas-González et al., 2020), fecundity (García León et al., 2018; Kainer et al., 2006; Nabe-Nielsen et al., 2009) and survival (Ingwell et al., 2010; Phillips et al., 2005), which constrains net above-ground productivity and biomass of woody tissue in tropical forests (Durán & Gianoli, 2013; van der Heijden et al., 2015). Moreover, by relying on the structural investments of trees to deploy leaves in the forest canopy, lianas invest fewer resources in the formation of carbon-dense stems and relatively more into developing an extensive leaf canopy (Rodríguez-Ronderos et al., 2016; Schnitzer et al., 2014; van der Heijden et al., 2013), thus failing to compensate for the biomass that they displace in trees (Schnitzer et al., 2014; van der Heijden et al., 2015, 2019; van der Heijden & Phillips, 2009).

Lianas are increasing in abundance, richness and biomass in tropical forests (Phillips et al., 2002; Schnitzer et al., 2021; Schnitzer & Bongers, 2011) – at least, this is what studies in Neotropical forests show, where the vast majority of liana research has been done. Increases in lianas may lead to changes in the functioning of forest ecosystems (Schnitzer et al., 2000; Schnitzer & Carson, 2010; van der Heijden et al., 2013), and further reduction of forest carbon stocks and sequestration (van der Heijden et al., 2015). Thus, lianas may have broad and important ramifications both for the global carbon cycle and rate of climate change and may be partly responsible for the observed decline in the carbon sink function of tropical forests (Brienen et al., 2015). As the ability of tropical forests to sequester carbon is important for mitigating climate change, and the increasing pressures upon tropical forests reduce their ability to do so (Lewis et al., 2015; Mitchard, 2018; Nakamura et al., 2017; Qie et al., 2017), we need to better understand these particularly carbon-rich tropical forest systems. It is, therefore, important to understand the distributions of lianas, and to determine what mechanisms may drive increases in lianas in the future.

Existing plot-scale studies (mostly in the Neotropics), show that lianas have highly clumped distributions, both at local scales (≤0.1-ha plot size, e.g. Putz, 1983, 1984a; Pérez-Salicrup et al., 2001) and (in the few studies conducted at) landscape scales (up to 50-ha plot size, e.g. Dalling et al., 2012; Ledo & Schnitzer, 2014; Marvin et al., 2016; Schnitzer et al., 2012). These non-random patterns presumably reflect underlying mechanisms driving liana distributions (Marshall et al., 2020; Putz, 1984b). Within-forest liana distributions may be strongly influenced by canopy gaps (Dalling et al., 2012; Ledo & Schnitzer, 2014; Schnitzer, 2005; Schnitzer & Carson, 2001; Schnitzer et al., 2012, 2021). Specifically, liana diversity and abundance, both in absolute terms and relative to trees, are thought to increase with the presence and size of canopy gaps (Babweteera et al., 2000; Hegarty & Caballe, 1991; Putz, 1984a). Lianas can capitalise on these disturbed areas as they are able to: (i) recruit into them early, and in large numbers, through a variety of methods, including clonal reproduction (Appanah & Putz, 1984; Rutishauser, 2011; Schnitzer et al., 2012; Yorke et al., 2013); and then (ii) grow rapidly in the high-resource environment (Schnitzer & Bongers, 2011). Indeed, lianas can maintain gaps in stalled regeneration for long periods of time (Schnitzer et al., 2000; Schnitzer & Carson, 2001), so higher liana loads may be expected in canopy gaps of lower vegetation height. Previous studies have also indicated that other biotic and abiotic factors may be important for shaping liana distributions. For example, lianas may be more abundant, have higher species richness and/or higher growth rates: (i) in areas with shallower slopes compared to those with steeper slopes (Addo-Fordjour et al., 2014; Dalling et al., 2012); (ii) in more fertile soils (Lai et al., 2017); and (iii) when close to other liana-infested trees (van der Heijden et al., 2008).

While previous studies have provided useful information on relationships between liana abundance and richness and these biotic and abiotic variables, our knowledge remains far from complete. We lack information on the influence and interaction of the multiple hypothesised influences on liana distributions at the landscape scale, particularly in tropical forest tree crowns. This is partly due to reliance on ground-based data collection, including liana stem measurements, as opposed to canopy occupancy, which can be difficult to assess from the ground (Marvin et al., 2016; van der Heijden et al., 2022; Waite et al., 2019). Liana canopy occupancy may be more directly related to liana–tree competition, however, as lianas deploy most of their leaves above those of their host trees (Avalos & Mulkey, 1999; Rodríguez-Ronderos et al., 2016), directly reducing the amount of light received and the photosynthetic capacity of their host trees (Avalos et al., 1999; Avalos & Mulkey, 1999; Fauset et al., 2017).

Uncertainties about the global implications of lianas for tropical forest ecology and on the global carbon cycle are exacerbated by the bias in existing liana research towards Neotropical forests (Marshall et al., 2020). Before we can generalise any trends from the work conducted in the Neotropics to estimates of the impact of lianas on global carbon dynamics, we first need to determine the transferability of the findings from the Neotropics to other regions. More research in other regions is essential for this. The forests of the Palaeotropics, and especially those of Southeast Asia, have received very little attention in this regard. Southeast Asian liana studies are particularly important, however, as these forests tend to have significantly higher above-ground biomass (Asia: 393.3 mean ± 109.3 SD Mg ha^{-1}) than Neotropical forests (287.8 mean ± 105.0 SD Mg ha^{-1}) due to the increased density of large trees (≥70 cm DBH; Slik et al., 2013). Furthermore, the forests of Southeast Asia have particularly high above-ground wood production; up to 0.43 Mg C ha^{-1} per year (Qie et al., 2017), approximately 50% greater than in Amazonia (Banin et al., 2014).

