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A view from above: using Unmanned Aerial Vehicles (UAVs) to enhance ecological understanding of lianas in tropical forest canopies

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Abstract

Lianas play integral roles in structuring community composition, forest regeneration, the maintenance of species diversity and whole-forest level ecosystem processes in tropical forests. With increasing disturbances to forests worldwide, the relative importance of lianas as players in many areas of forest dynamics is expected to increase, with important ramifications for the global carbon cycle. However, our knowledge of lianas is incomplete and biased: (i) towards the Neotropics; and (ii) against the canopy, yet the canopy is where lianas proliferate most. Research in these areas is hampered by the logistical difficulties of studying lianas; the fact that they are time-consuming to survey, and that it is difficult to quantify what is going on in the canopy. This thesis enhances ecological understanding of lianas in tropical forest tree crowns, focusing on the lesser studied Palaeotropics. The development of a novel method to enable faster, cheaper and more canopy-centred assessment of liana than possible with traditional assessment methods is vital for this.

A lightweight unmanned aerial vehicle (UAV) was used to assess liana infestation of tropical forest tree canopies in Sabah, Malaysia. By visually interpreting the images, the UAV-derived liana infestation estimates were compared with those derived from traditional ground methods of liana infestation assessment to determine the validity, strengths and weaknesses of using UAVs as a new method for assessing liana infestation of tree canopies. These data were then used to map and monitor liana load in tree crowns: (i) spatially, to elucidate liana-environmental relationships; and (ii) temporally, to monitor the canopy response, including changes in liana infestation, to El Niño drought.

UAV-derived estimates of liana infestation correlated strongly with ground-derived data at individual tree and plot level, and across multiple forest types and spatial resolutions. Furthermore, the UAV surveys improved liana infestation

assessment for upper canopy layers and were considerably faster and more cost-efficient than ground-based surveys. Liana infestation was significantly spatially aggregated, with tree canopy height and presence of canopy gaps being the most important variables influencing this. Taller trees were less often and less heavily infested by lianas while liana infestation occurred more often and to greater extents in close proximity to canopy gaps. Temporally, tree-level liana infestation and crown area showed significant increases in the aftermath of the 2015/16 El Niño whereas crown greenness and tree leaf cover showed a significant decrease. Furthermore, liana cover was significantly higher for trees that experienced mortality in the aftermath of the El Niño than for those that did not.

This thesis presents a novel UAV-based method of capturing data that can be used to assess liana infestation of tropical forest tree crowns at least as accurately as traditional ground data. This novel method promotes reproducibility of results and quality control, and enables additional variables to be derived from the image data. It is more cost-effective, time-efficient and covers larger geographical extents than traditional ground surveys, enabling more comprehensive monitoring of changes in liana infestation over space and time.

By utilising the new UAV method, this thesis presents: (i) the largest and most comprehensive continuous assessment of Palaeotropical tree crown liana infestation, and analysis of environmental variables that may influence this, to date; and (ii) the first study assessing short-term temporal change in liana canopy cover and associated alterations in the forest canopy using UAV image data. Examining how and why lianas are distributed in the forest canopy and how this changes through time may help us to determine what variables could determine increases in lianas with environmental change in the future, with important implications for tropical forest carbon storage and sequestration, and provide a step towards more comprehensive testing of ecological theory in tropical forests.

Chapter 1: Introduction

The overarching aim of this research is to enhance our ecological understanding of lianas in tropical forest tree crowns, focusing on the lesser studied Palaeotropics. To achieve this, a novel method to enable faster and cheaper assessment of liana infestation is developed using an unmanned aerial vehicle (UAV) and a rigorous, quantitative assessment of its capability to assess liana infestation in tropical forest tree canopies, and map this infestation through space and time, is conducted. This introductory chapter describes the value of tropical forests and their canopies, and the importance and role of lianas within them. Three main research questions are presented, each linking to one of the three research papers comprising Chapters 3–5 of the thesis. A review of the existing literature is given to provide context for each. The status of each of the three papers is then given, and an overview of the thesis structure is presented.

1.1 Background and Context

1.1.1 Importance of tropical forests and forest canopies

The study of tropical forests carries global importance, as these environments play a crucial role in the maintenance of biodiversity and provide unique local and global ecosystem services to all life on Earth (Ozanne et al., 2003; Lowman et al., 2013). Covering ~10% of Earth's dry land surface, they are arguably the most species-rich terrestrial environment on the planet (Brooks et al., 2002; Levin, 2013), providing buffered microclimates and complex microhabitats (Nakamura et al., 2017) that house more than half of Earth's terrestrial species (Schnitzer & Bongers, 2011; Lewis et al., 2015). Tropical forests also play a key role in local and regional hydrological patterns, influencing the hydrology of more than 45 million ha of land (Ozanne et al., 2003).

At a global scale, tropical forests also form a critical part of the global climate and the global carbon cycle (Beer et al., 2008; Pan et al., 2011; Marvin et al., 2016). Forest canopies constitute the functional interface between 90% of the Earth's terrestrial biomass and the atmosphere (Ozanne et al., 2003), playing a key role in forest atmospheric fluxes (Allen, 1996). Indeed, tropical forests exchange more carbon with the atmosphere than any other terrestrial biome (Beer et al., 2010; Pan et al., 2013) and account for a third of carbon fixed by photosynthesis (Dixon et al., 1994; Field et al., 1998; Beer et al., 2010; Wright, 2010; Schnitzer & Bongers, 2011; van der Heijden et al., 2015). A reported ~1.19 ± 0.41 Pg of carbon is absorbed by tropical forests each year (Pan et al., 2011). Tropical forests also store large amounts of carbon. They account for ~two-thirds of terrestrial live biomass (Beer et al., 2010; Pan et al., 2013), with an estimated ~200–300 Pg of carbon stored in living tropical trees (Pan et al., 2011; Saatchi et al., 2011; Baccini et al., 2012; Feldpaush et al., 2012; Avitabile et al., 2016; Michard, 2018). As such, tropical forests provide important ecosystem services, mediating the effects of anthropogenic activity on the Earth's climate and, as Schnitzer and Bongers (2011) note, any alteration to tropical forests has broad and important ramifications for species diversity and productivity, as well as the global climate and carbon cycles.

Despite their importance, forests and their canopies are one of the most threatened ecosystems on the planet (Brooks et al., 2002; Levin, 2013) and over half of the world's original forests have already been destroyed (Lowman et al., 2013). With the escalation of global environmental change and population pressures, the threats to forests and their canopies are increasing (Nakamura et al., 2017), reducing their ability to mediate anthropogenic driven climatic changes through the ecosystem services that they provide (Lewis et al., 2015, Mitchard, 2018). Indeed, it is now contested whether tropical forests constitute a carbon sink or source (e.g. Pan et al., 2011; Schimel et al., 2017; Baccini et al., 2017). Recent evidence suggests that intact and recovering tropical forests currently

balance carbon released through deforestation and degradation, so make an approximately neutral contribution to the global carbon cycle, overall (Mitchard, 2018). This research goes on to suggest, however, that, when considering multiple sources, tropical forests are likely become a carbon source in the near future as the intact forest sink declines in size (Grace et al., 2014; Sitch et al., 2015; Le Quéré et al., 2016; Baccini et al., 2017). Forest canopies may provide early warning indicators of environmental changes, however, as their declining health is a harbinger of environmental changes on a global scale, as well as a driver of further change (Foley et al., 2003; Janssen et al., 2008). Thus, improved understanding of global change impacts on forest ecosystems, of which the canopy plays an essential role, is fundamental (Mori et al., 2017), and improved monitoring of forest canopies is essential in order to capture any early warning signs.

1.1.2 Importance of lianas

Lianas may be one such early warning sign of declining tropical forest health. Lianas are a polyphyletic group of long-stemmed woody plants that occur in forests across the world. They are highest in abundance and richness in tropical forests where they typically constitute ~25% of the woody stem density (abundance) and species richness (Gentry, 1991; Appanah et al., 1992; Schnitzer & Bongers, 2002; van der Heijden et al., 2015). Lianas all share a common growth strategy: rooting in the soil at ground level before using the architecture of other plants for vertical support to climb to the forest canopy to access areas of forest with high light levels. Once in the canopy, lianas are known to also grow laterally between neighbouring tree crowns (Putz, 1984b; Campbell & Newbury, 1993), connecting multiple tree crowns and providing inter-canopy pathways for arboreal animals (Montgomery & Sunquist, 1978, Emmons & Gentry, 1983; Schnitzer et al., 2014).

Lianas have a variety of adaptations for attaching themselves to their host and climbing to the forest canopy. These include: (i) stem twining; (ii) clasping tendrils from the stem; (iii) leaf and branch modification; (iv) thorns and spines; (v) downward-pointing adhesive hairs; and (vi) adhesive, adventitious roots (Hegarty, 1991; DeWalt et al., 2000). This means that lianas, unlike trees, have relatively little internal structural support and can allocate more resources to reproduction, canopy development, and stem and root elongation (Ewers et al., 1991; Fisher, 1991). They, therefore, have a very high canopy:stem ratio, resulting in a higher proportion of photosynthetic biomass than is present in most woody plants.

The interactions between lianas and trees are of interest to ecologists due to the detrimental effects that lianas can have on their host tree (Lutz, 1943; Pérez-Salicrup, 2001). Even when lianas are relatively low in abundance, many studies have demonstrated a related decrease in tree growth, by up to 84%, (van der Heijden & Phillips, 2009; Ingwell et al., 2010; Schnitzer et al., 2014), fecundity (Kainer et al., 2006; Nabe-Nielsen et al., 2009), and survival (Phillips et al., 2005). Lianas influence trees via: (i) competition, slowing tree growth; (ii) increasing tree mortality rates by weighing down tree crowns, which puts mechanical strain (torque) on the stem and roots and increases branch snapping and pathogen susceptibility; (iii) connecting tree canopies, increasing the number and size of trees pulled down when liana-infested trees fall; and (iv) slowing rates of tree sapling growth in treefall gaps through the combined effects of shading and mechanical damage (Putz, 1984a; Carse et al., 2000). The first of these methods, liana–tree competition, is often more intense than tree–tree competition (Tobin et al., 2012). It occurs both above- and below-ground, for essential nutrients, water and light, and occurs in closed-canopy forest, treefall gaps and managed forests (Putz, 1984a; Lowe & Walker, 1977; Stevens, 1987; Dillenburg et al., 1993).

Not all trees are affected equally by lianas, however, as key characteristics, such as a rapid growth rate, flexible trunk, and large leaves allow some species to shed or avoid lianas (Putz, 1984b). Also, by increasing tree mortality and pulling down neighbouring trees in a treefall event, lianas create more and larger canopy gaps, as well as prolong the life of these gaps (Appanah & Putz, 1984). This indirectly promotes pioneer tree species by reducing competition from shade tolerant species and extending the opportunity for them to colonise (Schnitzer et al., 2000). Therefore, lianas appear to harm slow-growing, shade-tolerant species whilst not affecting, or even indirectly promoting, pioneer species (Laurance et al., 2001; Putz, 1984a; Schnitzer et al., 2000). In this way, lianas can change the relative competitive ability of tree species and alter tree communities (Putz, 1984a; Putz, 1984b; Clark & Clark, 1990; Schnitzer et al., 2000; Laurance et al., 2001; Schnitzer & Carson, 2001; Pérez-Salicrup, 2001).

As a result of the detrimental impact that lianas have on trees, lianas have a major impact on forest ecosystems by influencing carbon sequestration (Laurance, 1997; Gerwing & Farias, 2000). Firstly, by decreasing tree regeneration, growth and fecundity, and increasing tree mortality, lianas cause a loss of tree biomass from the ecosystem (Durán & Gianoli, 2013). This loss in tree biomass, however, is not offset by the increase in liana biomass. By relying on trees for structural support, lianas allocate a higher proportion of biomass to foliage production over carbon-dense stem production, and therefore have relatively slender stems and low wood density. As a result, lianas sequester far less carbon than trees (van der Heijden et al., 2013) contributing relatively little to forest-level biomass and further constraining above-ground forest primary productivity (van der Heijden et al., 2013). Indeed, Schnitzer et al. (2014) showed that lianas only contributed 24% of the tree biomass accumulation they displaced. Furthermore, following forest fragmentation in central Amazon, liana abundance greatly increased but liana above ground biomass (AGBM) increased by only 0.46 Mg ha^{-1} compared to a

decrease in tree AGBM of 36.1 Mg ha^{-1} (Laurance et al., 1997; Bongers et al., 2002). Lianas, therefore, play a large role in the forest carbon budget and can decrease the amount of carbon fixed by a given area of tropical forest, in some cases by as much as ~76%/year (van der Heijden et al., 2015). Additionally, lianas have short woody biomass residence times, with turnover rates as much as three times faster than trees (Phillips et al., 2005), meaning carbon sequestered in liana biomass will be released to the atmosphere much more quickly than carbon sequestered by trees.

Since the seminal study by Phillips et al. (2002) first documented the pattern, several long-term studies have indicated that lianas are now increasing in abundance and biomass in tropical forests (Schnitzer & Bongers, 2011). This has resulted in greater contribution of lianas to canopy leaf productivity, an increase in the number of tree crowns infested (Wright et al., 2004, Ingwell et al., 2010), increased tree turnover (Phillips et al., 2004), and shifted floristic composition (Laurance et al., 2004; Korner, 2004; Feeley et al., 2011). Therefore, the effects of lianas on trees at all life-history stages (recruitment, growth, reproduction and mortality), as well as the influence of lianas on tropical forest ecosystem processes, such as carbon sequestration, are likely to increase (Schnitzer & Bongers, 2002; Laurance et al., 2014). Although the mechanism(s) behind the increase in liana abundance and biomass are largely unknown, it is thought to be related to environmental change. Proposed putative mechanisms, that are likely operating synergistically, include: (i) increasing forest disturbance and turnover; (ii) increasing evapotranspirative demand due to increasing prevalence and severity of drought; (iii) increasing nutrient deposition; and (iv) elevated atmospheric CO_2 (Wright, 2010; Schnitzer & Bongers, 2011; Schnitzer et al., 2014).

In addition, lianas may be increasing not only as a result of such environmental changes but also because they facilitate their own increase by amplifying the

effects of environmental change, causing a positive feedback. In killing their host trees, lianas increase forest disturbance and the formation of canopy gaps: an environment in which they proliferate (Wright, 2005). Thus, the increase in lianas may set in motion a positive feedback of increased liana-induced tree mortality and disturbance resulting in greater liana regeneration. Therefore, lianas may themselves be a driver of further environmental change, both at a local and global scale, with potential impacts on the global carbon cycle and rate of climate change.

Research on tropical lianas is still in its early stages. Despite the effects that lianas have on the ecological communities of which they are a part, and the increasing size and abundance of lianas relative to trees, potentially leading to reduced forest carbon stocks, lianas remain understudied in tropical forest censuses and much remains unknown about the scale, cause, and impact of increasing liana populations (Marvin et al., 2016). Our knowledge of lianas is geographically inconsistent; in a 2011 review of previous liana studies, Schnitzer and Bongers noted a strong bias towards studies in Neotropical forests. Until Wright et al. (2015) no work had been done analysing liana change through time for an Asian forest. Since then more work on lianas in Southeast Asian forests has taken place (e.g. Addo-Fordjour et al., 2016; Lussetti et al., 2016; Magrach et al., 2016; O'Brien et al., 2018), but most studies still focus on the Neotropics. Thus, little is known whether the pattern of liana infestation in the Palaeotropics is similar to that in the Neotropics, and this thesis is valuable in targeting and adding to this body of work through liana censuses in Malaysia. By doing this, it could help to answer the question posed by Schnitzer and Bongers (2011) of whether differences in climate, plant composition and disturbance (both natural and anthropogenic) vary systematically among continents and drive differences in patterns of liana infestation between them.

Most studies of liana ecology focus on ground-based liana stem measurements rather than assessing liana canopy cover. This is due, in part, to the difficulties of collecting data on liana canopy cover from the ground (Marvin et al., 2016). Collecting liana canopy cover data is valuable, however, as it is more directly related to liana–tree competition than stem data. Stem data reflect the rooting point of lianas, which can be a considerable distance from their location in the canopy (Putz, 1984b; Campbell & Newbury, 1993). Liana canopy cover data, on the other hand, provide information on how lianas are distributed in the forest canopy, and the degree of liana infestation at a per-tree level. Such data will be useful for evaluating which areas of the forest and which individual trees lianas are likely to have the greatest effect on.

As discussed above, in the tropics, lianas play integral roles in structuring community composition, forest regeneration, the maintenance of species diversity and whole-forest level ecosystem processes. With increasing disturbances to forests worldwide, the relative importance of lianas as players in many areas of forest dynamics is expected to increase, with important ramifications for the global carbon cycle. However, our knowledge of lianas is incomplete and biased: (i) towards the Neotropics; and (ii) against the canopy, yet the canopy is where lianas proliferate most. Thus, knowledge gaps and questions for liana ecology still remain. Research on these questions is hampered, however, by the logistical difficulties of liana research; the fact that they are time-consuming to survey, and that it is difficult to quantify what is going on in the canopy. Therefore, in order to address the biases present, developing a method to improve the time- and cost-efficiency of liana surveys to aid in data collection is key. Such a method should enable greater ease in liana canopy cover assessment and may be used to add to our knowledge of liana spatial distribution patterns and their change through time.

1.2 Research Questions and Aims

Here, I identify three questions at the forefront of research on the study of liana ecology in tropical forests, and address them in three papers forming Chapters 3, 4, and 5 of this thesis. The questions and associated aims of each paper are:

(1) Can Unmanned Aerial Vehicles (UAVs) provide a new tool for assessing liana infestation in tropical forest canopies?

Aims: to assess the validity of using a consumer-grade UAV as a new method for collecting liana infestation data, by: (i) assessing inter-observer bias in classifying liana infestation from UAV images; (ii) evaluating the strength of the correlation between UAV- and ground-derived measures of liana infestation on individual tree- and plot levels, and for different canopy strata; and (iii) comparing input time and costs between ground and UAV surveys of liana infestation.

(2) What are the important influencing factors on the spatial distribution of liana infestation in Sabah, Malaysia?

Aims: to (i) test our expectation that liana infestation will be spatially aggregated across a 50 ha plot; (ii) evaluate the relative strengths of environmental variables to predict liana distributions and test our hypotheses concerning each; and (iii) evaluate how well UAV data are able to explain and predict liana distributions in comparison to traditional data (i.e. occupied airborne LiDAR and ground-collected data).

(3) How do liana infestation and other concurrent changes in tropical forest canopies change between years, and can UAVs monitor this?

Aims: to use the potential for UAVs to assess short-term change in tropical forest canopies to examine: (i) change in liana infestation; and (ii) associated changes in tree crown characteristics following the El Niño event of 2015/16.

Overall, this thesis aims to enhance our ecological understanding of lianas in tropical forest tree crowns, focusing on the lesser studied Palaeotropics. Integral to this is the development of a novel method to enable faster, cheaper and more canopy-centred assessment of lianas than possible with traditional assessment methods. Thus, this thesis aims to make both a methodological and substantive contribution to liana studies. The research into the development and testing of a novel UAV-based method for liana assessment (Chapter 3) is indicative of the methodological contribution, whilst the elucidation of liana-environmental relationships (Chapter 4) and temporal changes (Chapter 5) in a Palaeotropical forest canopy adds to our understanding of liana ecology. In the remainder of the Introduction, I detail each research question and present an overview of the relevant literature that forms the context in which the papers are written and their relevance to the state of the literature. I then present an overview of the current state of the papers forming Chapters 3–5 of the thesis and the overall structure of the thesis.

1.2.1 Can UAVs provide a new tool for assessing liana infestation in tropical forest canopies?

Despite the need for monitoring of forest canopies and liana infestation within them, the study of forest canopies has proven challenging. Alterations to forests can be relatively easily studied at ground level, but changes in other levels, and especially in canopies, can be very hard to survey. Therefore, research often remains limited to the understorey and thus, our current knowledge of forest functioning is biased towards this layer and many critical knowledge gaps remain for canopy science (Lowman et al., 2013; Marques et al., 2016; Nakamura et al., 2017). Indeed, Erwin (1983) labelled forest canopies 'the last biotic frontier' and, despite considerable advances in our understanding of canopy ecology, due in part to methodological improvements (Lowman et al., 2013), overall progress has remained slow. Thus, the forest canopy remains one of the world's least-known habitats (Ozanne et al., 2003; Lowman et al., 2012, Lowman et al., 2013).

This difficulty in assessing forest canopies and liana infestation within them is due, in part, to practical difficulties and the limited accessibility of canopies (Barker & Pinard, 2001; Lowman et al., 2012). Lowman and Nadkarni (1995) stated that, depending on the research question being addressed and the available budget, there are a wide variety of canopy access tools to choose from. This is even more true now, in 2019, but nonetheless many of the options available still suffer from the same limitations as addressed by Lowman and Nadkarni (1995). Existing methods for canopy data collection include: (i) high-tech canopy access; (ii) low-tech canopy access; (iii) ground-based observations; and (iv) air-based observations. For each, however, cost, safety, convenience, time, and disturbance are all factors that need to be considered and often have reciprocal negative impacts on each other (Table 1-1).

Table 1-1: Current techniques for study of tropical forest canopies. Generalised features of the four main methods for studying forest canopies are noted with their respective advantages and disadvantages detailed. Examples of literature that have used and/or commented on these methods are given.

Method	Advantages	Disadvantages	References
High-tech (e.g. cranes, towers, canopy walkways, hydraulic lifts, scaffolding, and booms)	- Permanent structures - Temporal replication - Relative ease of access to canopy - Allows collaborative work - Possibility to work at night and/or bad weather	- Limited spatial replication: static, and geographically sparse - Limited spatial scale: sampling cannot reach beyond limits of the structure - Can result in overuse of adjacent trees - Expensive to construct and maintain - Often large enough to alter the local microclimate	Perry & Williams, 1981; Parker et al., 1992; Koch et al., 1994; Lowman & Bouricius, 1995; Schowalter, 1995; Barker, 1997; Stork, 1997; Barker & Pinard, 2001; Stork, 2007; Lowman, 2009; Nakamura et al., 2017
Low-tech (e.g. bole-climbing, rope-climbing, ladders)	- Access to different canopy heights - Shifts easily between trees/sites - Easy to operate alone or in pairs - Easy to replicate between canopies - Relatively inexpensive	- No access to uppermost canopy - Requires time and effort - Only one researcher per rope - Requires specialist skills to operate safely - Limited sampling (must be in close proximity to rope) - Time-consuming	Lowman & Bouricius, 1995; Laman, 1995; Barker & Sutton, 1997; Barker, 1997; Anderson et al., 2015; Nakamura et al., 2017
Ground-based observations (e.g. litter-fall collections, visual est. via binoculars, radio tracking, photography/ hemispherical photography)	- Inexpensive - Safe - Low disturbance - Replicable	- Obscuration of top of canopy - Time-consuming	Munn, 1991; Lowman & Moffett, 1993; Barker & Sutton, 1997; Walther, 2003; Wright et al., 2004; van der Heijden et al., 2010; Cárdenas et al., 2015; Follstad Shah et al., 2017
Air-based observations (remote sensing) (e.g. aircraft, satellite)	- Replicable - Reduction of obscuring vegetation and view of top of the canopy - Low/no disturbance	- Cost-prohibitive - Restricted to specialists - Relatively coarse spatial and temporal resolutions - Cloud obscuration	Hansen & Loveland, 2012; Lehmann et al., 2015; Rocchini et al., 2015; Marvin et al., 2016; Nakamura et al., 2017

High-tech methods for canopy access (e.g. cranes, towers, canopy walkways, hydraulic lifts, scaffolding, and booms) tend to offer relatively safe, easily repeatable canopy access (Parker et al., 1992; Lowman & Bouricius, 1995; Stork, 1997; Stork, 2007). They are largely static, however, and thus limited in their ability to provide information on stand or landscape scale variation (Perry & Williams, 1981; Parker et al., 1992; Lowman & Bouricius, 1995; Schowalter, 1995; Barker, 1997). They are also time-consuming and relatively expensive to construct (Parker et al., 1992; Lowman & Bouricius, 1995; Barker, 1997; Lowman, 2009) and can cause large disturbances and modifications to the forest structure, microclimate, and arboreal animal movement (Perry & Williams, 1981; Parker et al., 1992; Koch et al., 1994; Barker, 1997; Barker & Pinard, 2001).

Low-tech canopy access methods (e.g. bole-climbing, rope-climbing, ladders) are inexpensive and can be deployed where they are needed, allowing increased replication, while typically causing less disturbance than high-tech methods (Lowman & Bouricius, 1995; Laman, 1995; Barker & Sutton, 1997; Barker 1997). However, they do not allow access to all parts of the canopy and are time-consuming and difficult to deploy and use, often requiring specialist skills, and are typically less safe and convenient than high-tech methods (Lowman & Bouricius, 1995; Laman, 1995; Barker & Sutton, 1997, Barker, 1997). They have a high potential for mistakes or malpractice, a wealth of examples of which can be found in the literature. This is particularly dangerous as any mistakes (even minor ones) can result in serious injury or death (Anderson et al., 2015).

Due to these difficulties, surveys designed to focus on the monitoring of forest canopies (especially over larger spatial extents) including liana studies, are often limited to ground-based observations. Examples include: litter fall collections (Wright et al., 2004; Cárdenas et al., 2015; Follstad Shah et al., 2017), radio tracking (Barker & Sutton, 1997), tape recordings (Walther, 2003), mist-nets

(Munn, 1991; Lowman & Moffett, 1993) and, most commonly for liana studies, visual data collection via binoculars (van der Heijden et al., 2010). These ground-based observations circumvent the issues of cost, safety and disturbance, but remain time-consuming and problematic. Remaining on the ground and attempting to examine the canopy through the understory necessarily means that: (i) these data cannot be expected to be accurate, as estimates rather than detailed measurements are taken, which are bound to miss many key details of the canopy and aspects of the ecology of the study species that are not detectable from the ground, or miss inconspicuous canopy species altogether (Walther, 2003; Lowman et al., 2013); and (ii) we have rather little idea about how accurate these data are, as good data for the canopy remain so rare.

Examining forest canopies from above via remote sensing opens a new avenue of research for canopy and liana studies. The definition of remote sensing, for the purpose of this thesis, is the observation of the Earth's surface from a distance with techniques using electromagnetic radiation for: (i) detection – identification of forms and anomalies; (ii) measurement – determining quantitative properties; and (iii) monitoring – repeated observation to assess change (Aggarwal, 2004; Sabins, 2007). Remote sensing approaches can be divided into: (i) passive systems, which record the amount of electromagnetic radiation naturally reflected and/or emitted from the Earth's surface; and (ii) active systems, which produce their own electromagnetic radiation and measure the intensity of the return signal (Rees, 2013).

Remote sensing revolutionised large-scale monitoring of forest canopies (Asner & Martin, 2009; Hansen et al., 2008; 2010; Asner & Alencar, 2010; Sanchez-Azofeifa et al., 2017) as platforms could: (i) assume a viewpoint above the canopy, to ideally examine it at a closer distance, and with less obscuration than possible from the ground (Nadkarni et al., 2011); and (ii) achieve suitable spatial and spectral

resolutions for examining large-scale phenomena. Using satellites or occupied aircraft in this way provides perspectives on the ecological phenomena that are difficult to study from the ground (Rocchini et al., 2015). These methods circumvent many of the limitations of the high- and low-tech methods described above, but they do have their own set of limitations. These platforms have relatively coarse spatial and temporal resolutions, with limited control over what time and area images will be captured (Matese et al., 2015), and suffer from cloud obscuration (particularly in moist forests) (Kussul et al., 2008). Lastly, to deploy an occupied aircraft or to utilise high-resolution satellite images is often very expensive and restricted to specialists, prohibiting the majority of individual researchers from using these technologies (Lowman & Schowalter, 2012).

Therefore, despite the variety of existing methods, the tops of emergent trees remain out of reach for many of them, several are limited in geographical and/or temporal coverage and by cost, and all are limited in spatial and/or temporal resolution. Thus, the highly heterogeneous and rapidly altering properties of canopies, such as lianas, remain exceedingly difficult to measure. Yet comprehensive monitoring of all aspects of forest canopies, including lianas, is essential for detecting and responding to global change. A limited number of studies have utilised occupied aircraft and satellite remote sensing for liana detection (e.g. Marvin et al., 2016), but they are restricted by the limitations of such technologies (as outlined above). As a result, we need a better method for comprehensive measuring and monitoring of canopies. Barker and Sutton (1997) commented that an ideal method would provide flexibility, safety, ease of use, and low establishment and operating costs, while preferably not resulting in damage to trees, epiphytes and other canopy residents.

UAVs have the potential to fulfil each of these requirements, providing a possible tool to map and monitor lianas at larger spatial scales and at more appropriate

temporal scales than is possible with traditional plot-based censuses, while overcoming the limitations of traditional satellite and airborne remote sensing. In 2005, McDermid et al., called for the utilisation of new technologies to advance aerial-surveying techniques and UAVs may answer this call, having been named as having the potential to revolutionise spatial and environmental sciences (Anderson & Gaston, 2013).

UAVs have evolved rapidly in recent years. Initially, demand and developments were driven primarily for military uses, but UAVs were soon recognised to have potential in the consumer market, as well as for scientific data collection purposes. This could be argued to have begun in the 1990s when NASA's Environmental Research Aircraft and Sensor Technology (ERAST) program noted the first major steps towards developing the protocols and capabilities for the use of UAVs in supporting scientific research (Robbins, 1997). Until this point, UAVs tended to be either: (i) capable of carrying powerful and accurate sensors, but large and very expensive; or (ii) small but lacking appropriate payloads to deliver precise/accurate data. Subsequent improvements in the miniaturisation of sensors and electronics resulted in numerous efforts among researchers to develop or modify UAVs for diverse applications (Watts, 2012). The recognition arising from this, that UAVs offer huge potential for many areas of scientific research, spurred significant demand for systems that combine the sensor quality typically found in large aircraft with the portability and cost advantages provided by smaller systems (Valavanis & Vachtsevanos, 2015).

Today, UAVs have become widely available, cheaper, and more user-friendly, with a wide array of options available, both in terms of the platform and sensor type. Various classification schemes for UAVs exist (e.g. Watts et al., 2012; Anderson & Gaston, 2013), but the simplest division is into the two most common types of UAV platform: rotor-based and fixed-wing UAVs. Both platform types exhibit a large

variety of sizes, prices, and sensor payloads, offering system-specific choice to suit particular research needs. Rotor-based UAVs feature an even number of rotor blades (usually four: quadcopters, or eight: octocopters) that spin to provide lift (Floreano & Wood, 2015). This UAV type can be controlled more precisely than their fixed-wing equivalents because the angular velocities of the numerous rotor blades can easily be adjusted (Kumar & Michael, 2012). This also means that rotor-based UAVs are able to ascend and descent vertically, as well as hover over fixed targets. Fixed-wing systems lack these abilities but can usually travel faster and longer than rotor-based systems, therefore covering more ground for surveys.

The benefits of UAV imaging include: (i) cost savings (from replacing humans with UAVs or buying/chartering satellite or airborne data); (ii) being non-labour intensive (including the ability to operate autonomously); (iii) the ability to acquire data from inaccessible environments (such as tall forest canopies); (iv) the higher spatial and temporal resolution of data (and control of these factors); (v) the increased speed of data collection; (vi) the replicability of data collection; (vii) the reduction in atmospheric interference; and (viii) user-control over system choice and flight parameters (Nakamura et al., 2017). Of course, the use of UAVs involves several operating constraints, namely: (i) the restricted payload and flying time; (ii) training required to effectively pilot UAVs; and (iii) risk of complete system loss when operating in adverse weather conditions or complex terrain.

Recent research has highlighted the emerging use of UAVs for enhancing ecological studies (Anderson & Gaston, 2013). UAVs have found applications in numerous fields, including ecosystem processes (e.g. Martin et al., 2011; Mayer et al., 2012; van der Kroonenberg et al., 2012), environmental monitoring and management (e.g. Rango et al., 2009; Chabot & Bird, 2013; Puttock et al., 2015), population ecology (e.g. Goebel et al., 2015; Linchant et al., 2015; Hodgson et al., 2016; 2017; Baena et al., 2017; Sardà-Palomera, 2017) and vegetation dynamics

(e.g. Mathews & Jensen, 2013; Bendig et al., 2014; Zarco-Tejada et al., 2014; Cunliffe et al., 2016; Jing et al., 2017). More recently, UAVs have been successfully adopted for use in tropical forest research. Already they have been shown to be useful for tropical forest monitoring (e.g. Zahawi et al., 2015; Zhang et al., 2016), assessing impacts of fire in tropical peatlands (e.g. Simpson et al., 2016), and determining forest structure (e.g. Ota et al., 2015; Kachamba et al., 2016; Otero et al., 2018).

In Chapter 3 of this thesis, the potential of a consumer-grade, rotary UAV to collect precise and accurate data on the presence and degree of liana infestation in tropical forest canopies in a cost-effective and time-efficient manner is tested for the first time, using ground-based observations as a benchmark. This method should be useful to a range of users including: (i) researchers interested in collecting such data on liana infestation; and (ii) forest managers who may seek to use such data to assist with selective liana cutting for improving yield in timber-producing forests or for forest management to increase carbon storage potential.

1.2.2 What are the important influencing factors on the spatial distribution of liana infestation in Sabah, Malaysia?

Determining the mechanisms responsible for the abundance and distribution of organisms is a central goal of ecology (Krebs, 1972; Brown, 1988). This has proven challenging for lianas due to the aforementioned difficulties in collecting data on liana infestation in tropical forest tree crowns. Perhaps as a result of this, although some previous research has taken place using both trees and lianas to test ecological theory (e.g. O'Brien et al., 1998; 2000; Field et al., 2005), most tests in tropical forests have been focussed exclusively on trees (e.g. Harms et al., 2001; Potts et al., 2004; John et al., 2007; Mangan et al., 2010; LeManna et al., 2017). This research has led to major advances in our understanding of the distribution and abundance of organisms (e.g. Johnson et al., 2017; Chen et al., 2018; Turner et al.,

2018). Analysing only one growth form, however, provides us with rather limited understanding because particular growth forms have convergent life-history traits that may differ from other growth forms (Schnitzer, 2018). Testing ecological theory on non-tree plant groups that co-occur with trees provides a way to address this.

Lianas provide both a complement and contrast to trees to test the generality of ecological theory. Lianas and trees have an overlapping range of functional characteristics (e.g. Gilbert et al., 2006; Asner & Martin, 2015; Isnard & Field, 2015) and are similar taxonomically (Gianoli, 2004; 2015). Lianas exhibit differences from trees in life-history strategies, however, expressing differences in anatomy and physiology (Zhu & Cao, 2009; 2010; Wyka et al., 2013; Angyalossy et al., 2015; Asner & Martin, 2015; Isnard & Field, 2015; Rowe & Speck, 2015; Santiago et al., 2015; Maréchaux et al., 2017). If we can determine the mechanisms that maintain species diversity and control distributions for lianas and determine whether these apply to both lianas and trees, we will be closer to formulating a general understanding of some of the fundamental questions in ecology.

Nakamura et al. (2017) state that rapid advances in our understanding of the mechanisms that drive the spatial and temporal dynamics of forests and their canopies may be envisaged with new technologies. UAVs may prove to be such a technology, by allowing for greater ease of data collection from tropical forest canopies than possible before, which may increase the rate and spatial scales at which we are able to collect liana infestation data. To date, most studies of liana ecology have been conducted at local scales (≤1 ha; e.g. Putz, 1984; Gentry, 1991; Pérez-Salicrup et al., 2001; Mascaro et al., 2004; di Porcia e Brugnera et al., 2019) and, therefore, rarely provide a sample size and spatial scale large enough to examine how lianas are distributed across a landscape and what processes may influence this distribution. The majority of previous studies of liana ecology also

focus on liana stem measurements, due to the difficulties in assessing liana canopy cover from the ground (Marvin et al., 2016; Waite et al., 2019). Liana canopy cover is more directly related to liana–tree competition, however, because liana stems can root a considerable distance away from their location in the canopy (Putz, 1984b; Campbell & Newbury, 1993). By examining how and why lianas are distributed in the forest canopy at a landscape-scale, we can develop our understanding of the mechanisms that may be driving this.

In Chapter 4 of this thesis, the largest and most comprehensive continuous assessment of Palaeotropical tree crown liana infestation, and analysis of environmental variables that may influence this, to date, is undertaken. This aims to enhance our knowledge of liana ecology at landscape scales, and to help us determine what variables may be important for determining increases in liana abundance with climate change into the future. This research may also provide a step towards more comprehensive testing of ecological theory in tropical forests.

1.2.3 How do liana infestation and other concurrent changes in tropical forest canopies alter between years, and can UAVs monitor this?