Determinants of liana load and spatial distribution in Southeast Asian forests may be expected to differ from their Neotropical counterparts due to the different biogeographical history of the regions and the ecological and structural differences between them. For example, unlike Neotropical forests, Southeast Asian forests are characterised by a greater prevalence of rattans, higher forest canopies and a dominance of dipterocarp species (Corlett & Primack, 2006, 2011). Rattan proliferation may occur at the expense of other lianas due to their ability to span larger inter-support gaps (Campbell et al., 2017), while a higher forest canopy with greater vertical separation may limit the ability of lianas to span adjacent tree crowns. Indeed, some suggestions of disparities are beginning to emerge between Neotropical and Southeast Asian forests. For example, research in the Neotropics has found that lianas infest larger trees more often, and to greater extents, than smaller trees (e.g. Pérez-Salicrup et al., 2001). However, Wright et al. (2015) found that dipterocarps, which tend to be the emergent trees in Southeast Asian forests, exhibited low liana loads in the Pasoh Forest Reserve, Malaysia. Thus, ecological and structural variation between and within Neotropical and Palaeotropics forests, including species composition, tree height and vertical crown separation, resulting from their distinct biogeographic and evolutionary histories, may fundamentally affect liana distributions. Studies are urgently needed to assess whether drivers of liana distributions are similar in both the Neo- and Palaeotropics (Marshall et al., 2017).

Here we present continuous landscape-level liana distribution data for 50-ha of Palaeotropical forest canopy in Danum Valley, Sabah, Malaysia. We use an unoccupied aerial vehicle equipped with remote sensing equipment (unoccupied aerial system; UAS) to capture high-resolution RGB imagery of the canopy. From this, we produce continuous, reliable, accurate and reproducible data on tree-level liana load (Waite et al., 2019) as well as concurrently capture tree-level variables, such as tree height, crown area, distance to nearest canopy gap and distance to nearest neighbouring tree containing lianas. We integrate these data with ground-collected topographic and soil data, and airborne-collected LiDAR data, in a comprehensive analytical framework using boosted regression trees (BRTs) to examine and predict what determines liana occurrence and load in tree crowns. To our knowledge, this is the first study to analyse multiple tree-level biotic factors, alongside abiotic factors that may affect liana spatial distribution in the forest canopy at an individual tree level at the landscape scale. This enhances our knowledge of which areas of the forest are being impacted by lianas the most, why, and how this may alter in the future.

Our objectives were to: (i) quantify the degree of spatial aggregation of liana load; and (ii) evaluate the relative strengths of multiple hypothesised drivers of liana distribution, including disturbance, tree characteristics, soil and topography and their ability to predict liana distributions in the forest canopy. Based on the literature discussed above, we expected larger canopy gaps with lower vegetation heights, lower slope angles, more fertile soils and presence of liana infested neighbouring trees to increase the presence and degree of liana load. Furthermore, we expected an increase in liana load with tree size below the emergent canopy layer but lower liana load in the largest, emergent trees.

2 | MATERIALS AND METHODS

2.1 | Study site

This study was conducted at Danum Valley Conservation Area ('Danum'; 4°57′N, 117°42′E) in Sabah, Malaysia (Figure 1). Danum has hosted a field centre and collaborative research programme since 1986 (Marsh & Greer, 1992). Danum is characterised by ~43,800 ha of uninhabited lowland, evergreen dipterocarp forest (Whitmore, 1975). The forest canopy height can reach upwards of 70 m (Milodowski et al., 2021) and the forest is dominated by Euphorbiaceae and Dipterocarpaceae in the understorey and canopy, respectively (Newbery et al., 1992). The most abundant species in the forest include *Mallotus miquelianus*, *Leea aculeata* and *Mallotus wrayi* and species contributing most to forest-level basal area include *Shorea johorensis*, *Parashorea malaanonan* and *Shorea parvifolia*. This heterogeneous, primary forest provides a suitable site to study the factors driving patterns of liana load in primary Southeast Asian forests. Specifically, here we focus on the 50-ha plot that is part of the CTFS-ForestGEO network. This plot was designed to provide a baseline for on-going studies of forest regeneration, carbon dynamics and biodiversity in adjacent logged forest and forest fragmented by oil palm plantations. The research presented here contributes to this by establishing a baseline of liana load for canopy and emergent trees.

2.2 | Soil and topographic (surface) data collection

Soil and topography data were collected from 2009–2018 (soil sampling: October 2016, analyses late 2016–2018; topographic data collection: 2009–2011) in the 50-ha plot. The topographic data (elevation in m) were collected from 1326 sample points distributed in a regular 20 x 20 m grid across the 50-ha plot using a laser compass survey station and survey poles (cf. Condit, 1998). The sample points were interpolated using Inverse Distance Weighting to produce a raster of 2.71 m resolution. Soil samples were collected from a total of 300 sample points. These were distributed mainly in a regular 50 × 50 m grid across the 50-ha plot (200 points). Each alternate grid point was paired with an additional sample point at 2, 8 or 20 m away (100 points; 1/3 of points at each distance) in a random compass direction from the grid to capture variation in soil properties at finer scales (cf. John et al., 2007). Exchangeable cations were quantified by extraction in 0.1 M BaCl2 and detection by ICP-OES spectrometry. Effective cation exchange capacity (%) was determined as the charge equivalents of calcium (Ca), potassium (K), magnesium (Mg) and sodium (Na) divided by total exchangeable cations. Available phosphorus (P) was determined by extraction in Bray-1 solution, with detection by automated molybdate colorimetry. Extractable copper (Cu) was determined by Mehlich-III extraction and detection by IC P-OES spectrometry. The soil data were interpolated using Ordinary Kriging using the R package GSTAT to produce raster layers at 2.71 m resolution (Supporting Information S1 and S2).

2.3 | Unoccupied aerial system data collection and processing

A DJI Phantom 3 Advanced was used to acquire images of the forest canopy. This is a lightweight, agile, inexpensive, commercially available quadcopter UAS with an integrated three-waveband (RGB) Sony EXMOR 1/2.3″ 12-megapixel camera. All flights took place between

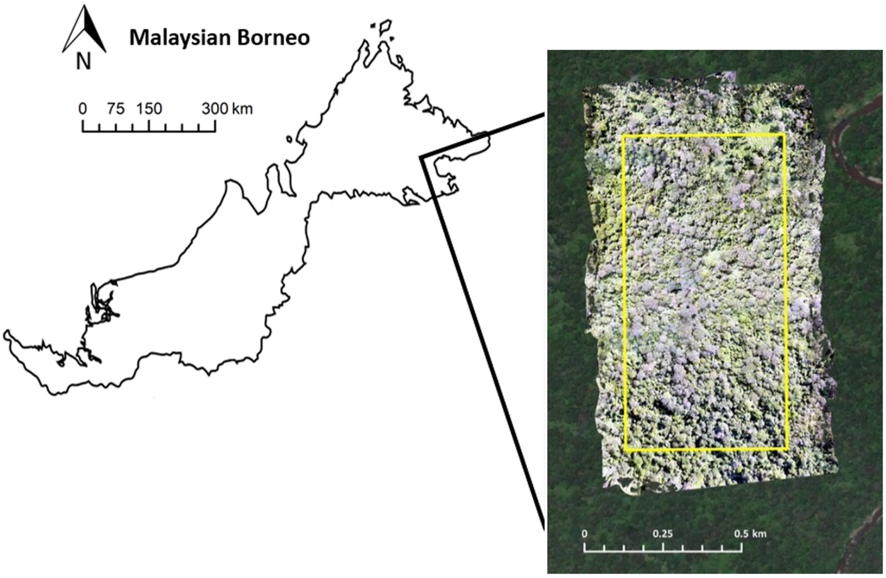

FIGURE 1 Location of the study site and 50-ha plot in Danum Valley Conservation Area, Sabah, Malaysia, Borneo, Southeast Asia. The orthomosaic created from our UAS survey of the 50-ha plot plus a 'buffer' of surrounding vegetation is shown overlaying satellite imagery. The 50-ha plot boundary is shown outlined in yellow. Satellite data source: DigitalGlobe WorldView2 RGB imagery.

14th and 16th June 2016. For details on the flight parameters, please see Waite et al. (2019) and Supporting Information S3. In total, 3884 images were captured covering the 50-ha plot and a buffer of surrounding forest. Using structure from motion photogrammetry, the images were assembled to form a single two-dimensional orthomosaic and processed to produce a digital terrain model and a digital surface model. These were used to produce a canopy height model geo-referenced to the WGS84 UTM Zone 50 N projected coordinate system, using Agisoft PhotoScan version 1.4.2. The resolution of UAS-derived data products was 0.17 m. More details on specific UAS flight parameters and the processing chain in Agisoft PhotoScan can be found in Waite et al. (2019). The orthomosaic was exported to ERDAS IMAGINE version 16.5.0 for visual identification and delineation of individual tree crowns.

2.4 | Derivation of liana load variables

On the orthomosaic, we visually identified and manually digitised the edges of every tree crown for which the majority of the crown was visible within the 50-ha plot. Thus, we created a shapefile for each individual tree crown. Any crowns $<25\,\text{m}^2$ in area or too shaded to accurately determine their edges and/or assess liana load were excluded from further analyses. In total, we used 2428 tree crowns located within the 50-ha plot boundary for this study.

For these tree crowns, we classified the liana cover of the crown via two methods: (i) liana presence/absence; and (ii) crown occupancy index (COI). The COI is a simple expression of liana load in the tree crown on an ordinal scale: (0) no lianas in the crown; (1) 1%–25%; (2) 26%–50%; (3) 51%–75%; and (4) >75% of the crown covered by liana leaves (Clark & Clark, 1990). We have previously shown that these UAS-derived measures accurately measure liana loads, being comparable (and most likely better in the higher canopy) to traditional ground-collected data at both the individual tree and plot level, as well as in different forest types and at different spatial resolutions, with little inter-observer bias (Waite et al., 2019).

As two observers were used to classify liana load across the 50-ha plot, we assessed inter-observer bias in classifying liana load from the UAS image data. Both observers classified the COI for 200 random trees and we used Kendall's coefficient of concordance (Kendall's *W*) to assess the concordance of the COI values recorded by the two observers. We found a high degree of concordance (Kendall's $W = 8.870$, $p = <0.001$, $n = 200$). Both observers recorded the same COI on 76.5% of occasions and when classifications differed, this was mostly by only one class (83.0%).