Tropical forest canopies are frequently affected by short-term environmental changes such as drought and fire events. With the predicted increase in the number and severity of such events (Stork et al., 2009; Phillips et al., 2009; Lee & McPhaden, 2010; Lowman et al., 2013; Mora et al., 2013; Corlett, 2016), an appropriate method of data capture is required. The method should be able to respond quickly to the events and capture data at the appropriate spatial and temporal resolution to meet the needs of the research. As described above, traditional occupied aircraft or satellite platforms may not offer this. Satellites capture data on defined paths with set return frequencies (Nadkarni et al., 2011), which may or may not operate at the temporal scale required (Kussul et al., 2008). Occupied aircraft offer user-set flight dates, but these are scheduled months in

advance with little ability to change this at short notice (Matese et al., 2015). The temporal frequency at which data can be acquired using UAV platforms is more flexible than with traditional platforms (Nakamura et al., 2017). Indeed, UAVs are already proving useful for monitoring short-term fire events (Simpson et al., 2016).

In Chapter 5 of this thesis, a UAV platform was used to collect image data of primary tropical forest in Sabah, Malaysia during and after the 2015/16 El Niño drought. This aims to assess, for the first time, the potential for UAVs to assess short-term change in tropical forests canopies including changes in liana canopy cover in the aftermath of this event, as well as concurrent changes in tree crown variables. Changing climatic conditions, and the associated increases in length and severity of droughts may alter liana infestation and liana impacts on tree canopies. This has important implications for tropical forest carbon storage and sequestration. The use of UAVs provides an effective, reproducible method to monitor changes in tropical forest canopies, providing an archive of imagery that can be built upon to develop time-series data for on-going research.

1.3 A Note on the Papers

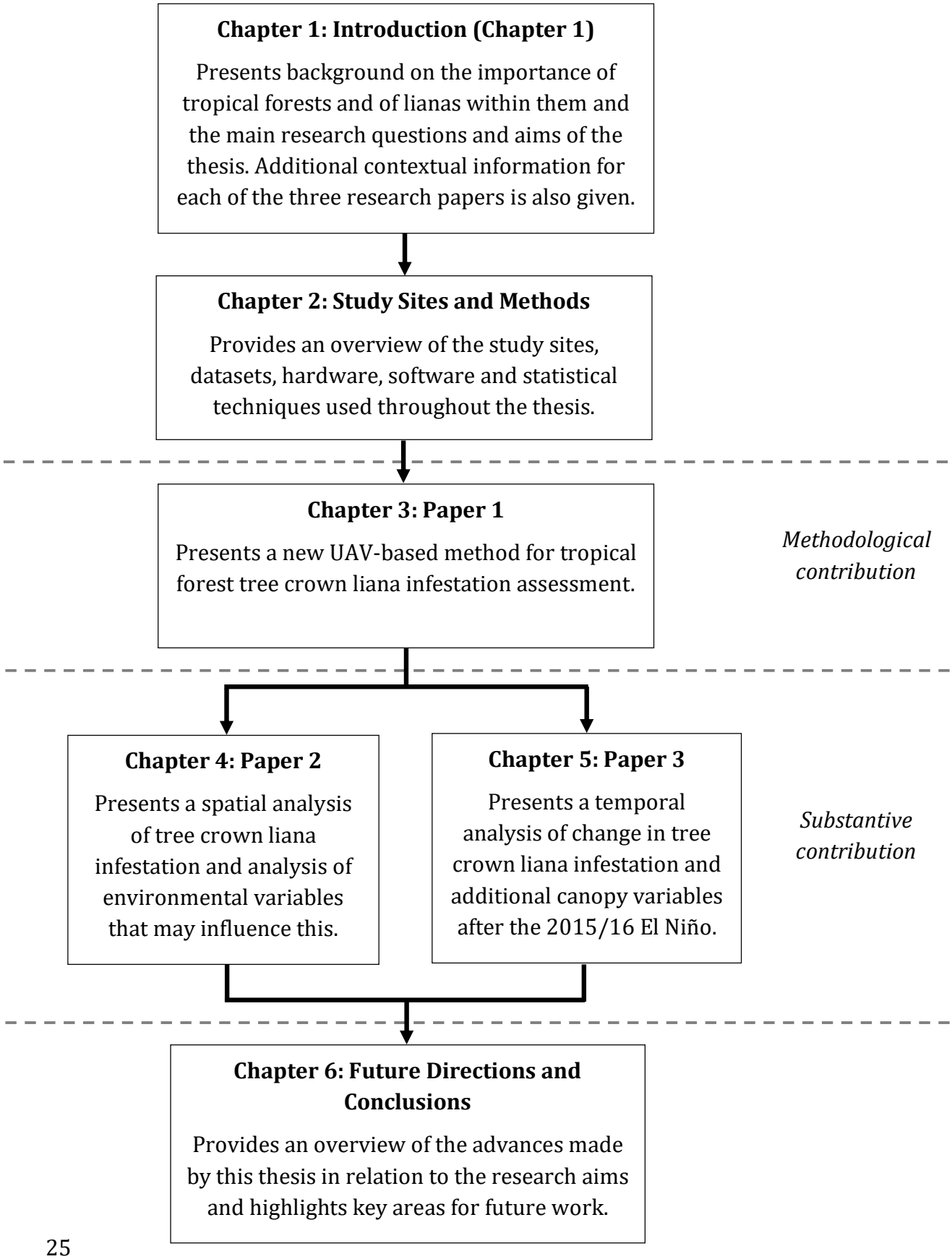
Each of the papers comprising this thesis, which are at various stages of the publication process, are outlined in Table 1-2. The format of the papers has been included as follows: (i) where a paper has been published, I have included the author's accepted manuscript, prior to the journal's typesetting process to keep formatting consistent; and (ii) where the manuscript is in the final stage of preparation but not yet submitted, the most recent version is presented. For (i) there may be, therefore, minor discrepancies between the published version of the paper and the author's accepted manuscript included herein as a result of the copy-editing process. The published version of the paper can be found in Appendix 1. Supporting Information for each paper is provided in Appendix 2.

Table 1-2: The current state of each of the three papers comprising the thesis.

Title	Status (Date accepted)	Journal or (Target Journal)	Page No
A view from above: Unmanned aerial vehicles (UAVs) provide a new tool for assessing liana infestation in tropical forest canopies	Published (2019)	*Journal of Applied Ecology*	41
A ladder to the sky: the roles of tree size and canopy gaps in liana infestation patterns of tropical forest canopy in Sabah, Malaysia	In prep	*Journal of Ecology*	66
Increase in liana infestation in Malaysian tropical forest tree crowns and concurrent canopy changes in the aftermath of the 2015/16 El Niño Event	In prep	*Ecology*	96

1.4 Thesis Structure

Figure 1-1: Overall structure of the thesis.



1.5 Chapter Summary

This chapter has provided an introduction to the main themes of this thesis. The importance of tropical forests and their canopies has been described, and the role of lianas within them has been detailed. The research questions behind the three research papers comprising Chapters 3–5 of this thesis have been given, as well as the overall aims of the thesis. Background information for each of the research papers has been presented, with the intention to provide additional context on the value each paper provides for the discipline. Finally, the status of each of the three papers was given, along with an overview of the structure of the thesis.

Chapter 2: Study Sites and Methods

This chapter provides an overview of the study sites, datasets, hardware, software and main statistical techniques utilised in this thesis. The information provided is intended to supplement that given in each of the papers, and to orient the reader in order to better understand and interpret the results therein. As such, more information related to that given here is presented in each paper, found in Chapters 3 (Paper 1), 4 (Paper 2) and 5 (Paper 3).

2.1 Study Sites

This research took place in two main locations: the Danum Valley Conservation Area and Sepilok Forest Reserve, located ~103 km apart in Sabah, Malaysia (Figure 2-1). The Malaysian state of Sabah occupies ~10% of the island of Borneo, covering an area of 73,631 km^2. At the end of the 1980s, forest cover in Sabah was ~44,750 km^2 (~60% of the state's land area), with 48% of this being designated as Permanent Forest Reserve (~33,585 km^2) or State Parks (~2450 km^2), distributed among primary forest types, including montane, coastal mangroves, freshwater swamps and lowland dipterocarp forests (Marsh & Greer, 1992). By 2010, due to logging and agricultural developments, forest cover was estimated to have dropped to ~37,600 km^2 or ~51% of the state's land area (Reynolds et al., 2011; Gaveau et al., 2014). This included a disproportionate loss of primary lowland dipterocarp forest; these forests occupied ~5,000 km^2 (6.8% of land area) in 1990 (Marsh & Greer, 1992) but by 2010, it was estimated that less than 700 km^2 remained (~0.95% of land area) (Reynolds et al., 2011). The existence and preservation of the Permanent Forest Reserves and State Parks protected some important forest sites, meaning that Sabah remains heavily forested relative to regional standards but, still, there remains little undisturbed lowland dipterocarp forest. Over half of the undisturbed lowland dipterocarp forest remaining is accounted for by the 438 km^2 Danum Valley Conservation Area.

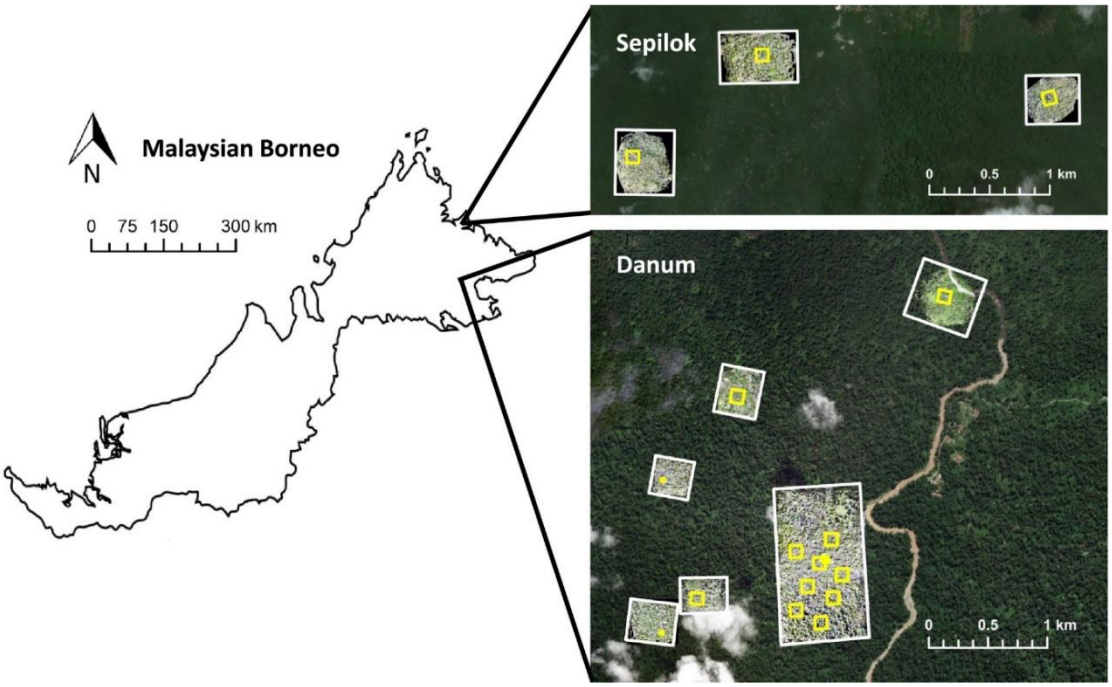


Figure 2-1: Location of the two study sites used in this thesis, Danum Valley Conservation Area and Sepilok Forest Reserve, which are located in the state of Sabah, Malaysia, on the island of Borneo, Southeast Asia. The orthomosaics created from the UAV surveys conducted (150 ha) are shown outlined in white on top of satellite imagery, and the field plots (14.15 ha) used in this thesis are outlined in yellow. Satellite imagery source: DigitalGlobe WorldView2 RGB imagery. Reproduced from Waite et al., 2019.

2.1.1 Danum Valley Conservation Area

In the southeast of the state of Sabah, the Sabah Foundation holds a 100-year-old timber concession of 9,730 km^2, 9.7% of which has been reserved for conservation. Included in this reservation is the 438 km^2 uninhabited area of lowland forest at Danum Valley: the Danum Valley Conservation Area (4˚57'N, 117˚42'E), which has been the site for a field centre and collaborative research programme since the opening of the Danum Valley Field Centre on the 29th August, 1986 (Marsh & Greer, 1992). Indeed, the scientific outputs from research at Danum Valley have made major contributions to multiple disciplines, and the Danum Valley Field Centre is widely regarded as the most productive and influential field station in the Palaeotropics (Reynolds et al., 2011).

Mean annual temperature at Danum Valley Conservation Area is 26.7°C, while mean annual rainfall is 2,844.1 mm. The rainfall pattern is influenced by the edge effects of two monsoons: the wettest months fall between November to March due to a north-eastern monsoon while drier, more consistent conditions occur due to a southwestern monsoon in June and July (Marsh & Greer, 1992; Walsh & Newbery, 1999; Clark & Walsh, 2006). The Danum Valley Conservation Area lies at a moderate elevation, with 9% of the area above 860 m above sea level (the conventional lower limit for montane forest) and another 36% at lower elevations on slopes exceeding 25°. There are three major summits in the Conservation Area; Mount Nicola (917 m) on the northern perimeter, Mount Danum (1,093 m) in the centre, and Mount Tribulation (861 m) in the upper Segama highlands to the southwest (Marsh & Greer, 1992). The terrain is generally rugged, set in a complex, actively eroding landscape with soils consisting of chromic and orthic luvisols, euthric cambisols and lithosols lying mainly on mudstone and sandstone (Newbery et al., 1992). The Danum Valley Conservation Area is characterised by lowland, evergreen mixed dipterocarp forest, with dipterocarps making up 88% of the total volume of large trees (Whitmore & Burnham, 1975).

The plots surveyed in this thesis correspond to existing plots set up throughout the Conservation Area. These are three 0.05 ha INDFORSUS plots, set up by an international research project funded by the European Commission (Foody et al., 2001), three 1 ha Amazon Forest Inventory Network (RAINFOR) plots, and the Centre for Tropical Forest Science (CTFS) 50 ha permanent research plot (Figure 2-1). For Paper 1 (Chapter 3), eight 1 ha plots within the CTFS 50 ha plot were used, whereas for Papers 2 and 3 (Chapters 4 and 5) the entire 50 ha plot was used. One of the benefits of utilising existing plots is that collaborations and analyses of multiple datasets become possible. Furthermore, by using existing plots the data collected, and research conducted, in this thesis will add to the body of knowledge present for these areas and can, in turn, be easily integrated into future studies.

2.1.2 Sepilok Forest Reserve

Sepilok Forest Reserve (5°52'N, 117°56'E) is a 4,924 ha protected area, located on the northeast coast of the island of Borneo and within Sabah, Malaysia. It is located 11 km west of the town of Sandakan, where mean annual temperature ranges from 26.7-27.2°C and mean annual rainfall averages 2,929 ± 134 mm. In a similar manner to the Danum Valley Conservation Area, the wettest months fall between November and February, (Nilus, 2004). Founded in 1931 by the Sabah Forest Department's Forest Research Centre, the reserve has been subjected to forest disturbance in the past, with 670 ha in the southern and north-eastern areas experiencing extraction of ~24,262 m^3 of trees via hand logging over the period 1919-1957 (Fox, 1973). The northern areas experienced additional disturbance when lianas and some non-timber trees were removed in several hundred hectares of forest in 1958.

Within the Sepilok Forest Reserve, covering elevations of 0-180 m, four different soil types give rise to four distinct forest types: alluvial lowland dipterocarp, sandstone hill dipterocarp, kerangas (heath) and mangrove. Plots surveyed in this thesis were located in the alluvial, sandstone hill and kerangas forest. Alluvial soils are red-yellow podzols, derived from low mudstone and sandstone (Iqbal et al., 2005). The topography of such areas is subdued, with low mudstone hills rising only 15 m. In stark contrast to this, the topography of the sandstone hills comprises steep slopes and narrow crests. These soils are derived from sandstone bedrock interbedded with mudstone, and red-yellow podzols dominate. Lithosols are present, however, in the upper slopes. Kerangas forest is restricted to the eastern portion of the Sepilok Forest Reserve, forming on podzols on the lower dip slopes of the sandstone cuesta landforms (DeWalt et al., 2006).

Each soil type has inherently different properties, arrayed along an axis of water and nutrient availability: alluvial > sandstone hill > kerangas. In the Sepilok Forest

Reserve, alluvial soils were found to be the most nutrient rich, with greater concentrations of total nitrogen, phosphorus and nitrate, as well as higher gravimetric soil water content and storage than sandstone soils (Dent, 2004; Baltzer et al., 2005). Sandy and coarse kerangas soils typically experience lower nutrient and water retention capacities than their more finely-textured alluvial counterparts (Whitmore & Burnham, 1975). These variances cause structural and compositional differences between the tree communities on the three soil types (Nilus, 2004). Generally, alluvial forest trees are less abundant and larger-stemmed than those in kerangas forest, while sandstone hill forest trees are intermediate in both number and size of stems (Fox, 1973). Tree species diversity follows the soil nutrient rankings, with alluvial forests possessing the highest diversity and kerangas forests the lowest.

In this thesis, three 1 ha plots were surveyed, corresponding to existing plots set up by DeWalt et al. (2006) in the alluvial, sandstone hill and kerangas forest (Figure 2-1). The use of plots in each of these distinct forest types provides the opportunity to assess the performance of the novel UAV-based method for collecting data on liana infestation across multiple forest types.

2.2 Datasets

An overview of the datasets used throughout this thesis is given in Table 2-1. These include pre-existing datasets, those I contributed to the collection of, and those that I collected in their entirety.

Table 2-1: An overview of the datasets used throughout this thesis. The type of dataset, as well as the plots (described above) covered by each are indicated. Information is given on the person(s) responsible for the data collection, the funding source, date of collection, any additional relevant details and whether the datasets were existing or are novel to the thesis. Finally, the paper(s) in which the datasets are used is indicated.