2.5 | Derivation of potential drivers of spatial liana load patterns

We compiled 18 variables quantifying potential drivers of liana spatial distribution in the forest canopy, using UAS-derived and field-collected (surface) data (Supporting Information S1). These variables included the following: distances from individual tree crowns to their nearest canopy gap, for different gap areas and depths; distances to nearest infested neighbouring trees; crown area; mean top of crown height; mean slope angle; and soil chemical variables. Details on these variables and the methods used to derive them are given in Supporting Information S1. To assess the efficacy of the UAS data, airborne LiDAR data were used. Airborne LiDAR data were collected in November 2014 and processed to produce a DTM with a 1 m resolution. An additional 11 variables were derived from these LiDAR data, comparable to those derived from the UAS data (Supporting Information S1). Details on the airborne LiDAR data collection and processing can be found in Supporting Information S4. All variables were derived on an individual-tree crown basis. All raster files for analysis were prepared using ArcGIS version 10.4 and subsequently processed and analysed in R version 4.1.0 (R Core Team, 2021).

For the surface topography and soil variables, we used the tree crown shapefiles to determine the extent of the area of influence. Due to difference in root system size, soil and topography influence larger trees over a greater spatial extent than smaller trees. Using tree crown size to capture this variation is appropriate as it typically scales with root system size (Denslow, 1980). Furthermore, most lianas root below the crown of their host (e.g. Alvira et al., 2004; 52.4% of liana stems in our ground survey had their last rooting point within 1 m of the tree stem of their host) and so would be largely subject to the topographical and soil values in the same area. We overlaid the tree crown shapefiles on the soil chemistry and topography rasters and took the mean value of all pixels comprising the tree crown. The final soil chemical variables (Supporting Information S1) were selected from a wider range of soil variables after exploratory analyses showed that they explained the majority of variation in the data and are relatively independent of one another. We did not consider climate variables in this analysis because they operate at larger spatial scales. Microclimatic variation may have some impact on liana growth patterns; we assumed that this is largely captured via other included drivers, such as topography and canopy data, as shown by Jucker et al. (2018).

2.6 | Analysis

To test whether liana infested tree crowns were spatially aggregated across the 50-ha plot, we calculated an inverse distance matrix for each individual tree (centroid) with its associated COI. We then calculated one-sided Moran's *I* (Moran, 1950) using the R package APE version 5.3 (Paradis & Schliep, 2018) with a null hypothesis assuming no spatial aggregation, and an alternative hypothesis that liana loads are more spatially aggregated than expected by chance. Due to the complex dataset, with largely unknown relationships and variable interactions, we used boosted regression tree (BRT) models, which allowed us to efficiently analyse liana spatial distribution patterns in relation to the predictor variables (Supporting Information S1). BRTs are an ensemble modelling, machine-learning technique which combines two algorithms: regression trees and boosting, to combine a collection of models with improved predictive performance that can deliver meaningful ecological insights (Elith et al., 2008; Leathwick et al., 2006).

BRT models were fitted for two main predictor sets: (i) surface and UAS-derived variables; and (ii) UAS-derived variables only. To assess the efficacy of UAS-derived variables to explain and predict liana distributions compared to other, more traditional and highly calibrated remote sensing data collection techniques, BRT models were also fitted on; (iii) surface and LiDAR-derived variables. The BRT models were fitted to both liana response variables: (i) liana presence/absence; and (ii) COI. The predictor sets used in the modelling are summarised in Supporting Information S1. To test the prediction from Neotropical research that the tree height–liana load relationship would be positive below the emergent layer (see Introduction), we repeated the analyses, removing those trees over 50 m (n = 223; 9.2% of individuals), which is the top height of the canopy for non-emergent trees (Coomes et al., 2017). The function gbm in the R package GBM version 2.1.5 (Greenwell et al., 2019) was used for the BRT analyses. This function was used to balance predictive performance with model fit, while discouraging overfitting, by using regularisation methods (Hastie et al., 2009) and shrinkage procedures as each tree is added to control the number of terms and produce parsimonious models. During model calibration, we tested different combinations of bag fraction (0.1, 0.5, 0.6, 0.75), learning rate (0.005, 0.001, 0.0001) and tree complexity (1, 2, 3, 4, 5) to determine the optimum number of trees. The optimal parameters were selected for each model predictor set based on explained deviance and AUC.

To quantify the modelled effects of individual predictor variables, their relative influence values, which indicate model contribution of variables to the model outcome, were obtained. Relative influence values are based on weighting the number of times a predictor is selected for splitting a tree according to the improvement to the model as a result of each split, averaged over all trees (Friedman & Meulman, 2003). They allow these complex ensemble models to be easily interpreted. The relative influence of each predictor variable is scaled so that the sum adds to 100; higher numbers indicate a stronger influence on the response and a value of 100 for a single variable would indicate it contributed solely to the final model.

As well as evaluation from internal fit statistics (i.e. self-statistics, R^2) model performance was evaluated using 10-fold cross-validation. Both self-statistics and cross-validation values range from 0 to 1, where a higher number suggests a better model; a value of 1 would be a model that: (i) explains all of the variation in the data for self-statistics; or (ii) predicts perfectly to a subset of data in the same area in cross-validation. Additionally, to test whether model fit reflected more than spatial autocorrelation of the variables, we reassessed the fits of the BRT models by geographically separating calibration and evaluation data and calculated the percentage deviance explained. The division of the data into evaluation and calibration data sets was made by the method described in the R package *ENMeval* for 'Checkerboard1' (Muscarella et al., 2014). This partitions the data into two bins following a checkerboard grid pattern. Using variograms, we determined the maximum range of autocorrelation in our environment to be 181 m. We ensured that the cell blocks in our checkerboard exceeded this to protect against autocorrelative effects. This resulted in relatively balanced training and evaluation sets (training set: 1235 data points; evaluation set: 1193 data points).