Dataset	Plots Covered	Collected By (Funded By)	Date of Collection	Details	Existing or Novel	Paper Used In
LiDAR Data	All plots in Danum	NERC Airborne Research Facility (ARF) (NERC)	2014	LiDAR data were collected from a Dornier 228 aircraft, using the Leica ALS50-II LiDAR system capable of simultaneous discrete and full waveform recording. The full waveform data were delivered as LAS 1.3 (binary data) files.	Existing	Paper 2
Soil Data	50 ha Plot, Danum	David Burslem, Ben Turner, Jim Dalling, Xubing Liu and Graham Zemunik (NERC grant NE/M004848/1)	2016	D. Burslem, B. Turner, J. Dalling and two postdocs, X. Liu and G. Zemunik, collected the soil samples in the field. All soil analyses were conducted in Ben Turner's lab in Panama (late 2016–2018).	Existing	Paper 2
Topographic Data	50 ha Plot, Danum	Danum Valley Research Assistant team (HSBC Malaysia and the University of Zurich)	2009–2011	A team of research assistants led by Alex Karolus collected topographic data.	Existing	Paper 2

Liana Ground Surveys						
(i)	All plots in Danum (eight 1 ha plots within 50 ha plot)	Catherine Waite and Geertje van der Heijden (University of Nottingham, PhD Award to C.W and Anne McLaren Research Fellowship to G.v.d.H)	2016	G. van der Heijden was responsible for original plan to collect liana stem measurements on the ground. C. Waite proposed additional collection of more detailed crown infestation assessments in order to link ground-based liana assessments to UAV data	Novel	Paper 1
(ii)	All plots in Sepilok	Catherine Waite (University of Nottingham, PhD Award)	2016		Novel	Paper 1
UAV Surveys						
(i)	All plots in Danum (entire 50 ha plot)	Catherine Waite (University of Nottingham, PhD Award)	2016	C. Waite collected UAV data in 2016 for use in this thesis. In 2017, C. Waite was invited to act as a Research Assistant and contribute to the NERC-funded Spatio-TEmporal Dynamics of Forest Response to ENSO Drought (STEED) project, collecting additional UAV data for use in publications resulting from the STEED project as well as this thesis.	Novel	Papers 1, 2, & 3
(ii)	All plots in Sepilok	Catherine Waite (University of Nottingham, PhD Award)	2016		Novel	Paper 1
(iii)	All plots in Danum (entire 50 ha plot)	Catherine Waite (Research Assistant for NERC STEED Grant)	2017		Novel	Paper 3
UAV Image Processing	All plots in Danum and Sepilok (entire 50 ha plot)	Catherine Waite (University of Nottingham, PhD Award)	2016–2017	All images collected during the UAV surveys were processed to form: (i) orthomosaics; (ii) digital elevation models; (iii) digital terrain models; (iv) digital surface models; (v) point clouds; and (vi) 3D models, for every plot.	Novel	Papers 1, 2 & 3

2.3 UAV Hardware and Software Specifications

A suitable UAV for environmental research should be robust, stable, flight-programmable and possess a high-quality sensor (Anderson & Gaston, 2013; Hodgson & Koh, 2016). For accurate and precise data capture, a rotor-based UAV is the most appropriate and best suited type as they experience less in-flight vibration than their fixed-wing equivalents (Wallace et al., 2011). As well as this, the specific nature of data collection for this thesis necessitates the use of UAVs in a dense tropical forest. Therefore, it was determined that a suitable UAV would be small and lightweight, to increase portability and allow easier transportation to the plots, and ensure easier manoeuvrability during flight in the tropical forest.

An aim of this research was to develop a new method of liana assessment that would be rapid and cost-effective, as well as accessible to other users such as scientists and forest managers. Therefore, to ensure the new method would not be cost-prohibitive, and would be most easily transferable, a consumer-grade UAV was necessary. As the world's leading professional and consumer UAV manufacturer, DJI offers a range of UAV models. Utilising a DJI UAV model increases the transferability of the new method. It will be easier for others to obtain either the same UAV, or (as is often the case given the rapidly developing technology) later versions of the UAV that may include additional features or updated payload specifications, but will adhere to the same core principles as the model used for this research. The need for an accessible, consumer-grade UAV also precludes the use of expensive sensor-types such as multispectral or LiDAR. As a result, a three-waveband red-green-blue (RGB) sensor was suitable.

As a result of these considerations, the UAV selected was a small, lightweight, agile, consumer-grade quadcopter UAV: a DJI Phantom 3 Advanced, equipped with an integrated three-waveband (RGB) high-quality camera, mounted on a three-axis, gyro-stabilised gimbal. In addition to the quadcopter itself, a flight controller and

downlink monitor were essential components of the UAV system, allowing for flight-planning and control of the UAV in the field. An SD card was also necessary for image storage.

As well as the base UAV system components, additional equipment and external software was sourced. The DJI Phantom 3 Advanced exhibits maximum flight times of ~23 minutes, so additional batteries and portable charging hubs were required for prolonged field surveys such as those undertaken in this thesis. A total of five additional batteries were purchased to bring the total to six batteries, allowing a total flight time ~2 hours per day. Also, propeller damage is quite common in UAV flights, even those taking place in open spaces. The operating environment of this research is dense tropical forest which increases the risk of propeller damage, so spare propellers were purchased to allow surveying to continue with minimal interruptions in case of damage. A purpose-designed backpack to house the UAV, flight controller, additional batteries, charger, and propeller sets was used to protect the UAV in transit and enhance portability in the field. The DJI purpose-built software (DJI GO) enables calibration and control of the UAV in manual situations but has limited automated abilities. Therefore, separate software was required to allow for pre-flight planning and automation of the UAV surveys. The software selected for this was Map Pilot for DJI versions 1.5.1 – 2.4.2, a low-cost surveying app with the capability to fulfil these requirements.

The UAV and integrated sensor, together with the battery, remote controller and operating software, work synergistically to comprise a system capable of flight planning, aerial surveying, image capture and storage. The hardware and software specifications of this UAV system are given below in Table 2-2.

Table 2-2: UAV hardware and software specifications. Individual components of the UAV system (including the aircraft, camera, remote controller, battery, and associated software) are listed alongside their specifications, as provided by the manufacturers (DJI and Map Pilot).

Aircraft	
Weight (inc. battery & propellers)	1280 g
Diagonal Size (propellers excluded)	350 mm
Max Ascent Speed	5 m/s
Max Descent Speed	3 m/s
Max Speed	16 m/s
Max Tilt Angle	35°
Max Flight Time	~23 min
Operating Temperature Range	0° – 40°C
Satellite Positioning Systems	GPS/GLONASS
Camera	
Sensor	1/2.3" CMOS 12.4 megapixel
Lens	94° field of view 20 mm f/2.8 focus
ISO Range	100-3200 (video) 100-1600 (photo)
Electronic Shutter Speed	8 – 1/8000s
Image size	4000x3000
Photo	JPEG, DNG (RAW)
Video	MP4, MOV (MPEG-4 AVC/H.264)
Supported SD Cards	Micro SD Max capacity: 64 GB Class 10 or UHS-1 rating required
Remote Controller	
Operating Frequency	2.4000 – 2.483 GHz
Max Transmission Distance	FCC Compliant: 3.1 mi (5 km) CE Compliant: 2.2 mi (3.5 km) (Unobstructed, free of interference)

Battery	6000 mAh LiPo 2S
Video Output Port	USB
Battery	
Capacity	4480 mAh
Voltage	15.2 V
Type	LiPo 4S
Energy	68 Wh
Net weight	365 g
Max Charging Power	100 W
App (for UAV setup and calibration)	
Mobile App	DJI GO
Live View Working Frequency	2.4 GHz ISM
Live View Quality	720P @ 30fps
Latency	200 ms (depending on conditions and mobile device)
Required Operating Systems	iOS 8.0 or later Android 4.1.2 or later
App (for automated surveys)	
Mobile App	Map Pilot for DJI
Required Operating Systems	iOS 11.0 or later

2.4 UAV Image Processing

As a result of the UAV surveys conducted in 2016 and 2017, a total of 37,094 UAV images (198.1 GB) were collected. Image processing was used to create: (i) orthomosaics; (ii) digital terrain models; (iii) digital surface models; (iv) digital elevation models; (v) point clouds; and (vi) 3D models, for each individual plot. A buffer of surrounding forest was included for all plots to minimise edge effects. All products were geo-referenced to the WGS84 UTM Zone 50N projected coordinate system. Image processing was undertaken using the program Agisoft Photoscan versions 1.3.0 – 1.4.2 (Agisoft LLC). This is computer vision Structure from Motion

(SfM) software, which uses the fundamental principles of photogrammetry, combined with robust algorithms from computer vision. In doing so, it uses bundle adjustment algorithms to simultaneously solve for the location of images with respect to each other, and to the objects viewed within them. Using an incremental approach, features in individual images are matched to corresponding features in additional images and are extracted, with the same process repeated on sequential image pairs, incorporating more images at each iteration until a seamless panorama is produced (Dandios & Ellis, 2013; Bemis et al., 2014; DeBell et al., 2015; Song et al., 2016). SfM-photogrammetry enables the matching of points from images of differing scales, view angles and orientations, and has therefore proven advantageous for use with UAV imagery (Rosnell & Honkavaara, 2012; Turner et al., 2012; Fonstad et al., 2013). Published literature using SfM-photogrammetry for ecological and conservation assessments started to emerge ~2011, but have already proven revolutionary (Anderson & Gaston, 2013), and include applications in the fields of vegetation dynamics (e.g. Mathews & Jensen, 2013; Bendig et al., 2014; Zarco-Tejada et al., 2014; Cunliffe et al., 2016; Jing et al., 2017) and population ecology (e.g. Hodgson et al., 2016; Baena et al., 2017).

2.5 Statistical Analyses

The research papers comprising Chapters 3–5 of this thesis make both a substantive and methodological contribution to research on lianas in tropical forests. Appropriate statistical analyses were integral to these papers, and needed to be capable of validating the novel UAV method by examining the concordance between data collected by the UAV and traditional ground-based data in Paper 1 (Chapter 3), and modelling the relationships between liana infestation and environmental variables (Paper 2, Chapter 4) and how these may change through time (Paper 3, Chapter 5). Commonplace statistical analyses are not addressed here but are presented within the relevant paper(s) in which they are used.

Detailed below is additional information on two of the main statistical analysis techniques employed in this thesis, which are less commonplace. This provides background on the use of these statistical methods, and their relevance to the particular research questions to which they are applied in each of the papers.

2.5.1 Modell II regression

When the explanatory and response variables of a regression equation are both not controlled by the research, there are errors associated with the measurements of x and y. Such is the case in the first paper of this thesis (Chapter 3). Here, the ability of UAVs to be used as a tool to identify liana infestation is tested using traditional ground-based measurements as a benchmark. Both methods of assessment (ground-based and UAV-based) result in estimates of crown liana cover and, therefore, both contain errors. Ordinary Least Squares (OLS) regression, where varying y values (i.e. UAV-derived data) are compared to fixed (i.e. 'true') x values (i.e. ground-derived data), would be inappropriate as it underestimates the slope of the linear relationship between the variables when both contain error (Legendre & Legendre, 1998). Instead, for situations such as this, Modell II regression should be used to take account of measurement errors in both the x and y variables.

2.5.2 Boosted regression tree modelling

Ecologists frequently use models to detect and describe patterns, identifying variables with the most explanatory power, and to predict to new situations. In cases such as that presented by Paper 2 (Chapter 4), where complex datasets with largely unknown relationships and potential variable interactions are present, it is appropriate to use statistical modelling techniques capable of fitting nonlinear relationships between a response and its predictors, as well as determining variable interactions.

Boosted regression tree modelling (BRT) is a combination of statistical and machine learning techniques. The method differs from conventional regression, which aims to fit a single, parsimonious model, and instead uses an ensemble method for statistical model fitting. BRT combines the strength of two algorithms: (i) regression trees (models that relate a response to their predictor by recursive binary spits); and (ii) boosting (an adaptive method for combining many simple models to improve predictive performance). A BRT model can be understood as an additive regression model in which each individual term is a simple regression tree, fitted in a forward, stagewise fashion. To avoid overfitting to training data, tree models are trained on one subset of the data and evaluated on another, in a process that may be repeated many times (Jafari et al., 2014).

Advantages of the BRT method include the ability to: (i) handle different types of predictor variables; (ii) accommodate missing data; (iii) fit complex, nonlinear relationships; and (iv) automatically handle interaction effects between predictors with; (v) no need for prior data transformations or elimination of outliers (Leathwick et al., 2006; Elith et al., 2008). Although BRT models are complex, they can be summarised in ways that give powerful ecological insights, and their predictive performance is superior to most traditional modelling methods (Elith et al., 2008).

2.6 Chapter Summary

This chapter has provided information on the study sites, datasets, hardware, software and main statistical techniques utilised in this thesis. This should provide a good basis to understand the study location and datasets, and well as specifics of the UAV-platform and software that will be referred to throughout this thesis. Further details of the methods specific to each paper are given in the following Chapters (3–5), accompanied by subsequent in-depth analyses and discussions.

Chapter 3: A view from above: Unmanned Aerial Vehicles (UAVs) provide a new tool for assessing liana infestation in tropical forest canopies

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Authors' Contributions: C.E.W., G.M.F.v.d.H., R.F., and D.S.B. designed the research; C.E.W. performed the UAV data capture and processing, analysed the data, and wrote the paper; G.M.F.v.d.H. was responsible for ground data collection; all authors developed the analytical approach, contributed to manuscript revisions, and approved publication.

3.1 Abstract

1. Tropical forests store and sequester large quantities of carbon, mitigating climate change. Lianas (woody vines) are important tropical forest components, most conspicuous in the canopy. Lianas reduce forest carbon uptake and their recent increase may, therefore, limit forest carbon storage with global consequences for climate change. Liana infestation of tree crowns is traditionally assessed from the ground, which is labour-intensive and difficult, particularly for upper canopy layers.

2. We used a lightweight unmanned aerial vehicle (UAV) to assess liana infestation of tree canopies from above. It was a commercially available quadcopter UAV with an integrated, standard three-waveband camera to collect aerial image data for 150 ha of tropical forest canopy. By visually interpreting the images, we assessed the degree of liana infestation for 14.15 ha of forest for which ground-based estimates were collected simultaneously. We compared the UAV liana infestation estimates with those from the ground to determine the validity, strengths and weaknesses of using UAVs as a new method for assessing liana infestation of tree canopies.

3. Estimates of liana infestation from the UAV correlated strongly with ground-based surveys at the individual tree and plot level, and across multiple forest types and spatial resolutions, improving liana infestation assessment for upper canopy layers. Importantly, UAV-based surveys, including the image collection, processing and visual interpretation, were considerably faster and more cost-efficient than ground-based surveys.

4. *Synthesis and applications.* Unmanned aerial vehicle image data of tree canopies can be easily captured and used to assess liana infestation at least as accurately as traditional ground data. This novel method promotes reproducibility

of results and quality control, and enables additional variables to be derived from the image data. It is more cost-effective, time-efficient and covers larger geographical extents than traditional ground surveys, enabling more comprehensive monitoring of changes in liana infestation over space and time. This is important for assessing liana impacts on the global carbon balance, and particularly useful for forest management where knowledge of the location and change in liana infestation can be used for tailored, targeted and effective management of tropical forests for enhanced carbon sequestration (e.g. REDD+ projects), timber concessions and forest restoration.

3.2 Introduction

Tropical forests and their canopies play a crucial role in the maintenance and provision of unique biodiversity and essential ecosystem services to all life on Earth (Lowman & Schowalter, 2012; Ozanne et al., 2003). One of the most important ecosystem services that tropical forests provide is their ability to store and sequester carbon (Pan et al., 2011). Managing tropical forests for carbon sequestration, therefore, provides a key opportunity to mitigate some of the effects of climate change resulting from increasing atmospheric CO_2 concentrations (Canadell & Raupauch, 2008).

Lianas (woody vines) are conspicuous components of tropical forests, where they peak in abundance, biomass and species richness (Schnitzer & Bongers, 2002). Lianas use the structural biomass of trees to deploy leaves in the canopy, thus investing relatively more resources in producing an extensive leaf canopy than in woody tissue. Lianas, therefore, disproportionately contribute to the forest canopy: liana leaves can comprise up to 30% of forest leaf area but only up to 5% of woody stem biomass of tropical forests (van der Heijden et al., 2013). Liana abundance and biomass have increased over the last few decades (Schnitzer & Bongers, 2011). Consequently, lianas have proliferated in the forest canopy,

indicated by an increase in their contribution to leaf productivity, as well as in the number of tree crowns infested (Ingwell et al., 2010; Wright et al., 2004). Partly due to their extensive canopies, lianas aggressively compete with trees, reducing tree growth (Ingwell et al., 2010; van der Heijden & Phillips, 2009), fecundity (Kainer et al., 2014), survival (Ingwell et al., 2010; Phillips et al., 2005) and, consequently, forest biomass and net carbon uptake (van der Heijden et al., 2015). Lianas pose a particular problem for managed forests, where they can substantially hinder carbon sequestration and forest restoration (e.g. Marshall et al., 2017). Liana cutting is often used to enhance carbon uptake (van der Heijden et al., 2015; Marshall et al., 2017); however, this is expensive and labour-intensive to perform over large extents. The ability to identify where liana management would be most beneficial would, therefore, help target management of tropical forests.

Being able to accurately monitor the presence and degree of liana infestation in forest canopies over time and space is, therefore, important for determining whether and where liana impacts are high and/or may be increasing, particularly in managed tropical forests. Due to practical difficulties in accessing tropical forest canopies (Nakamura et al., 2017), assessing liana canopy infestation is traditionally done by ground-based surveys (e.g. van der Heijden et al., 2010). These are labour- and time-intensive, and consequently limited in their spatial and temporal coverage, and lianas, therefore, remain understudied in tropical forests (Marvin et al., 2016). Furthermore, the stratified nature of tropical forests often limits the visibility of canopy and emergent tree crowns, affecting the reliability of ground-based estimates for them. As these larger trees tend to store and sequester the most carbon and, due to high light conditions in their crown, often harbour lianas (van der Heijden et al., 2008), reliable assessment of liana infestation for top-of-the-canopy trees is especially important.

Assessing lianas from a vantage point above the canopy should be feasible using remote sensing platforms which offer views of the canopy with much less obscuration by vegetation than possible from the ground (Nadkarni et al., 2011). However, satellite and many airborne platforms generally provide data which are too coarse in temporal or spatial resolution for this task, too expensive at very fine resolutions, and frequently suffer from cloud obscuration, especially in moist forests. Workarounds exist: using hyperspectral and LiDAR sensors, the Carnegie Airborne Observatory (CAO) was able to accurately map heavy liana infestation across the forests of Panama (Marvin et al., 2016). The use of such sensors is very expensive and restricted to specialists, however, prohibiting their accessibility to the majority of researchers and forest managers. Furthermore, such remote sensing campaigns are typically carried out as one-time operations, so frequent monitoring is difficult (Xue & Su, 2017).