To address a potential bias in UAS imagery of representing all the tallest trees (most visible on the imagery) and missing some understorey trees, we collected field survey data on tree diameter at breast height (DBH), tree species and liana COI for all trees ≥10 cm DBH in a subset of our study area. Species were identified largely through field sample collection and comparison to herbarium reference collections. For a small number of species, where field teams could confidently identify them, samples were not routinely collected. These data were collected contemporaneously with the UAS data collection. We tested for differences in median COI between five DBH size classes (10–20 cm, 20–30 cm, 30–40 cm, 40–60 cm and >60 cm), roughly corresponding to understorey, lower-canopy, mid-canopy, upper-canopy and emergent trees. Finally, to test whether any observed differences to Neotropical studies in the relationship between tree size and liana load is due to the prevalence of dipterocarp species, we repeated the analyses removing the dipterocarp species from the dataset (8.2% of individuals; 4.1% of species).

3 | RESULTS

We delineated 2428 tree crowns ≥25 m^2 in area (mean = 48.6 individuals ha^{-1}) across the 50-ha plot (Figure 2). In total, 1243 trees (51.2%) with crowns visible on the UAS-derived imagery were infested by lianas (Figure 2). Trees were distributed unevenly between each of the COI classes as follows: 0 (0% liana canopy cover): 1185 trees/48.8%; 1 (1%–25% liana canopy cover): 706 trees/29.1%; 2 (26%–50% liana canopy cover): 237 trees/9.8%; 3 (51%–75% liana canopy cover): 129 trees/5.3%; 4 (>75% liana canopy cover): 171 trees/7.0%. Overall, we found that liana-infested tree crowns were spatially aggregated across the 50-ha plot (Moran's I = 0.036, p = ≤0.001; Figure 2).

3.1 | Boosted regression tree model performance

The BRT models built on the: (i) surface and UAS-derived variables; and (ii) UAS-derived variables only had similar internal fits based on the self-statistics and cross-validation statistics across both liana load classifications (Table 1). The same was found for the BRT model built on the surface and LiDAR-derived variables (Table 1). Model performance across each of the predictor sets was similar. The self-statistics values (internal model fit; R^2) ranged 0.58–0.64 (UAS only), 0.59–0.70 (UAS and surface) and 0.55–0.69 (LiDAR and surface) and the models accounted for 44%–52% (UAS only), 45%–54% (UAS and surface) and 42%–53% (LiDAR and surface) of the variation in liana load. When examining whether model performance was subject to autocorrelation of the predictor variables, model evaluation using

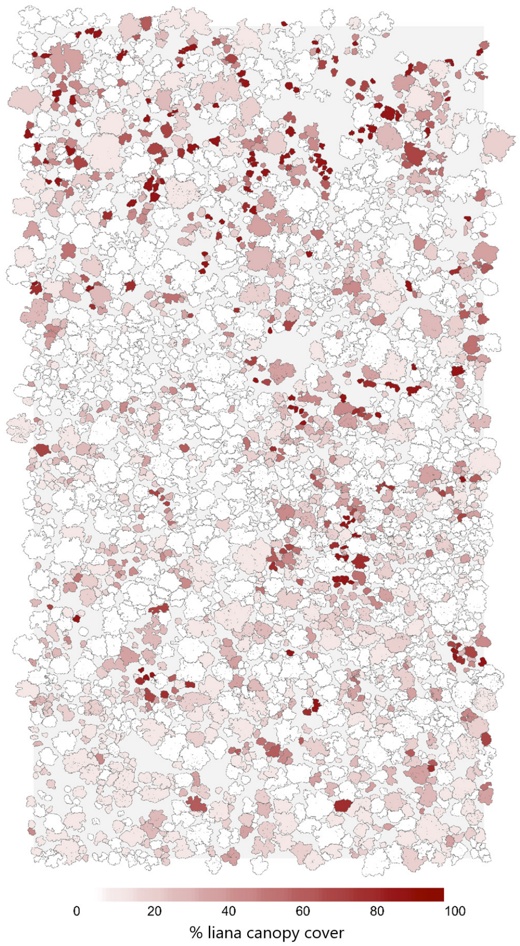

FIGURE 2 The location and liana load level of all tree crowns ≥25 m^2 visible from UAS imagery located within the 50-ha plot (*n* = 2428). The plot is indicated with grey shading. The red colour ramp indicates liana load, from 0% to 100% of the tree crown covered by liana leaves (darker red = more heavily infested tree crowns).

geographically separated evaluation data resulted in only slightly lower percentage deviance explained than those models evaluated through cross-validation (Table 1).

3.2 | Variable importance

Tree height was by far the strongest predictor of liana load, dominating the BRT models across both liana assessment methods (Table 1; Figure 3; Supporting Information S5 and S6). It had the highest relative influence values of any predictor variable, always exceeding 34.60% and with a maximum of 45.39% for the COI model built with UAS data only (Table 1; Figure 3; Supporting Information S5). The negative relationship with liana occupancy and load shows that taller trees (~35–65 m) were less often, and to a lesser extent, infested by lianas than shorter trees (~<15 m). The negative relationship between tree height and liana load held across all predictor sets when removing the emergent trees (>50 m height), with relative influence values remaining over 32%.

TABLE 1 Boosted regression tree (BRT) model results across both liana load assessments (liana presence/absence [P/A], and crown occupancy index [COI]) for the different predictor sets (UAS data, UAS and surface data, and LiDAR and surface data). Model prediction validated with cross-validation (CV) and geographically separated evaluation data (GEV) are shown, the values of which are given alongside the internal model fit. The dominant variables, i.e. those with the highest relative influence (RI), are shown, with the RI values given in brackets.