Unmanned Aerial Vehicles (UAVs) with sensors overcome most of the aforementioned limitations of remote sensing platforms (Cunliffe et al., 2016). They can acquire remotely sensed data from relatively inaccessible environments, and thus are useful for measuring and (long-term) monitoring of forest canopies (Kachamba et al., 2016; Paneque-Gálvez et al., 2014; Zahawi et al., 2015; Zhang et al., 2016). Additionally, UAVs can capture data at even finer temporal and spatial resolutions than satellite and manned-airborne remote sensing (Nakamura et al., 2017). This is especially important because visually distinguishing lianas from trees requires ultra-fine resolution (mm-cm) image data: liana leaves grow among the leaves of the trees in which they are located, becoming embedded in the canopy, and are also heterogeneous in nature, as lianas are phylogenetically and functionally highly diverse (Burnham, 2004; Gentry, 1991). Because their physical traits vary, leaves of a given liana species may look very different or very similar to other liana species or the tree in which they are located. Additional textural context, such as leaf shape or arrangement, could allow improved discrimination

of liana leaves from tree leaves in cases where spectral discrimination is unfeasible. Thus, UAVs and the enhanced spatial resolution they offer are potentially effective for assessing canopy-level liana infestation. However, even though UAVs have been used to study other canopy phenomena (e.g., Zahawi et al., 2015); thus far, they have not been used to study lianas.

Here we examine, for the first time, the applicability of UAV-derived image data to assess the presence and degree of liana infestation in tropical tree canopies, using ground-based observations as a benchmark. Specifically we aim to assess the validity of utilising a consumer-grade UAV and camera as a new method for collecting data on liana infestation, by: (i) assessing inter-observer bias in classifying liana infestation from UAV images (reproducibility between observers); (ii) evaluating the strength of the correlation between UAV- and ground-derived measures of liana infestation on individual tree- and plot-levels, and for different canopy strata (accuracy and reproducibility against benchmarked method); and (iii) comparing input time and costs between ground and UAV surveys of liana infestation (efficiency against a benchmarked method).

3.3 Methods

3.3.1 Study sites

Ground and UAV-based surveys were conducted in two sites across eastern Sabah, Malaysia: Danum Valley Conservation Area (Danum) (4°57’ N, 117°42’ E) and Sepilok Forest Reserve (Sepilok) (5°52’ N, 117°56’ E) (Figure 3-1). Danum is characterised by lowland, evergreen dipterocarp forest, covering ~43,800 ha, and Sepilok by alluvial lowland dipterocarp, sandstone hill dipterocarp, and kerangas forests, covering ~4,300 ha. We surveyed seventeen plots: eight 1 ha plots located in the Center for Tropical Forest Science (CTFS) 50 ha plot, three additional 1 ha plots (Berry et al., 2008), and three 0.05 ha circular plots (Foody et al., 2001) in

Danum and three 1 ha plots in Sepilok located in the alluvial, sandstone hill, and kerangas forests (Nilus, 2004).

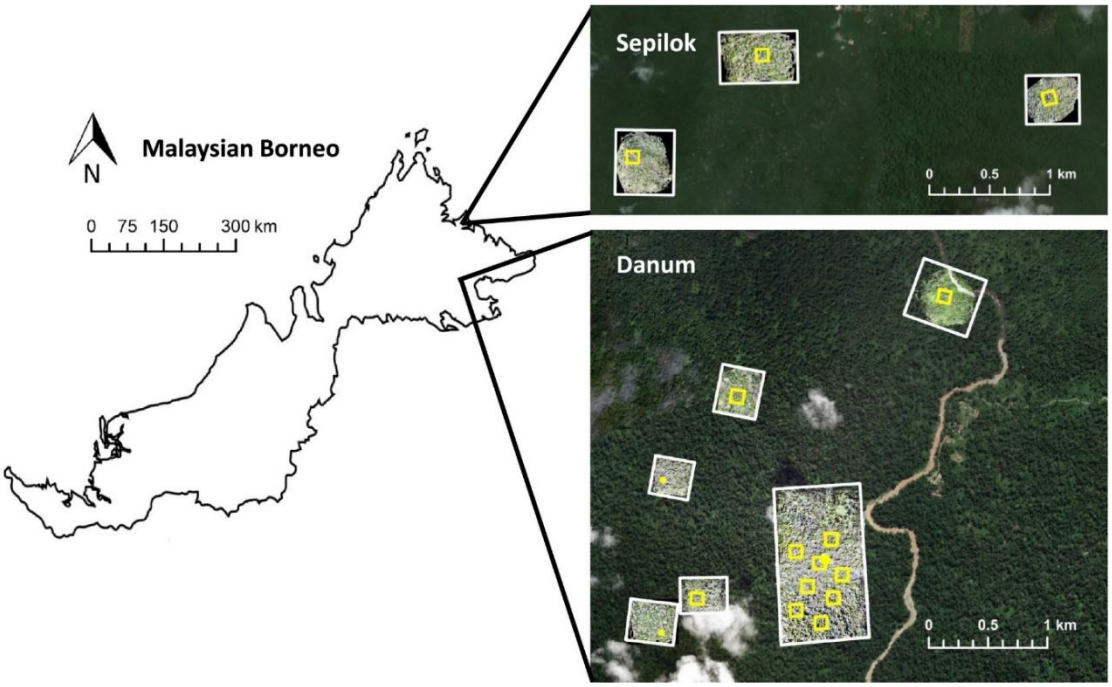


Figure 3-1: Location of the 2 study sites and 17 plots, which are in the state of Sabah, Malaysia, on the island of Borneo, Southeast Asia. The orthomosaics created from the UAV survey (150 ha) are shown outlined in white on top of satellite imagery, and the plots (14.15 ha) outlined in yellow. Satellite imagery source: DigitalGlobe WorldView2 RGB imagery.

3.3.2 Ground-based data collection and liana assessments

We classified the liana load carried by each tree ≥10cm diameter at breast height (DBH) within the plots using two methods: (i) crown occupancy index (COI); and (ii) percentage liana cover (%LC). The COI expresses liana load in the tree crown on a simple five-point 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). This index is widely used in liana research and accurately measures liana loads at both the individual tree- and site-level with little inter-observer bias (van der Heijden et al., 2010). Percentage liana cover (%LC) is a more detailed estimate, expressed as the mean of four compass quadrants into which the tree

crown is visually spilt and percentage of the crown covered by lianas estimated to the nearest 5% (cf. Marvin et al., 2016).

The plot corners (or mid-points for the 0.05 ha plots) and individual trees ≥10cm DBH within each plot were georeferenced using a handheld GPS unit (Garmin eTrex Vista HCx), allowing individual tree crowns to be identified and cross-referenced in the UAV images. We also assigned each tree ≥10cm DBH a value indicating the light level its crown received using the crown illumination index (CII) (Clark & Clark, 1992). This ordinal-scale index is more-or-less equivalent to canopy stature (1 = understorey, 2 = lower canopy, 3 = mid canopy, 4 = upper canopy, 5 = emergent); it helped identify individual trees on the UAV image data and allowed comparison across different tree canopy statures. Tree maps of the plots, measuring the distance of each trunk to the south-easternmost plot corner on the x and y axis were also used to help locate the trees in the UAV image data.

The CII, COI and %LC values were assigned by two independent observers, who discussed their estimates in the field and agreed final values for each tree. Due to time-constraints in the field, in one of the Danum plots %LC data were not collected, and in the Sepilok plots we only collected data for higher canopy-level trees.

3.3.3 UAV data collection and liana assessments

We acquired images of the forest canopy using a lightweight, agile, inexpensive, commercially available quadcopter UAV: a DJI Phantom 3 Advanced equipped with an integrated three-waveband (RGB) camera, mounted on a 3-axis, gyro-stabilised gimbal. The high-quality Sony EXMOR 1/2.3" 12-megapixel camera has a narrow 94^{o} field of view lens (35 mm format equivalent: 20 mm) reducing 'fish-eye' image distortion, and an f/2.8 aperture and 8s–1/8000s shutter speed reducing image blur. The UAV possesses GPS and GLONASS positioning to enable autonomous

flights of up to ~23 minutes. Each image is geo-tagged with the GPS location and altitude of the UAV at the point of capture.

The plots were flown using the automatic mapping software Map Pilot version 1.5.1, with predetermined flight plans with the same parameters (speed: 4 m/s; image overlap at ground-level: 90% forward, 90% side; altitude: 30 m and 60 m above canopy surface) in parallel tracks that covered the plot and a 'buffer' of surrounding vegetation to minimise edge-effects affecting the images of the plot in processing. High image overlap at ground-level was necessary to maintain adequate overlap for producing orthomosaics at canopy-level (for more information see Appendix 2 S2.3.1). We identified canopy gaps large enough to allow the UAV to be launched/landed, and manually piloted it through, to ensure maximal pilot control and minimal risk of collisions. The flights were conducted during calm conditions to prevent wind effects on leaves (McNeil, 2016) and, where possible, when there was even cloud cover to ensure diffuse radiation and minimise shadowing in the canopy – improving clarity in the images and aiding liana identification. All flights took place concurrently with the ground assessments in May and June 2016. Additional details on the UAV surveys, and our experiences and recommendations for using UAVs for research, are in Appendix S2.1.

In total 6,094 and 1,344 images taken 30 m and 60 m above the canopy were captured with spatial resolutions of ~10 mm/pixel and ~20 mm/pixel, covering ~150 ha and ~50 ha of forest, respectively, within which the plots cover 14.15 ha. The images were assembled to form a single two-dimensional orthorectified image (orthomosaic) for each plot, geo-referenced to the WGS84 UTM Zone 50N projected coordinate system, using Agisoft PhotoScan version 1.3.0. An example Agisoft PhotoScan output is in Appendix S2.2. The orthomosaics were exported into ArcGIS version 10.4 to identify individual trees (supplemented by the original

images, to provide multiple views from different angles, where necessary). The 30 m data were used for all analyses; the 60 m data were used to compare different spatial resolutions.

For each individual tree, COI and %LC values were determined by visual image interpretation using the same method used on the ground but applied from above. Interpreting the images in this way is beneficial because it: (i) matches the visual assessment used on the ground; and (ii) harnesses the power of human interpretation skills, which is especially important as no algorithm has been developed to automate liana infestation identification in tree canopies from RGB image data. Any trees for which ground data were collected, but which were obscured by larger trees and not visible on the UAV image data, were excluded from further analysis on individual tree-levels but retained for plot-level comparisons of UAV and ground surveys.

3.3.4 Analysis

We used Kendall's coefficient of concordance (Kendall's W) and Spearman's rank test, respectively, to assess the concordance of COI and %LC values recorded by different observers. Kendall's W was also used to assess the concordance in COI values derived from the ground and UAV surveys. We used Model II regression to test the relationship between the UAV and the ground-derived %LC values. Model II regression performs better than standard Model I (OLS) regression when there are errors associated with both variables (Legendre & Legendre, 1998), with the estimated model having the same slope and r^2 values independent of which way round the axes are. To further evaluate the relationship between the UAV- and ground-based methods, we also calculated the RMSE with respect to the 1:1 line with lower RMSE values indicating greater concordance between the UAV and ground methods.

3.4 Results

Liana load data were collected in 17 plots across 4 forest types, via both ground- and UAV-based methods, for more than 3,500 trees. The ultra-fine spatial resolution (10 mm/pixel) of the UAV data rendered each tree crown recognisable and individual leaves clearly identifiable (Figure 3-2). Liana load could, therefore, be assessed: trees without liana infestation (Figure 3-2a) could be distinguished from liana-infested trees (Figure 3-2b). This remained true when using the coarser ~20 mm/pixel spatial resolution.



Figure 3-2: An example image taken using the DJI Phantom 3 Advanced. Two sections of the image have been selected to show a (a) liana–free and (b) liana–infested tree crown (indicated by a white border). The yellow border in (b) indicates the liana leaves.

3.4.1 Reproducibility (between observers)

We assessed inter-observer bias in classifying liana load from the UAV image data; bias in ground-based surveys was examined previously by van der Heijden et al. (2010) and therefore not assessed here. Three independent observers with differing levels of experience in liana identification classified the COI and %LC for 200 randomly selected trees. We used Kendall's coefficient of concordance (Kendall's W) and Spearman's rank test, respectively, to assess the concordance of COI and %LC values recorded by different observers, finding high degrees of concordance for both measures (Table 3-1). The same COI was recorded by all observers on 75% of occasions and on only 2% of occasions did all observers classify liana load differently. When classifications differed, this was most often by only one class (86%).

Table 3-1: Degree of concordance between different observers (obs) in independently assessing liana infestation of tree crowns in UAV image data using crown occupancy index (COI) and percentage liana cover (%LC). Differences in COI and %LC were assessed with Kendall's W and Spearman's rank tests, respectively.

	COI		**%LC**	
	W	**p**	**r**	**p**
All	0.950	<0.001		
Obs. 1 & 2	0.966	<0.001	0.961	<0.001
Obs. 1 & 3	0.966	<0.001	0.942	<0.001
Obs. 2 & 3	0.955	<0.001	0.927	<0.001

3.4.2 Reproducibility (against a benchmarked method)

There was high concordance of COI scores between UAV and ground surveys for the full dataset (Kendall's W = 0.947, $p < 0.001$, n = 3,555; Tables 3-2 and 3-3), with liana load scored the same on 71.1% of occasions. Classifications differed by one class for 26.1%, and by two or more classes for 2.8% of the trees. The most frequent differences between UAV and ground surveys (43.2% of trees that differed) were when COI was scored 0 (liana-free) by ground-based surveys and 1 (low infestation) by UAV surveys (Tables 3-2 and 3-3). Similar trends were found for Danum and the different forest types in Sepilok separately (Appendix S2.3.1).

Table 3-2: Percentage of trees in each of the crown occupancy index (COI) classes for the ground (G) and UAV surveys, and the degree of concordance between the surveys (Kendall's W) for the full dataset (All trees) and the dataset partitioned by canopy strata. $p < 0.001$ for all comparisons.

			COI 0 (%)		COI 1 (%)		COI 2 (%)		COI 3 (%)		COI 4 (%)	
	N	W	G	UAV	G	UAV	G	UAV	G	UAV	G	UAV
All trees	3,555	0.947	44.6	34.5	13.0	24.7	12.3	11.4	12.1	12.8	18.0	16.6
Lower	1,841	0.968	33.9	31.6	16.2	22.0	15.2	13.5	13.1	14.0	22.0	19.0
Mid	989	0.936	44.5	29.6	11.0	26.7	11.2	11.7	13.6	14.3	19.5	17.7
Upper	412	0.909	61.2	39.6	10.2	28.9	7.8	7.0	10.0	10.2	10.9	14.3
Emergent	313	0.750	86.9	60.7	4.2	29.1	4.2	3.8	3.2	4.5	1.6	1.9

Table 3-3: Error matrix showing the number of trees classified in each crown occupancy index (COI) class for the ground and UAV surveys for the full dataset. Counts in bold indicate when the two methods produced the same score.

		Ground Data COI				
		0	**1**	**2**	**3**	**4**
UAV data COI	**0**	**1164**	54	7	2	0
	1	390	**358**	109	16	5
	2	25	43	**227**	93	18
	3	9	6	85	**259**	96
	4	1	1	8	59	**520**

We used Model II regression and calculated RMSE with respect to the 1:1 line to test the relationship between the UAV and the ground-derived %LC values. We found a strong relationship between ground- and UAV-based assessments of %LC for the full dataset ($r^2 = 0.867$, $p < 0.001$, n = 3,320; Figure 3-3), for different forest types separately (Appendix S2.3.2) and when using a coarser spatial resolution (Appendix S2.3.3). Although UAV- and ground-based classifications were similar for more heavily infested trees, UAV-based %LC classification was higher for lightly infested trees, with the regression line significantly below the 1:1 line for %LC below 40% (Figure 3-3). This was mainly caused by the high number of tree crowns classed as liana-free by the ground survey but as low-level liana infestation by the UAV survey.

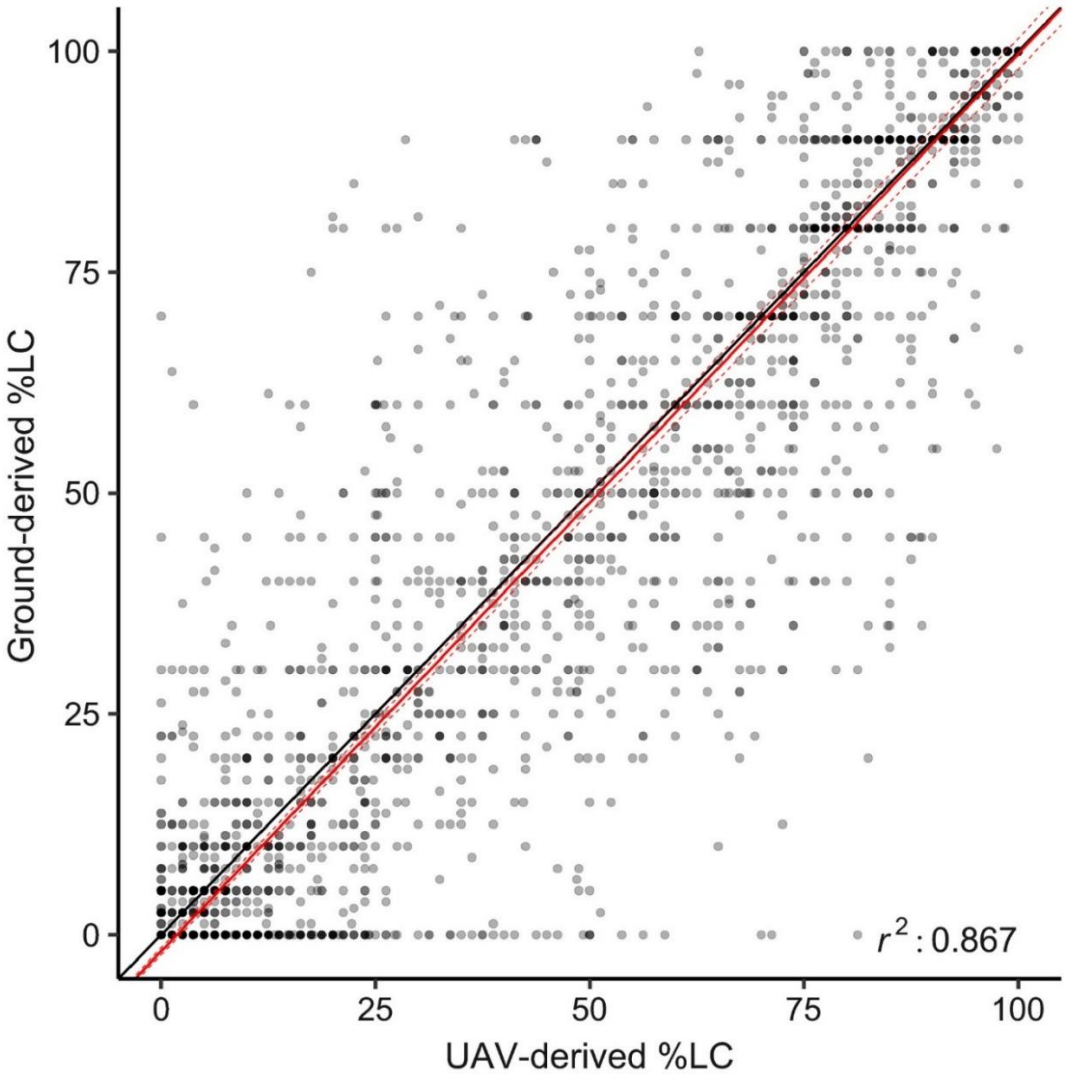


Figure 3-3: Relationship between the UAV-derived percentage liana cover (%LC) and the ground-derived percentage liana cover (%LC). The solid red line is the Model II regression line, and its associated r^2 is reported, dashed red lines are the 95% confidence intervals, and the black line is the 1:1 line (i.e., perfect match). n = 3,320; RMSE (with respect to the 1:1 line) = 12.73. Darker dots indicate more data points with similar ground and UAV values.