	UAS					UAS and surface					LiDAR and surface				
	Percentage deviance explained		Internal model fit	Predictor with highest RI	Predictor with 2nd highest RI	Percentage deviance explained		Internal model fit	Predictor with highest RI	Predictor with 2nd highest RI	Percentage deviance explained		Internal model fit	Predictor with highest RI	Predictor with 2nd highest RI
	CV	GEV				CV	GEV				CV	GEV			
P/A	0.44	0.42	0.58	Tree height (41.10%)	Distance to nearest infested neighbour (9.72%)	0.45	0.42	0.59	Tree height (40.04%)	Distance to nearest infested neighbour (8.86%)	0.42	0.40	0.55	Tree height (41.36%)	Distance to gaps <2 m height, >500 m^2 (10.19%)
COI	0.52	0.43	0.64	Tree height (45.39%)	Distance to gaps 5–10 m height, >500 m^2 (9.06%)	0.54	0.44	0.70	Tree height (34.60%)	Distance to gaps 5–10 m height, >500 m^2 (8.96%)	0.53	0.42	0.69	Tree height (35.49%)	Distance to gaps <2 m height, >500 m^2 (7.93%)

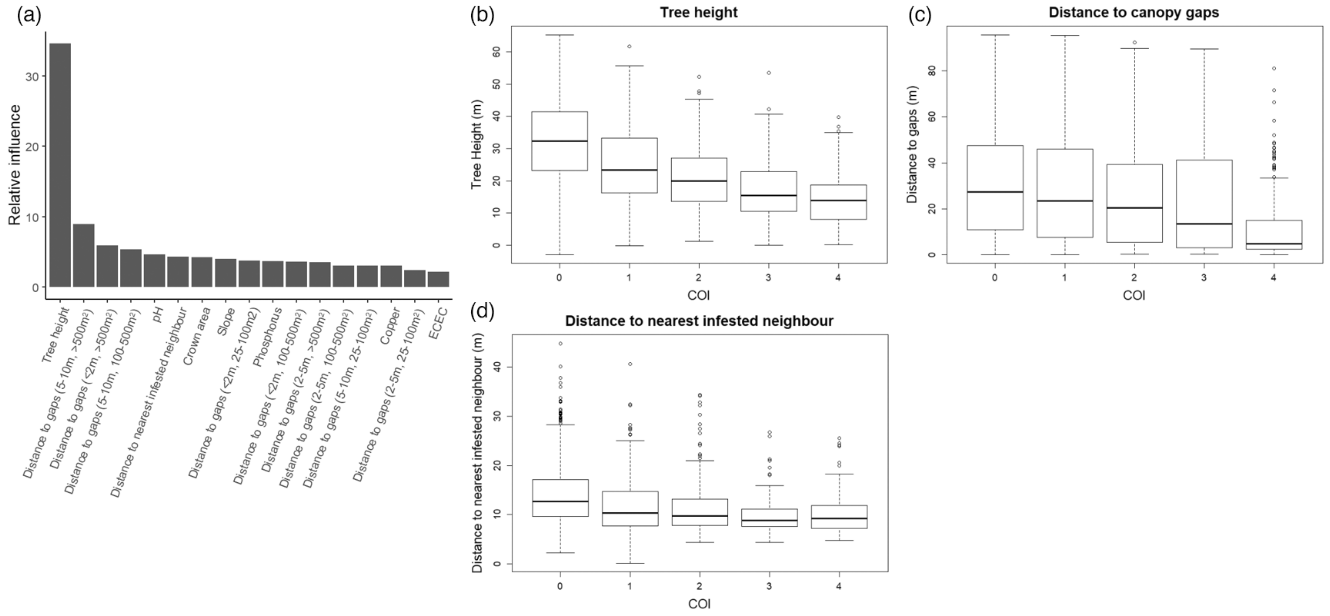

FIGURE 3 (a) Variable importance plot for the boosted regression tree (BRT) model built for liana COI (Crown Occupancy Index: (0) no lianas in the crown; (1) 1%–25%; (2) 26%–50%; (3) 51%–75%; and (4) >75% of the crown covered by liana leaves) on the UAS and surface data. Variable importance plots for the additional BRT models built on different predictor sets and liana response variables can be found in Supporting Information S6. The relative influence of each variable (full description given in Supporting Information S1) is scaled so that the sum adds to 100, with higher numbers indicating a stronger influence on the response. Boxplots show the relationship between the COI classes and: (b) tree height; (c) distance to gaps (5–10 m in height and >500 m^2); and (d) distance to the nearest neighbouring tree crown with lianas present. Wilcoxon rank sum tests with Bonferroni correction indicate that all COI classes differ in median height (p = <0.05).

When analysing the ground-collected data to address a potential bias in the UAS imagery of representing all of the tallest trees and missing some understorey trees, we found a peak in the lower canopy, with a general decline in liana load with increasing DBH 20–30 cm upwards (Supporting Information S7). Similar results were found when removing dipterocarp species from the analyses, although the number of significant differences between DBH classes was reduced (Supporting Information S7).

Other variables with high relative influence values were gap variables, particularly those for the largest gap areas, for the models fitted for liana COI (Table 1; Figure 3; Supporting Information S5 and S6). The gap variable with the highest relative influence for both predictor sets was that representing gaps 5–10 m in height and >500 m^2 in area (UAS only = 9.06%; UAS and surface = 8.96%; Figure 3; Supporting Information S5). Distance to the nearest infested neighbour was important in the models fitted for liana presence/absence, with relative influence values of 9.72% and 8.86% in the models built on the UAS data only, and UAS and surface data, respectively (Figure 3; Supporting Information S5 and S6). All these variables displayed negative relationships with liana load, indicating that as distance from gaps and infested neighbours increased, trees were less often, and to a lesser extent, infested with lianas.

The modelled contributions of topographic variables were all <5% (Figure 3; Supporting Information S5 and S6). Modelled influences from soil variables were also low (<5% model contribution), with the exception of soil copper concentration with a relative influence value of 5.22% for liana presence/absence in the LiDAR and surface combined model (Figure 3; Supporting Information S5 and S6).

4 | DISCUSSION

Here we present a landscape-scale analysis comprising multiple potential biotic and abiotic drivers of liana spatial distributions in a Southeast Asian forest canopy. Liana load of tree crowns was spatially aggregated (Figure 2), similar to studies conducted in other tropical forests around the world (Ledo & Schnitzer, 2014; Pérez-Salicrup & De Meijere, 2005; Schnitzer et al., 2012). Liana load increased in trees growing near gaps and other infested trees, but the most important driver of liana load was tree height. In contrast to Neotropical studies (e.g. Addo-Fordjour et al., 2009; Pérez-Salicrup et al., 2001; Pérez-Salicrup & De Meijere, 2005; van der Heijden et al., 2008), we found that shorter trees (~<15 m), which tend to have small crowns, are more likely to support lianas and carry a larger liana load than larger trees (~35–65 m), which tend to have larger crowns. These latter findings alter our understanding of the mechanisms driving liana canopy load, showing that they may differ between biogeographically distinct regions.

The negative relationship between tree height and liana load in this study (Figure 3), which we found whether or not we included emergent trees in our analysis, may reflect differences in forest structure and composition between Neotropical and Southeast Asian forests (Corlett & Primack, 2006, 2011). For example, Southeast Asian forests are characterised by emergent dipterocarps which are less often infested by lianas (Wright et al., 2015). A mechanism behind this may be that adult dipterocarps have tall branch-free boles, lacking trellises to support climbing lianas (Campbell & Newbery, 1993; Hallé & Ng, 1981) and/or that lower branches, and thereby lianas, are shed as trees shift from monopodial to sympodial growth during their ontogeny. However, the fact that the relationship with tree height was robust to exclusion of dipterocarps (Supporting Information S7) suggests that this is not the only mechanism. Instead, our results suggest this may be part of a more general decrease of liana load with increasing tree height in this Southeast Asian forest. The overall canopy is taller in Southeast Asian tropical forests compared with Neotropical forests, often reaching >50–70 m with more vertical separation between tree crowns (Coomes et al., 2017). This potentially presents fewer opportunities for lianas to spread from one tree crown to another and may lead to the observation that lianas are more predominant in the lower canopy layers. Further research in other Palaeotropical forests is needed to test the generality of this fundamental difference from Neotropical forests.

The second most important driver of liana canopy distributions was canopy gaps, in the models built on liana COI (Table 1; Figure 3; Supporting Information S5 and S6). Degree of liana load increased closer to canopy gaps, which represent past disturbances in the forest. This finding is consistent with research in the Neotropics (Dalling et al., 2012; Schnitzer, 2005; Schnitzer et al., 2012; Schnitzer et al., 2021; Schnitzer & Carson, 2001) and may indicate similarity in patterns of liana load in relation to canopy gaps between Southeast Asian and Neotropical forests. Large gaps, >500 m^2 in area, with vegetation 5–10 m in height, had the highest relative influence in the models fitted for liana COI, although the relative influence was reduced in the models fitted for liana presence/absence (Figure 3; Supporting Information S5 and S6). The size and vegetation height of these gaps mean that they are unlikely to be particularly recent. This may indicate that lianas have impacted tree regeneration in these gaps and that these gaps are stalled in a low-canopy state (e.g. Schnitzer et al., 2000, 2021). A higher relative influence is expected in the models fitted for liana COI, as we observe, because greater liana loads are expected in older gaps, whereas simple liana presence (possibly at lower levels of liana load) may be more related to gaps of any size and age. For the models built on liana presence/absence, proximity to another liana-infested tree was the second most important driver of liana canopy distribution, increasing the probability of nearby trees to also carry lianas in their crown (Table 1; Figure 3; Supporting Information S5 and S6). This agrees with previous research and may result from lianas: (i) traversing adjacent crowns; (ii) descending, re-rooting and climbing into a different tree crown; or (iii) different stems from the same liana infesting different trees (van der Heijden et al., 2008).

Soil and topography variables were not significant drivers of liana canopy presence and load (Figure 3; Supporting Information S5 and S6). Relationships between soil fertility and liana growth are inconsistent (Fadrique & Homeier, 2016) and, as lianas may be more ecologically generalist than trees, this may result in a lack of clear relationships with soil variables in some cases (Macía et al., 2007). Some research has shown that soil fertility can increase liana abundance or growth (DeWalt et al., 2006; Lai et al., 2017; Laurance et al., 2001) while others have shown liana density to be unrelated to soil fertility (van der Heijden & Phillips, 2009). These studies examined multiple plots over landscape to regional scales, including early successional and old growth forests, and likely captured a greater range of variation in nutrients than present in our study. Interestingly, in a comparable 50-ha plot study in the Neotropics, Dalling et al. (2012) found that, relative to trees, lianas were only weakly associated with local variation in topography and soil chemistry, a finding similar to our study. The use of finer scale soil and topographic data consistent with the resolution of our remotely sensed variables could potentially alter these findings; however, the spatial extent over which individual lianas access soil resources is poorly studied.