Since canopies of taller trees can be hard to see from the ground due to the stratified nature of tropical forests canopies, we also compared ground and UAV survey results for tree crowns located in different canopy strata. We found strong agreement between ground- and UAV-derived COI values (Kendall's W > 0.9) for all canopy stature classes except emergent trees (Kendall's W = 0.750; Table 3-2; Appendix S2.3.4a-d). The most common differences were again when COI was classed as 0 by the ground survey and 1 by the UAV survey, especially in the higher canopy strata (this was up to seven times more likely for emergent trees). Agreement between the two methods was greater for tree crowns in the lower canopy layers, and for more heavily infested individuals in upper canopy strata (Table 3-2; Appendix S2.3.4a-d). These patterns were also evident when comparing the %LC values; although ground- and UAV-derived %LC values were strongly related for all four canopy strata (Figure 3-4), the regression line deviated significantly from the 1:1 line for upper canopy and emergent trees. This was again caused by many trees classified as liana-free in the ground-based surveys and with low levels of liana infestation in the UAV-based surveys (Figure 3-4c&d).

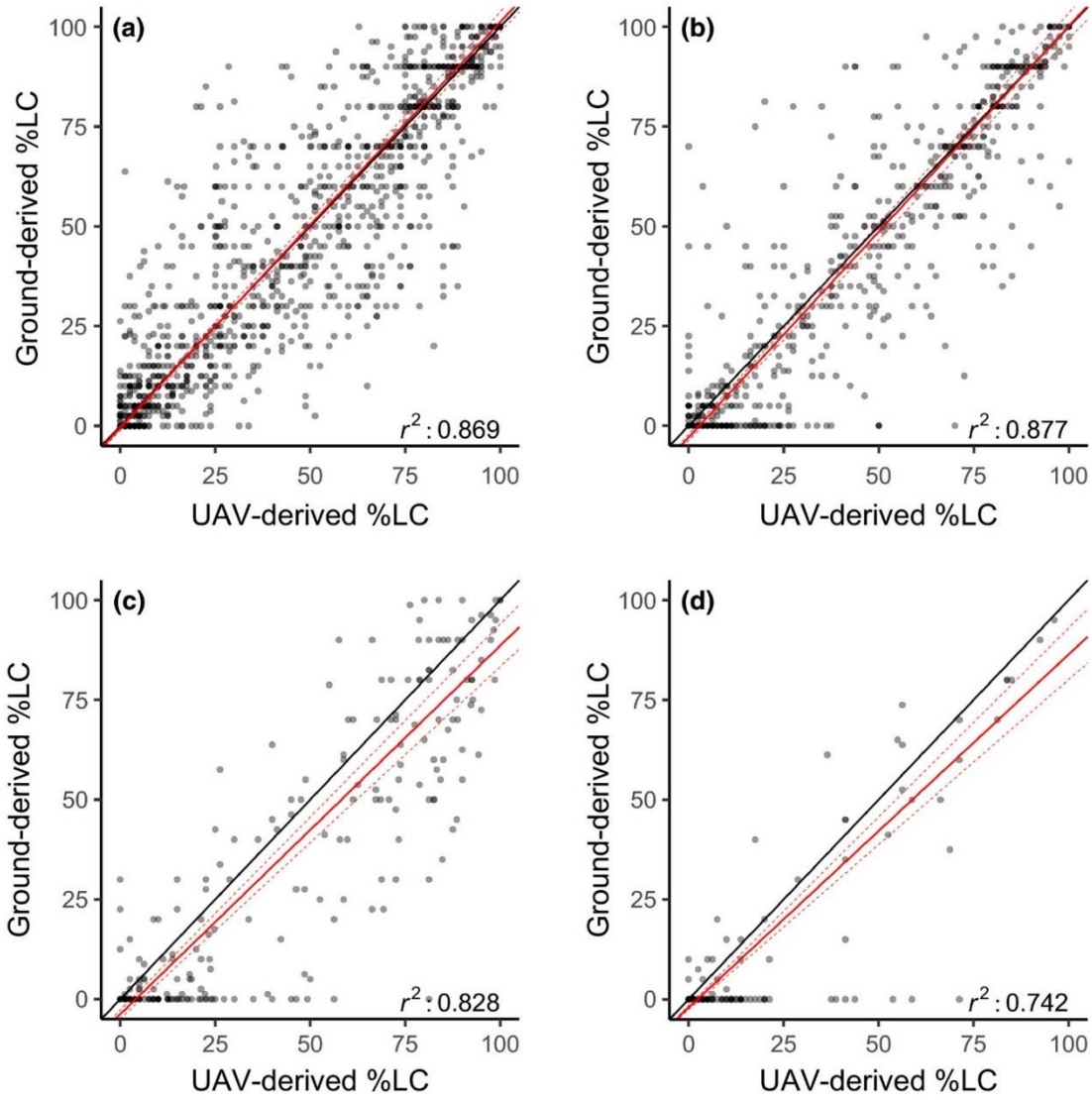


Figure 3-4: Relationships between the UAV-derived percentage liana cover (%LC) and the ground-derived percentage liana cover (%LC) for (a) lower canopy (N = 1,711; RMSE (with respect to the 1:1 line) = 12.79), (b) mid canopy (N = 931; RMSE (with respect to the 1:1 line) = 12.47), (c) upper canopy (N = 380; RMSE (with respect to the 1:1 line) = 14.96), (d) emergent trees (N = 298; RMSE (with respect to the 1:1 line) = 9.79). Solid red lines are the Model II regression lines with their associated r^2s reported, dashed red lines are the 95% confidence intervals, and black lines are the 1:1 lines (i.e., perfect match). Darker dots indicate more data points with similar ground and UAV values.

At plot level, there was a strong, positive relationship between ground- and UAV-based classifications of: (i) the proportion of liana infested trees per plot, and plot-level; (ii) mean COI; and (iii) %LC values (r^2 = 0.719; 0.899; 0.920, respectively; Figure 3-5). This indicates that, although fewer tree crowns (of smaller trees) are discernible in the UAV image data (mean trees/ha: ground = 360; UAV = 270), the UAV method is nonetheless suitable for plot-level analysis. UAV-derived plot-level estimates of liana infestation were higher (i.e. under the 1:1 line in Figure 3-5) than ground-based estimates for almost all plots, with the difference more pronounced for plots with lower liana infestation.

3.4.3 Efficiency

The UAV method was particularly time-efficient, with liana infestation assessment on average more than five times faster than the ground-based method, including both field and lab time (Table 3-4). Field campaigns are typically the most costly and time-limited phases of ecological research, and here the efficiency of the UAV survey over the ground survey is particularly enhanced. It reduces field time by 98.6% and the fixed costs of UAV hardware and software are recovered in the first 5.5 1 ha plots, with further UAV surveys costing 5.5% as much as the ground survey (Table 3-4). As fixed costs decrease with developments in UAV technology and popularity, the break-even point will occur even sooner than the 5.5 1 ha plots in this study.

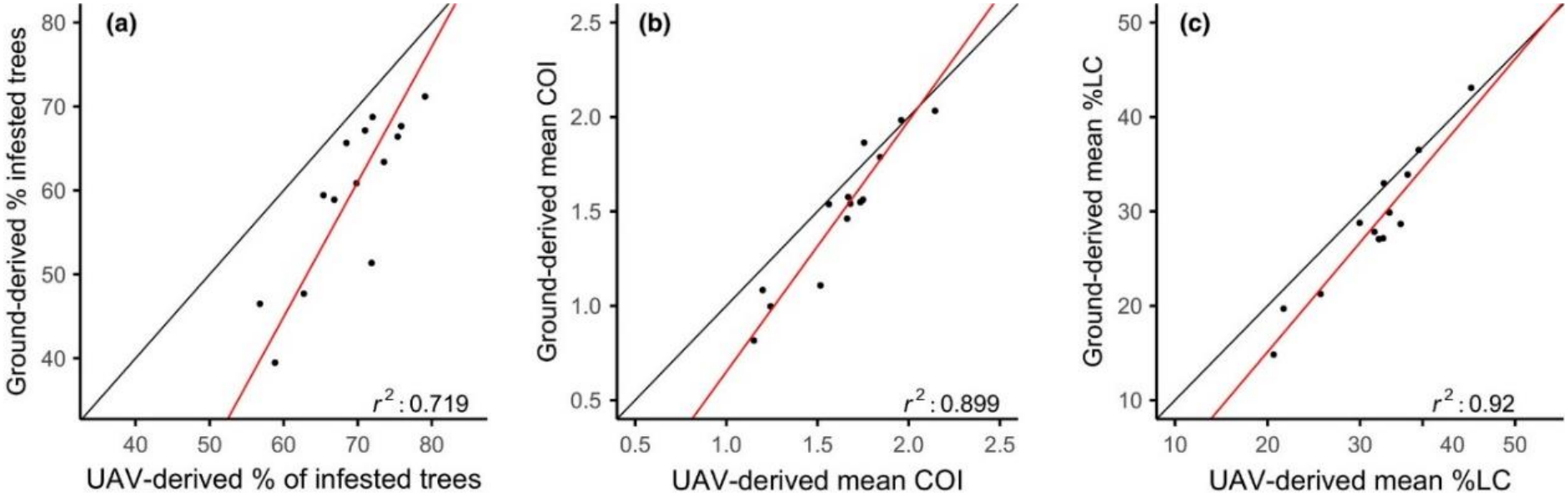


Figure 3-5: Relationships between ground- and UAV-derived plot-level (a) proportion of infested trees (%; n = 14; RMSE (with respect to the 1:1 line) = 10.86), (b) mean liana crown occupancy index (COI; n = 14; RMSE (with respect to the 1:1 line) = 0.19), and (c) mean percentage liana cover (%LC; n = 13; RMSE (with respect to the 1:1 line) = 3.68) for the Danum Valley Conservation Area plots. The Model II regression lines are shown in red, with their associated r^2s reported, and the 1:1 lines in black. The 1:1 line fell within the 95% confidence bands, but as intervals were large they were excluded from the graph.

Table 3-4: Efficiency comparison of the time taken and costs required to collect crown occupancy index (COI) and percentage liana cover (%LC) using ground-based and UAV-based methods for a 1 ha plot, including the fixed costs (field and UAV equipment and processing software) required for the whole campaign (14.15 ha for ground; 150 ha for UAV). All timings are reported in 'person-hours' (i.e. time taken to collect data considering number of people required) and exclude time to walk to the plots. All costs exclude international travel and costs/ha have been calculated based on number of days required at each plot with daily rates of £14.10 and £27.75 for accommodation/subsistence and field assistant costs, respectively. To replicate most grant budget costings, field assistant wages have been costed whereas researcher input time has not.

	Ground			UAV		
	Time/ha (h)	**Fixed costs (£)**	**Cost/ha (£)**	**Time/ha (h)**	**Fixed costs (£)**	**Cost/ha (£)**
Field*						
Accommodation/subsistence	-	-	84.60	-	-	4.70**
Field assistants	-	-	166.50	-	-	9.25**
UAV flight (inc. take-off/landing)	-	-	-	0.5	1336	-
COI and %LC assessments	40	450	-	-	-	-
Lab						
Data type up	5	-	-	-	-	-
Processing image data	-	-	-	9	427.10	-
Mapping trees on orthomosaics	-	-	-	1	-	-
COI and %LC assessment	-	-	-	2	-	-
Total	**45**	**450**	**251.10**	**12.5**	**1763.10**	**13.95**

*Training time is not included as it is not measured per ha. We found 5 hours ground and 2 hours UAV training was sufficient. Ground-measurement training must take place in the field; UAV training can take place beforehand, although some flight training in a tropical forest is recommended.

**We found it possible to survey three 1 ha plots, at two altitudes in a single day. To generate costs/ha, we have divided the daily accommodation/subsistence and field assistant costs by three.

3.5 Discussion

Here we demonstrate, for the first time, that UAVs can be used as an accurate, accessible, agile, cost-effective and time-efficient new tool for collecting data on liana infestation of tropical tree crowns, overcoming limitations of existing methods. Liana load derived from UAV surveys and traditional ground surveys were strongly related at both individual tree- and plot-level (Tables 3-2 and 3-3; Figures 3-3 and 3-4). Furthermore, we found little inter-observer bias in visual classifications of liana loads derived from UAV image data regardless of liana expertise or previous experience of liana surveys (Table 3-1), indicating high reproducibility of the UAV method. Additionally, the UAV method was much more time-efficient than the ground-based method, particularly in the field, and considerably more cost-efficient over multiple surveys (Table 3-4), with initial investment recouped within the first six plots. The UAV also remains cheaper than most suitable satellite or manned aerial survey image data. Thus, UAVs make liana data collection more accessible to a wider variety of researchers and forest managers and may, therefore, enable canopy monitoring and mapping of lianas on unprecedented spatial and temporal scales.

At the plot level, UAV-based surveys consistently classed percent liana infestation higher than ground-based surveys (Figure 3-5). There are two explanations for this. Firstly, UAVs were better at recognising low-level liana infestation (Tables 3-2 and 3-3; Figures 3-3 and 3-4). Secondly, plot-level estimates of liana infestation from ground surveys included understorey trees not visible on the UAV image data. As understorey trees are less frequently infested by lianas than larger trees (van der Heijden et al., 2008), their inclusion in ground surveys reduces plot-level values of percent liana infestation. Despite these differences between the ground- and UAV-based surveys, there was a strong positive relationship between their results for plot-level liana infestation. This suggests either method can be used to

compare plot-level liana infestation rates across sites (c.f. van der Heijden et al., 2010) provided the same method is used.

The fine spatial resolution of UAV image data, combined with the top-of-the-canopy view, provides an enhanced perspective to study liana infestation. This makes UAVs particularly useful for silvicultural systems, where liana cutting is routinely performed for improving timber and fruit production (Kainer et al., 2014; Sist et al., 2003; Verwer et al., 2008), and for forest management or restoration purposes, where liana cutting has been shown to regenerate biomass (Marshall et al., 2017). With UAVs, users can quickly, efficiently and accurately pinpoint which trees or areas suffer from heavy liana infestation, and those at risk of heavy liana infestation in the future. This is feasible over much larger areas than normally possible with ground-based methods, enabling better targeting of management practices such as liana cutting, and saving time, effort and money.

UAVs improve liana infestation assessment for canopy and emergent trees, compared to ground surveys (Table 3-2; Figure 3-4c&d; Appendix S2.3.4c&d). These tall trees store and sequester the most carbon and are the main commercial species. Liana-induced changes in them may, therefore, be an important mechanism affecting forest-level and tree-level carbon storage and sequestration, for which UAVs represent a particularly useful management tool. Successful liana management may also help to increase timber and fruit productivity, and carbon storage and sequestration of degraded forests (van der Heijden et al., 2015). In particular, UAVs increased our ability to detect low-level liana infestation in these trees, which is particularly difficult from the ground as they are often partly obscured by shorter canopy layers (Table 3-3; Figure 3-4c&d). Although lianas exert limited effects at low levels (<50% crown coverage; e.g. Ingwell et al., 2010), identifying them quickly is important as infestation progression is likely as lianas

utilise each other to climb into the tree crown (Putz, 1984), stressing the importance of repeated surveys of liana infestation.

UAVs answer this need, offering user-controlled deployment times, potential for high temporal frequency and an increased likelihood of recognising low-level liana infestation (Table 3-2; Figure 3-4c&d). This allows for a flexible approach to liana management, tailoring it for trees or areas of forests at risk of heavy liana infestation. The new technique also facilitates monitoring and assessment of the success of management practices after they are put in place (Zahawi et al., 2015), including changing where management efforts are concentrated, as spatial patterns of liana infestation change over time. It will also help track temporal changes, not only in liana infestation, but in wider canopy phenomena, such as tree crown shape and area, and timber, fruit, and forest-level biomass productivity and phenology, over shorter time-scales than is possible with ground-based surveys. The ability to track temporal changes enables investigation of the effects of short-term phenomena, such as drought events, on liana infestation and other processes in the canopy. The image data also represent an archive of detailed information about the forest canopy that allows: (i) reproducibility as people can check previous results; (ii) additional metrics to be derived, for example 3D models or digital elevation models (Appendix S2.2.5); and (iii) users to go back in time and measure variables that were not measured at the time but are later deemed important. For example, orang-utan nests are clearly visible in our imagery (Appendix S2.3.5).

Advances in UAV technology and competitive price pressures are likely to improve the current UAV method and expand its applicability for forest management. We cannot specify at what resolution lianas (or other canopy phenomena) become indistinguishable (lianas remained clearly identifiable in our coarser spatial resolution images; Appendix S2.3.3), but the advent of newer UAVs with larger

high-resolution image sensors, bright lenses and zoom lens technology will enable even higher flights while retaining the ability to identify lianas, which may increase area coverage (it is unlikely that this will be possible using satellite data in the next few decades). Further research could usefully investigate this for lianas, as well as for other canopy phenomena. The wide array of UAV platforms and sensors already available (Pajares, 2015) allows tailoring of system choice towards individual research and/or monitoring requirements. Additionally, rapid advances in the miniaturisation of hyperspectral and LiDAR sensors increasingly enable them to be mounted on UAVs (Sankey et al., 2017) alongside RGB cameras, and predicted future price drops will increase their accessibility. While RGB images allow visual species identification (Baena et al., 2017; Getzin et al., 2012), multispectral or hyperspectral sensors may allow this to be automated (Baena et al., 2017; Sankey et al., 2018), further increasing the speed and ease of liana identification. Future work could test whether a suitably equipped UAV could automate mapping of liana infestation and changes in infestation similarly to the approach adopted by Marvin et al. (2016) using airborne-collected data, but at much finer spatial and temporal resolutions, and at a small fraction of the cost. Also, as liana and tree species differ spectrally (e.g. Sánchez-Azofeifa et al., 2009), hyperspectral UAVs may help discern liana and tree species, supporting monitoring of tropical forest biodiversity, which is particularly important for the management of degraded forests (e.g. Marshall et al., 2017). With the emergence of new platform and sensor capabilities, the opportunities for using UAVs in both liana, and canopy research more generally, will increase. Thus, the UAV method presented here offers a wealth of opportunities for forest canopy research and monitoring, including liana monitoring, over space and time to assist with tailored management of tropical forests, and forms a firm foundation for exploiting future advances.

3.6 Conclusions

The recent proliferation of lianas, coupled with their large impacts on the carbon balance and cycle of tropical forests, has made it important to study liana infestation of tree canopies more comprehensively and frequently than feasible with current methods. Here we show, for the first time, how capturing RGB images of tree canopies via an inexpensive, lightweight UAV can be used accurately and efficiently to assess liana infestation and help make such data collection more accessible. Liana infestation data derived from UAV image data are at least as accurate as traditional ground data, and superior in assessing liana infestation of tree crowns in upper canopy layers, enabling future advances in liana and tropical forest ecology research. The support for frequent surveys, data archiving, wealth of additional data captured, and larger geographical extent covered will enable more detailed monitoring of liana infestation and forest canopies over space and time with the potential to revolutionise both liana and canopy research. These advantages will be enhanced by rapidly developing protocols for UAV use in science (Duffy et al., 2018) and the potential for additional sensors offered by UAV platforms. UAVs also provide potential for tailored and targeted liana management protocols to effectively manage liana infestation to aid restoration of degraded forests, silvicultural systems, and projects designed to increase carbon storage and sequestration in tropical forests.

Chapter 4: A ladder to the sky: the roles of tree size and canopy gaps in liana infestation patterns of tropical forest canopy in Sabah, Malaysia

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Authors' Contributions: C.E.W. designed the research, performed the UAV data collection and image processing, developed the analytical approach, analysed the data, and wrote the paper; C.E.W. and G.M.F.v.d.H. collected the data from the UAV images; D.S.B. was responsible for the occupied aircraft data provision through a NERC Direct Access grant; D.B. was responsible for the ground data collection, assisted by B.T. and J.D.; R.N. provided logistical support in obtaining permits for the work; C.E.W., R.F., D.S.B., and G.M.F.v.d.H. contributed to manuscript revisions.

4.1 Abstract

Lianas are key components in tropical forests where they are increasing in abundance. Relatively little is known about landscape-level liana distributions in tropical forest tree crowns, especially in the Palaeotropics. A new method for data collection of liana infestation using Unmanned Aerial Vehicles (UAVs) has increased the speed at which reliable, accurate, reproducible, liana data can be collected, as well as reducing the cost of such data collection. Now we have the opportunity to determine, for the first time, landscape-level distributions and spatial patterns of liana canopy cover and test the main hypotheses and ideas about what determines liana occurrence and abundance in tree crowns.

We used a commercially available UAV to collect image data and, through Structure from Motion photogrammetry and visual image analysis, assessed liana load in the canopy for 50 ha of tropical forest in Sabah, Malaysia and derived multiple environmental variables including tree height, crown area, canopy gap area and height. Comparable variables were produced from an occupied aircraft LiDAR sensor and soil data were provided from ground surveys. Using the environmental data from the UAV, occupied aircraft and ground surveys, we: (i) evaluated the relative strengths of the environmental variables to predict liana distributions and tested hypotheses concerning each; and (ii) evaluated how well UAV data were able to explain and predict liana distributions in comparison to the traditional occupied airborne LiDAR and ground-collected data.

Liana infestation was significantly aggregated across the 50 ha plot, with tree canopy height being the most important variable influencing this; taller trees were less often and less heavily infested by lianas. Presence of canopy gaps was also important in influencing liana distributions, with liana infestation occurring more often and to greater extents in close proximity to them. Examining how and why lianas are distributed in the forest canopy at landscape-scales may help us to

determine what variables may determine increases in lianas with environmental change in the future and provide a step towards more comprehensive testing of ecological theory in tropical forests.

4.2 Introduction

One of the central goals in ecology is to determine the mechanisms responsible for the abundance and distribution of organisms (Krebs, 1972; Brown, 1988). Most studies testing ecological theory in tropical forests focus on trees. Determining such mechanisms for lianas will lead to new insights into how and when these varied mechanisms operate, and may contribute to a more comprehensive understanding of the maintenance of plant species diversity and the factors that control plant species distributions (Schnitzer, 2018). Lianas (woody vines) are a key component of tropical forests, where they peak in abundance, biomass, richness and species diversity (Gentry, 1991; Schnitzer & Bongers, 2002) and are an important agent in changing carbon cycling in tropical forests. However, lianas have presented a problem for ecologists because they are time-consuming and difficult to survey from the ground, and therefore relatively little is known about their spatial distributions in tree crowns or the mechanisms that may influence this. Recently, a new method using UAVs to collect liana data has increased the speed at which reliable, accurate, reproducible, liana data can be collected, as well as reducing the cost of such data collection (Waite et al., 2019). Now we have the opportunity to determine, for the first time, continuous landscape-level distributions and spatial patterns of liana canopy cover and test the main hypotheses and ideas about what determines liana occurrence and abundance in tree crowns.

Lianas contribute relatively little to forest-level biomass as they rely on the structural investments of trees to deploy leaves in the forest canopy. In doing so, lianas invest fewer resources in the formation of carbon-dense stems, and

relatively more into developing an extensive leaf canopy (van der Heijden et al., 2013). Furthermore, lianas can decrease the amount of carbon fixed by a given area of tropical forest via liana–tree competition, both above- and below-ground, for resources such as essential nutrients, water and light, which can be more intensive than tree–tree competition (Tobin et al., 2012). Such competition can reduce individual tree growth by up to 84% (van der Heijden & Phillips, 2009; Ingwell et al., 2010; Schnitzer et al., 2014), fecundity (Kainer et al., 2006; Nabe-Nielsen et al., 2009), and survival (Phillips et al., 2005). Lianas, therefore, constrain above-ground forest primary productivity and forest biomass (Durán & Gianoli, 2013) and can reduce net carbon uptake by ~76%/year (van der Heijden et al., 2015).

This reduction in carbon uptake and storage may be exacerbated because lianas are increasing in abundance, richness and biomass in tropical forests (Phillips et al., 2002; Schnitzer & Bongers, 2011). This observed increasing size and abundance of lianas relative to trees may lead to changes in the functioning of forest ecosystems (Schnitzer et al., 2000; Schnitzer & Carson, 2010; van der Heijden et al., 2013), and to reduced forest carbon stocks (van der Heijden et al., 2015). Lianas thus have broad and important ramifications for the global carbon cycle and the 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). It is therefore important to understand the distributions of lianas, to help us to determine what variables may determine increases in lianas with environmental change in the future.

Landscape-scale liana spatial distribution in forest canopies and the mechanisms driving that distribution remain largely unknown. Building on research conducted in small-scale plots, studies at a ≤50 ha plot size have taken place (e.g. Dalling et al., 2012; Schnitzer et al., 2012; Ledo & Schnitzer, 2014; Marvin et al., 2016), but

our knowledge remains incomplete. Currently, knowledge from these studies, together with that from small-scale studies conducted across the globe, is that lianas have highly clumped distributions and are significantly spatially aggregated within the plots that have been examined (e.g. Putz, 1983; Putz, 1984a; Caballe, 1986; Clark & Clark, 1990; Hegarty & Caballe, 1991; Sokal & Rohlf, 1995; Pérez-Salicrup et al., 2001; Pérez-Salicrup & De Meijere, 2005; Schnitzer et al., 2012; Ledo & Schnitzer, 2014). This indicates that lianas are not randomly distributed, and that there are underlying mechanisms driving their patterning (Putz, 1984b).

Perhaps the most widely referenced mechanism thought to influence liana patterning (giving rise to spatial aggregation) is disturbance; within-forest liana distributions may be strongly influenced by the occurrence of canopy gaps (Schnitzer & Carson, 2001; Schnitzer, 2005; Dalling et al., 2012; Schnitzer et al., 2012; Ledo & Schnitzer, 2014). Specifically, liana abundance (density), both in absolute terms and relative to trees, and diversity (species richness), tend to increase with the presence and size of canopy gaps (Putz, 1984a; Hegarty & Caballe, 1991; Babweteera et al., 2000). This literature led to the first hypothesis of our study. Lianas capitalise on these disturbed areas and may become abundant in gaps 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). Long-distance clonal recruitment enables gap occupation as >90% of adult lianas falling into the understorey following a canopy disturbance or treefall event survive and can then produce an abundance of new stems in the gap (Putz, 1984a; Schnitzer et al., 2000; Phillips et al., 2005; Ingwell et al., 2010). Capitalising on this, upon arrival in a treefall gap, liana growth rate and vegetative stem production far exceed those of trees. This allows them to proliferate and grow rapidly in the high-resource environment; thus enabling them to eventually climb successfully back to the

forest canopy (Putz, 1984a, Schnitzer et al., 2000; 2004). As a result, immediate arrival of lianas into treefall gaps, and rapid proliferation following, may lead to lianas being higher in density and diversity in gaps than in the intact forest (Schnitzer & Bongers, 2000; Schnitzer & Carson, 2000; Schnitzer et al., 2000).

Previous studies have indicated that other factors, both biotic and abiotic, are also potentially important for shaping liana distributions. Such abiotic factors include soil fertility (Balfour & Bond, 1993; Gentry, 1991), and biotic factors include host tree susceptibility to climbers, including height, trunk roughness, and canopy size (Hegarty & Caballe, 1991; Putz, 1984b; Newberry, 1993; Carse et al., 2000; Siebert, 2005; van der Heijden & Phillips, 2008). These studies have provided useful information on liana-(a)biotic interactions, but we are, so far, lacking information on the influence and interaction of these multiple environmental variables on liana distributions in tropical forest tree crowns at the landscape level. The interactions between lianas and (a)biotic factors form the basis for hypotheses 4–6 of this study.

One of the key gaps in our knowledge of liana spatial distributions and potential factors influencing this, is that the vast majority of the existing work outlined above has been undertaken in Neotropical forests. The forests of the Palaeotropics, and especially those of Southeast Asia, have received very little attention. These forests are distinct ecological entities, however, with key differences, for example the prevalence of dipterocarp dominance in Southeast Asian tropical forests (Corlett & Primack, 2006; 2011). The spatial distributions of lianas, therefore, may be determined by different factors in Southeast Asia than in the Neotropics. Examining this will help to answer the question posed by Schnitzer and Bongers (2011) of whether differences between continents drive differences in patterns of liana infestation. This is important as Palaeotropical forests have significantly higher aboveground 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 (≥70 cm DBH) trees (Slik et al., 2013). Indeed, the forests of Southeast Asia have particularly high aboveground wood production, 49% greater in the forests of Borneo than those in Amazonia (Banin et al., 2014). With the importance of carbon storage in tropical forests for mitigating climate change, and the increasing pressures upon tropical forests reducing their ability to do so (Levin, 2013; Nakamura et al., 2017; Lewis et al., 2015; Mitchard, 2018), it is important that we understand these carbon-rich systems.

Furthermore, most work on liana ecology focuses on liana stem measurements rather than liana canopy cover, due to the difficulties in assessing liana canopy cover from the ground (Marvin et al., 2016; Waite et al., 2019). Liana canopy cover is more directly related to liana–tree competition, however, because liana stems can root a considerable distance away from their location in the canopy (Putz, 1984b; Campbell & Newbury, 1993). By examining how and why lianas are distributed in the forest canopy, we can enhance our knowledge of which areas of the forest are being impacted by lianas the most, and how this may alter in the future.

Previous studies have been limited in their examination of factors that may determine liana distributions at landscape-level for two main reasons: (i) they lack the examination of Palaeotropical forests, particularly those of Southeast Asia; and (ii) they focus on liana stem assessments rather than liana canopy cover, which is more directly related to liana–tree competition. These limitations can be circumvented by using UAVs to aid data collection in Palaeotropical forests. The use of UAVs affords the efficient collection of accurate data on liana distributions in tropical tree crowns (Waite et al., 2019) and their integration with multiple environmental variables (derived from UAV imagery, but also from other

techniques such as manned airborne LiDAR, as well as ground-based measurements).

Here we present the first continuous landscape-level liana distribution data for the Palaeotropics, focussed on the primary rainforests at Danum Valley, Sabah, Malaysian Borneo. To our knowledge, this is the first study analysing multiple tree-level biotic factors such as tree height and crown area, alongside abiotic factors that may affect liana spatial distribution at the landscape-scale. Our specific aims were to: (i) test the expectation that liana infestation will exhibit a spatially aggregated pattern across the 50 ha plot; (ii) evaluate the relative strengths of a set of environmental variables to predict liana spatial distributions and test our hypotheses concerning each variable (Table 4-1); and (iii) evaluate how well UAV data are able to explain and predict liana distributions in comparison to other traditional data collection techniques (i.e. occupied airborne LiDAR and ground-collected data).

Table 4-1: The method of deriving each of the environmental variables, the rationale for their inclusion in the study, and the associated hypotheses of their relationships to liana presence–absence and degree of liana infestation (liana crown occupancy index (COI) and percentage liana cover (%LC)) influencing liana spatial distribution. The disturbance variables are multiple canopy gap heights (<2 m, <5 m, and <10 m) and areas (25–100 m^2, 100–500 m^2, >500 m^2).

[Category] Variable name	**Method of derivation**	**Rationale**	**Hypotheses**
[Disturbance] <2m height, 25–100m^2; <2m height, 100–500m^2; <2m height, >500m^2 <5m height, 25–100m^2; <5m height, 100–500m^2; <5m height, >500m^2 <10m height, 25–100m^2; <10m height, 100–500m^2; <10m height, >500m^2	Canopy gaps were derived by thresholding the LiDAR and UAV canopy height models (CHMs) at different heights (<2 m, <5 m and <10 m) and areas (25-100 m^2, 100-500 m^2, >500 m^2) to produce 18 layers (9 LiDAR, 9 UAV) containing individual gaps as polygons. The distance of each tree crown centroid to its nearest gap edge (in m) was calculated (using both the LiDAR- and UAV-derived gap data) using the dist2line function in the package geosphere version 1.5.1 (Hijmans et al., 2019) in R version 3.5.1. This makes the most ecological sense as lianas may be present throughout gaps, including the edge, and commonly infest crowns by climbing the trunk which, in the absence of knowing the exact trunk location, is likely near the centroid of the tree crown.	Canopy gaps influence liana spatial distributions. Including several gap height and area variables is important as they may affect liana distributions differently. Larger gaps may indicate higher levels of disturbance and a positive relationship between gap size and liana infestation is expected (Babweteera et al., 2000). Lower gaps may indicate more recent disturbance than higher gaps. Higher gaps may therefore have provided more time for lianas to infest surrounding tree crowns and may be more highly correlated with liana presence and degree of infestation.	H1. (Putz, 1984a). The shorter the distance to gaps, the higher the likelihood of liana infestation (liana presence–absence) and the higher the levels of liana infestation (COI and %LC). a) Larger gaps will be more highly correlated with liana infestation b) Higher gaps will be more highly correlated with liana infestation.
[Tree variables] Mean crown height	Tree crown height was calculated using the canopy height models (CHMs) derived from the LiDAR and UAV data. The tree crown shapefiles were overlaid on the CHM rasters and elevation values for each pixel comprising the tree crown were taken. The mean value for each tree crown was used as we feel it is slightly more impervious to small errors (branches protruding above the canopy, errors in the LiDAR pulse readings or UAV point cloud etc.) than maximum or minimum values.	Lianas infest taller trees more often and to greater extents than shorter trees (e.g. Pérez-Salicrup et al., 2001). This could be due to the positive relationship between tree age and height: older trees have had more time exposed to liana pressures, and thus a higher chance of liana infestation. As lianas can use one another as trellises, the degree of infestation rises once one liana has reached a tree crown (van der Heijden et al., 2008).	H2. The greater the tree height, the higher the chance of liana infestation (liana presence–absence) and the higher the levels of liana infestation (COI and %LC).

Crown area	Tree crown area was calculated by determining the size of the pixels comprising the orthomosaic and multiplying this by the number of pixels in the crown. This is not a calibrated measure but as it is only used as a comparison between relative tree sizes to examine potential differences in liana infestation, specific, calibrated, values are not necessary.	Large tree crowns have been shown to have higher chances of being infested by lianas due to the larger area of exposure to potential infestation than in smaller crowns. As lianas can use one another as trellises, the degree of infestation rises once one liana has reached a tree crown (van der Heijden et al., 2008).	H3. The larger the tree crown area, the higher the likelihood (liana presence–absence) and level of liana infestation (COI and %LC).
[Soil and Topography] Mean slope angle	Slope values were derived from the ground-collected topographic data, the LiDAR data, and the UAV data using ArcGIS version 10.4. For the ground data, the data collected from the sample points were interpolated using Inverse Distance Weighting. For the LiDAR and UAV data, slope was calculated from the digital terrain models. The tree crown shapefiles were overlain on the three raster layers (ground-, LiDAR-, UAV-derived slope) and values for each pixel comprising the tree crown taken. The mean value of all pixels was then taken for each tree crown as, due to the layers being interpolations with no true minimum or maximum, it is the most accurate and reliable metric.	Slope may affect liana infestation negatively or positively (or both). Steep areas promote trees with smaller root systems, shorter heights and smaller crowns with a greater risk of falling (disturbance). However, flat areas promote the largest trees (dipterocarps) which result in the largest and longest lasting gaps when they fall. Both outcomes may promote liana presence and it is likely that no clear relationships between slope and liana infestation will be observed.	H4. The lower the slope angle, the higher the likelihood (liana presence–absence) and level of liana infestation (COI and %LC). OR The higher the slope angle, the higher the likelihood (liana presence–absence) and level of liana infestation (COI and %LC).
ECEC Copper Phosphorus pH	The data collected from the ground sample points were interpolated using Kriging in ArcGIS version 10.4. The tree crown shapefiles were overlain on these interpolated raster layers and values for each pixel comprising the tree crown taken. The mean value of all pixels was then taken for each tree crown as, due to the layers being interpolations with no true min or max, it is the most accurate and reliable metric.	Soil infertility, and low levels of Phosphorus in particular, can inhibit both tree and liana growth (Pasquini et al., 2015). Lianas are more ecologically generalist than trees along soil gradients, however, so are unlikely to display any clear relationships with soil variables (Macía, 2007).	H5. (Macía, 2007). There will be little to no effect of the soil variables on liana infestation (liana presence–absence) or degree of liana infestation (COI and %LC).
[Surrounding environment] Distance to nearest infested neighbour	The distance from each individual tree to its nearest neighbour that was infested with lianas was calculated using the nndist function in the package spatstat version 1.61 (Baddeley et al., 2015) in R version 3.5.1.	Proximity to an infested tree increases the probability of liana infestation of the target tree. This can occur by lianas: (i) moving laterally from the infested to the target crown; or (ii) descending, re-rooting and climbing up into the target tree crown.	H6. The shorter the distance to the trees' nearest infested neighbour, the greater the chance and levels of liana infestation (liana presence–absence, COI and %LC).