A limitation of this study is that only the trees >25 m^2, with all or most of their canopy visible from above, were included. This means that all adult emergent trees were included but some understorey trees were not. Our sample is, therefore, biased towards the taller trees and may not be fully comparable to ground-based studies. As a check of robustness of our findings to this issue, we used a ground-collected dataset covering a subset of our study area, where data on DBH, liana COI and % liana canopy cover for all trees ≥10 cm DBH were collected, thus including understorey trees that may not be visible on the UAS imagery. Although we could not examine the relationship between tree height and liana load with these ground-collected data, DBH is a useful proxy as it has been shown to be strongly related to tree height (Banin et al., 2012). Thus, the five DBH size classes roughly correspond to understorey, lower-canopy, mid-canopy, upper-canopy and emergent trees. We observed an initial increase in median COI between the two smallest DBH classes, and a reduction in median COI with increasing DBH across all other classes, regardless of the inclusion of dipterocarps in the analysis (Supporting Information S7). This indicates that the highest liana loads are found in the lower-canopy (20–30 cm DBH), rather than the understorey (10–20 cm DBH). Above the understorey, we found a similar negative relationship between tree height and liana load as was observed with the UAS data, indicating a fundamental difference in liana distribution from Neotropical forests. This does not appear to match previous work that indicates lianas tend to proliferate in higher light conditions (Putz, 1984a; Rodríguez-Ronderos et al., 2016), and in older trees that have had more time to become infested by lianas and for lianas present in their crown to spread more widely (Visser et al., 2017). These explanations have largely stemmed from the Neotropics, however, and perhaps do not apply here.

Of consideration is whether full calibration of UAS data using ground control points is necessary, as it is very difficult in tropical forests, due to complex terrain and dense vegetation cover (Baena et al., 2018). Comparisons between LiDAR-derived and UAS-derived digital terrain models and canopy height models showed strong relationships (Supporting Information S8) and the BRT models built using LiDAR-derived data, which are commonly accepted as gold standard (Philipson et al., 2020), and those using UAS-derived data, which were not fully calibrated, performed very similarly to one another, accounting for comparable amounts of variation in liana load (Table 1). They also performed very similarly in predicting liana load (Table 1). This indicates that difficulties in calibrating UAS data did not affect our results, and that UASs may, therefore, make collecting data on liana load, and on the variables that may determine liana spatial patterns in forest canopies, more accessible to a wider variety of users and enable faster, cheaper and more reliable (less affected by cloud cover) mapping than is possible with either ground- or LiDAR-derived data.

The models had slightly lowered predictive performance on geographically separated evaluation data (Table 1), indicating that, as expected, predictions of liana load are less precise in areas beyond those in which the models were trained. However, this slight reduction in the precision of liana load estimates does not preclude the models from being useful when broad assessments of liana load are needed, for example in helping to indicate areas of higher liana load that may be potentially important for future research. The ability to distinguish areas likely to support high liana load may also be useful to inform practices involving liana cutting for improved timber and fruit production (Kainer et al., 2014; Sist et al., 2003; Verwer et al., 2008) or carbon sequestration (Marshall et al., 2017). Here, liana cutting may be targeted and confined to relatively small areas where liana load is greatest, and liana effects strongest, to maximise the benefits of the management technique. The ability to pinpoint areas with high liana load via UAS would minimise time spent in the field searching for them and, thus, reduce input cost and time. The models would likely be most useful in other lowland dipterocarp forests in Southeast Asia, with similar forest structure to our study area. We expect that performance may degrade when extrapolating to different forest types and structures, for example African and Neotropical forests.

This work underlines the importance of combined ground and remote-sensing data for understanding the emerging and critical impacts of lianas at large scales. The use of UASs and the comprehensive analytical framework employed here to examine what determines liana occurrence and load and predict liana load at individual tree crown level may allow extension of the research into other locations and/or forest types, such as logged forests. This would increase our knowledge of liana spatial distributions, and their drivers, and may assist in providing a more comprehensive understanding of the factors that control plant species distributions more generally. This may prove particularly pertinent as lianas may continue to increase with future climate change and, given their interaction with aboveground carbon stocks, alter tropical forest functioning with serious implications for tropical forest carbon storage.

AUTHOR CONTRIBUTIONS

Catherine E. Waite, Doreen S. Boyd, Richard Field and Geertje M. F. van der Heijden designed the research; Catherine E. Waite performed the UAS data collection, processed the UAS images and analysed the data; Catherine E. Waite and Geertje M. F. van der Heijden extracted tree crown data and liana load estimates from the UAS images; Catherine E. Waite, Geertje M. F. van der Heijden and M. Elizabeth Rodríguez-Ronderos collected the ground liana cover data; Catherine E. Waite, Doreen S. Boyd, Geertje M. F. van der Heijden and Richard Field developed the analytical approach; Doreen S. Boyd contributed the occupied aircraft LiDAR data through a NERC ARSF direct access grant to Doreen S. Boyd and David F. R. P. Burslem (NERC MA14/11); David F. R. P. Burslem was responsible for the soil and topography data, assisted by James W. Dalling; Reuben Nilus provided logistical support in obtaining permits for the work; Catherine E. Waite wrote the paper with contributions from all authors. This work was a component of Catherine E. Waite's PhD, which was supervised by Doreen S. Boyd and Richard Field.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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