4.3 Methods

4.3.1 Study site

This study took place at Danum Valley Conservation Area (Danum) (4°57' N, 117°42' E) in Sabah, Malaysia (Figure 4-1). Danum has been the site for a field centre and collaborative research programme since 1986 (Marsh & Greer, 1992). Situated in a complex landscape with rugged terrain and stable soils (Newbery et al., 1992), Danum is characterised by ~43,800 ha of uninhabited lowland, evergreen dipterocarp forest (Whitmore, 1975). This is a heterogeneous, primary forest and therefore provides a suitable study site to examine the factors driving patterns of liana infestation in primary palaeotropical forests. Specifically, we studied the Center for Tropical Forest Science 50 ha plot, established in 2010. 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 aim by establishing the baseline liana load of canopy and emergent trees.

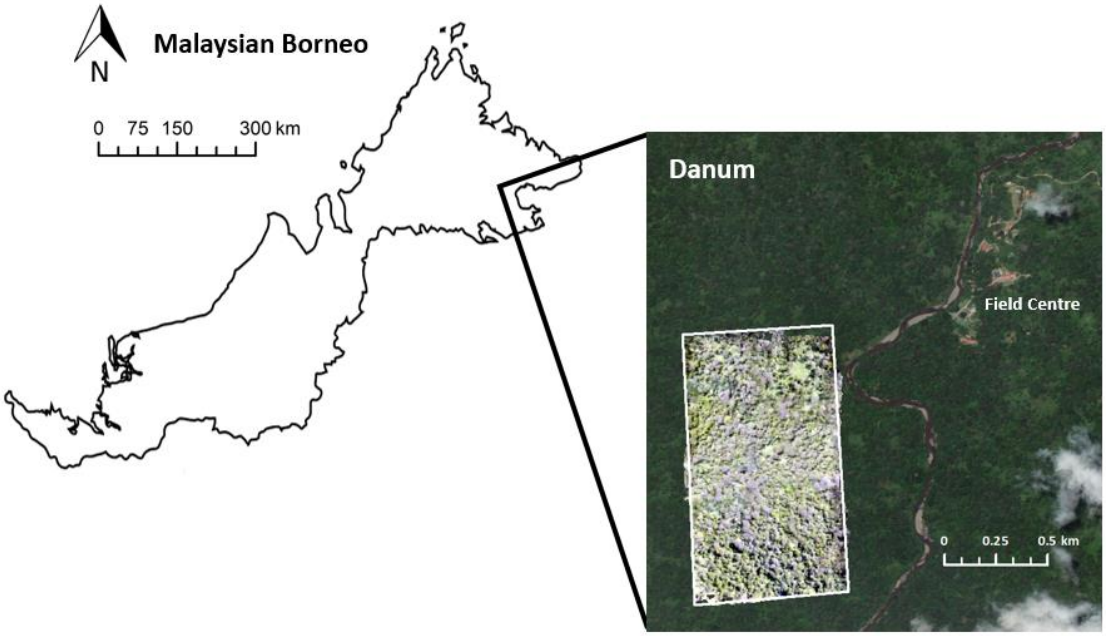


Figure 4-1: Location of the study site and 50 ha plot, which are located in the state of Sabah, Malaysia, on the island of Borneo, Southeast Asia. The orthomosaic created from our UAV survey of the 50 ha plot is shown outlined in white on top of satellite imagery of the Danum Valley Conservation Area. Satellite imagery source: DigitalGlobe WorldView2 RGB imagery.

4.3.2 Ground soil and topographic data collection

Ground surveys were undertaken in the 50 ha plot with soil and topographic data collected from 2009-2018 (soil sampling: October 2016, analyses late 2016-2018; topographic data collection: 2009–2011). Data collected consisted of: (i) topographic data (elevation in m); and (ii) soil samples, which were subsequently processed with barium chloride extract to give soil data for pH, phosphorus (mg/kg), copper (mg/kg), and ECEC (cmol/kg). The topographic data were collected from 1,326 sample points distributed in a regular 20 x 20 m grid across the 50 ha plot, and the soil data were collected from 300 sample points distributed mainly in a regular 50 x 50 m grid across the 50 ha plot (total of 200 points), supplemented with extra sample points (total of an additional 100 points) at short distances to capture short-range variation.

4.3.3 Occupied aircraft-based LiDAR data collection and processing

LiDAR data for Danum were acquired by the Natural Environment Research Council Airborne Research Facility (NERC ARF) during their 2014 Malaysia Campaign. The data were captured from a Dornier 228 aircraft, recording 10 flight lines over ~64 minutes at an average altitude of 2378 m (7802 ft). During flight, the aircraft's position was recorded using a differential GPS, with positional information relayed from a base station with a known position, and the aircraft's orientation (roll, pitch, and bearing) recorded through the Inertial Measuring Unit (IMU). The conditions were favourable during the survey, with the resultant images only affected by 3% cloud and 5% shadow, none of which affects the 50 ha plot. The sensors on-board the aircraft included the Leica ALS50-II LiDAR system (1064 nm; hit rate: 2.03 points/m^2; ~15 cm in Z). The data from this system were pre-processed by NERC's Data Analysis Node and supplied in LAS 1.2 (binary data) and ASCII file formats with horizontal and vertical datum projected in WGS84 UTM Zone 50N. These were processed in LAStools to provide a canopy height model (CHM) and digital terrain model (DTM) that were clipped to the extent of the 50 ha plot. Outliers were eliminated and the data were filtered to identify ground and non-ground hits. Normalised above-ground heights were calculated by interpolating the ground points into a surface using the adaptive triangulated irregular network (TIN) filtering algorithm, and subtracting this from the non-ground points.

4.3.4 UAV-based data collection and processing

We used a DJI Phantom 3 Advanced to acquire images of the forest canopy. This is a lightweight, agile, inexpensive, commercially available quadcopter UAV with an integrated three-waveband (RGB) Sony EXMOR 1/2.3" 12-megapixel camera. Its narrow 94^o field of view lens and fast 1/8000s shutter speed reduce 'fish-eye' image distortion and image blur. On-board GPS and GLONASS positioning enables

autonomous flights (up to ~23 minutes) and geo-tagging of acquired images with the GPS location and elevation of the UAV at the point of capture.

The flight plan for the survey of the 50 ha plot was designed with, and flown using, Map Pilot software version 1.5.1. It consisted of 9 individual flights with the same parameters (altitude: 30 m above the canopy surface; speed: 4 m/s; image overlap: 90% forward, 90% side). Each consisted of parallel tracks, covering a portion of the 50 ha plot (overlapping with other flights to allow image matching and stitching of multiple flights into one orthomosaic) and a 'buffer' of surrounding vegetation, outside the 50 ha plot, to minimise edge-effects affecting the images of the plot in processing. The flight tracks were uploaded to the UAV and the surveys flown autonomously, with the exception of launch and landing; here we identified canopy gaps large enough to launch/land the UAV, and manually piloted it through the gaps, to ensure maximal pilot control and minimal risk of collisions. The flights were conducted during calm conditions and, where possible, under even cloud cover to prevent wind effects on leaves (McNeil, 2016) and ensure diffuse radiation and less shadow on the ground. This produced images of greater clarity, aiding liana identification. All flights took place between 14th and 16th June 2016.

In total, 3,884 images were captured covering the 50 ha plot, and a ~50 ha buffer of surrounding forest, with a spatial resolution of ~12.4 mm/pixel. Using Structure from Motion photogrammetry, the images were assembled to form a single two-dimensional orthomosaic and processed to produce a DTM and a digital surface model (DSM) which were both used to produce a CHM geo-referenced to the WGS84 UTM Zone 50N projected coordinate system, using Agisoft PhotoScan version 1.4.2. More details on specific UAV flight parameter choices 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.

4.3.5 Derivation of liana load variables

On the orthomosaic, we visually identified and manually digitised the edges of every tree crown within the 50 ha area, where the whole (or majority) of the canopy was visible, to create shapefiles for each individual tree crown (tree crown shapefiles). Any tree crowns <25 m^2 in area or too shaded to accurately determine the edge of the tree crown and/or assess visually for liana infestation were excluded from further analysis. In total, we used 2,428 tree crowns located within the 50 ha boundary for this study.

For these trees, we classified the liana cover of the tree crown via three methods: (i) liana presence–absence; (ii) crown occupancy index (COI); and (iii) percentage liana cover (%LC). 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). %LC is a more detailed estimate: the tree crown is visually split into four compass quadrants and the percentage covered by lianas is estimated to the nearest 5% for each, before a mean is taken for the whole crown (Marvin et al., 2016, Waite et al., 2019). We have previously shown that these UAV-derived measures of liana infestation accurately measure liana loads, being comparable with traditional ground-collected data (and, arguably, better in the higher canopy) 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 UAV image data to ensure that there is no bias between the two halves of the plot. The two observers classified the COI and %LC for 200 random trees and we used Kendall's coefficient of concordance (Kendall's W) and a paired-samples t-test, respectively, to assess the concordance of COI and difference in %LC values recorded by the two

observers. We found a high degree of concordance for COI (Kendall's W = 8.870, p = < 0.001, n = 200) and no difference in %LC classification between observers (t = -1.802, p = 0.072; df = 199). Both observers recorded the same COI on 76.5% of occasions and when classifications differed, this was mostly by only one class (83.0%).

4.3.6 Derivation of environmental variables

We compiled 29 environmental variables across three predictor sets: (i) LiDAR-; (ii) Ground-; and (iii) UAV-derived data, as potential predictors for this analysis (Table 4-2). All were derived on an individual-tree (per crown) basis. The method of deriving these variables, the rationale behind their inclusion and the associated hypotheses of their impact on liana distributions that we are testing are given in Table 4-1. All raster files for analysis were prepared using ArcGIS version 10.4 and subsequently processed and analysed in R version 3.5.1 (R Core Team, 2019). For variables measuring variation in the surrounding area (i.e. slope and soil), we used the tree crown shapefiles to determine the extent of the area of influence. This was because soil and topography will have a larger geographical extent of influence on larger trees than smaller trees, and the relative sizes of the tree crowns are appropriate for capturing this variation. Most lianas (90%) have been show to root below the crown of their host (e.g. Alvira et al., 2004) and, in addition to this, our field data show that the majority of lianas root within 1-2m from the tree trunk (i.e. under the area the canopy covers). The root systems of the trees typically scale with tree crown size (van der Heijden & Phillips, 2009).

We have not considered climate variables in this analysis as we assume that most of these variables operate at spatial scales too large for this study. Microclimatic variation may have some impact on liana growth patterns; we assume that this is better captured via the environmental variables we have used (especially topography) than by climate variables.

Table 4-2: The environmental variables and their associated predictor sets used in the Boosted Regression Tree (BRT) models.

Predictor Set	[Category] Variable name	Units
LiDAR	**[Distance to gaps]**	m
	<2m height, 25 – 100m^2; <2m height, 100 – 500m^2; <2m height, >500m^2	
	<5m height, 25 – 100m^2; <5m height, 100 – 500m^2; <5m height, >500m^2	
	<10m height, 25 – 100m^2; <10m height, 100 – 500m^2; <10m height, >500m^2	
	[Crown height]	m
	Mean crown height	
	[Topography]	o
	Mean slope angle	
Ground	**[Topography]**	o
	Mean slope angle	
	[Soil]	
	ECEC	cmol/kg
	Copper	mg/kg
	Phosphorus	mg/kg
	pH	
UAV	**[Distance to gaps]**	m
	<2m height, 25 – 100m^2; <2m height, 100 – 500m^2; <2m height, >500m^2	
	<5m height, 25 – 100m^2; <5m height, 100 – 500m^2; <5m height, >500m^2	
	<10m height, 25 – 100m^2; <10m height, 100 – 500m^2; <10m height, >500m^2	
	[Crown height]	m
	Mean crown height	
	[Topography]	o
	Mean slope angle	
	[Surrounding environment]	m
	Distance to nearest infested neighbour	
	[Crown area]	m^2

4.3.7 Analysis

To test our expectation that the distribution of liana-infested tree crowns across the 50 ha plot will exhibit a spatially aggregated pattern, we calculated an inverse distance matrix for each individual tree with its associated %LC. We then calculated Moran's I (Moran, 1950) using the command Moran.I in the package ape version 5.3 (Paradis & Schliep, 2018) in R. Boosted regression tree (BRT) models were used to analyse liana spatial distribution patterns in relation to the predictor variables and address our hypotheses H1–6 (Table 4-1). This machine-learning technique is an ensemble modelling method using regression trees and boosting to combine a collection of models with improved predictive performance that are capable of delivering powerful ecological insights (Leathwick et al., 2006; Elith et al., 2008). BRTs are appropriate and efficient for use here, due to the complex dataset with largely unknown relationships with variable interactions. Additionally, BRTs explicitly consider and report interactions between variables, which can indicate important combined effects, and handle non-linearity and collinearity relatively well in relation to other methods (Elith et al., 2008; Dormann et al., 2013). Furthermore, this technique is appropriate for both binary and continuous response variables (liana presence–absence, COI, and %LC, respectively).

BRT models were fitted in R for three predictor sets: (i) ground and LiDAR-derived variables; (ii) ground-derived and UAV-derived variables; and (iii) UAV-derived variables only. All were fitted to each liana response variable: (i) liana presence–absence; (ii) COI; and (iii) %LC. All predictor sets used in the modelling are summarised in Table 4-2. The function gbm.step in the gbm package version 2.1.5 (Greenwell et al., 2019) was used. This function balances predictive performance with model fit, while discouraging overfitting, by using regularisation methods (Hastie et al., 2001), and uses shrinkage procedures as each tree is added to control the number of terms and produce parsimonious models. After

experimenting with model settings, we used a tree complexity of 3, learning rate of 0.005, bag fraction of 0.5 and default values for all other arguments.

To quantify the model effects of individual explanatory variables, the relative influence (RI) values, which indicate model contribution of each predictor on the model outcome, were obtained from gbm.step. RI 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, and averaged over all trees (Friedman & Meulman, 2003), and allow these complex ensemble models to be easily interpreted. The relative influence of each variable is scaled so that the sum adds to 100, with higher numbers indicating a stronger influence on the response, (a value of 100 for a predictor would mean that it contributed solely to the final model). Where the model contribution reflected a negative relationship with liana presence–absence, COI or %LC, we made the RI value negative for display purposes.

Internal fit statistics (self-statistics, SS) were used to assess internal model fit. We then evaluated our models using 10-fold cross-validation (CV). Both SS and CV are included in the gbm package and their values range from 0 to 1, where a higher number suggests a better model: a value of 1 would be a model that explains all of the variation in the data (SS) or predicts very well to new data in the same area (CV). CV randomly subsamples the data according to the user-defined bag fraction (here 0.5). This means 50% of the data were used to parameterise the model and the other 50% to evaluate it. This is repeated ten times and the final cross-validation correlation statistic is the mean Pearson correlation coefficient between the training and testing data across these ten runs.

Additionally, to test whether model fit reflected more than spatial autocorrelation of the variables, we reassessed the fits of all the BRT models by geographically separating calibration and evaluation data and calculated the percentage deviance

explained and the area under the receiver operating characteristic curve. The division of the data into evaluation and calibration data sets was made by following the method described in ENMeval (Muscarella et al., 2014) for 'Checkerboard1'. This partitions the data into two bins following a checkerboard grid pattern. It does not ensure a balanced number of occurrences/data points in each bin but we ended with a fairly balanced training and evaluation set (training set: 1235 data points; evaluation set: 1193 data points).

4.4 Results

We delineated 2,428 tree crowns ≥ 25m^2 area (mean = 48.6 individuals ha^{-1}), ranging in liana infestation from 0-100% across the 50 ha plot (Figure 4-2). For each, we derived values for the environmental predictor variables (Table 4-2) and assessed the liana load of the tree crown. In total, 1,243 trees (51.2%) were infested by lianas at any level: COI 1 = 705 trees (29.0%), COI 2 = 237 trees (9.8%), COI 3 = 129 trees (5.3%), COI 4 = 171 trees (7.0%) (Figure 4-2). We found that liana-infested tree crowns were positively spatially aggregated across the 50 ha plot (Moran's I = 0.036, $p \leq 0.001$).

4.4.1 BRT self-statistics and cross-validation

The BRT models built on the separate predictor sets generally had similar, good internal fits (SS) and relatively good cross-validation (CV) statistics across all liana load classifications (Table 4-3). SS increased from 0.55–0.73 when more precise measures of liana infestation (% liana cover [%LC]) were used compared with simple presence/absence of lianas. The variance accounted for by these models (as indicated by the CV) also increased with increased precision of liana load classification from 43 to 54%. The best models were those that combined UAV and ground-derived variables, with SS ranging from 0.60-0.73 and accounting for between 45% and 54%, with the models that used more precise liana classifications scoring higher. The models built on the combined LiDAR and

ground data performed similarly to those built only on the UAV-derived variables. The SS values for these models ranged from 0.55–0.70 (LiDAR and Ground) and 0.58–0.66 (UAV only) and the models accounted for between 43–54% (LiDAR and Ground) and 44–52% (UAV only) of variation in liana load. When examining whether model performance was subject to autocorrelation of the predictor variables, model evaluation using independent data resulted in a lower percentage deviance explained that those models evaluated through cross-validation (Table 4-4).

4.4.2 Variable importance

Canopy height dominated all of the BRT models across all predictor sets and liana assessment methods (Tables 4-3 and 4-5). It had the highest relative influence values of any environmental variable, regardless of predictor set, always exceeding -32% and with a maximum of -42.36% for the LiDAR-derived canopy height in the combined LiDAR and ground data model (Tables 4-3 and 4-5). The negative relationships with liana infestation show that taller trees were less infested with lianas than shorter trees.

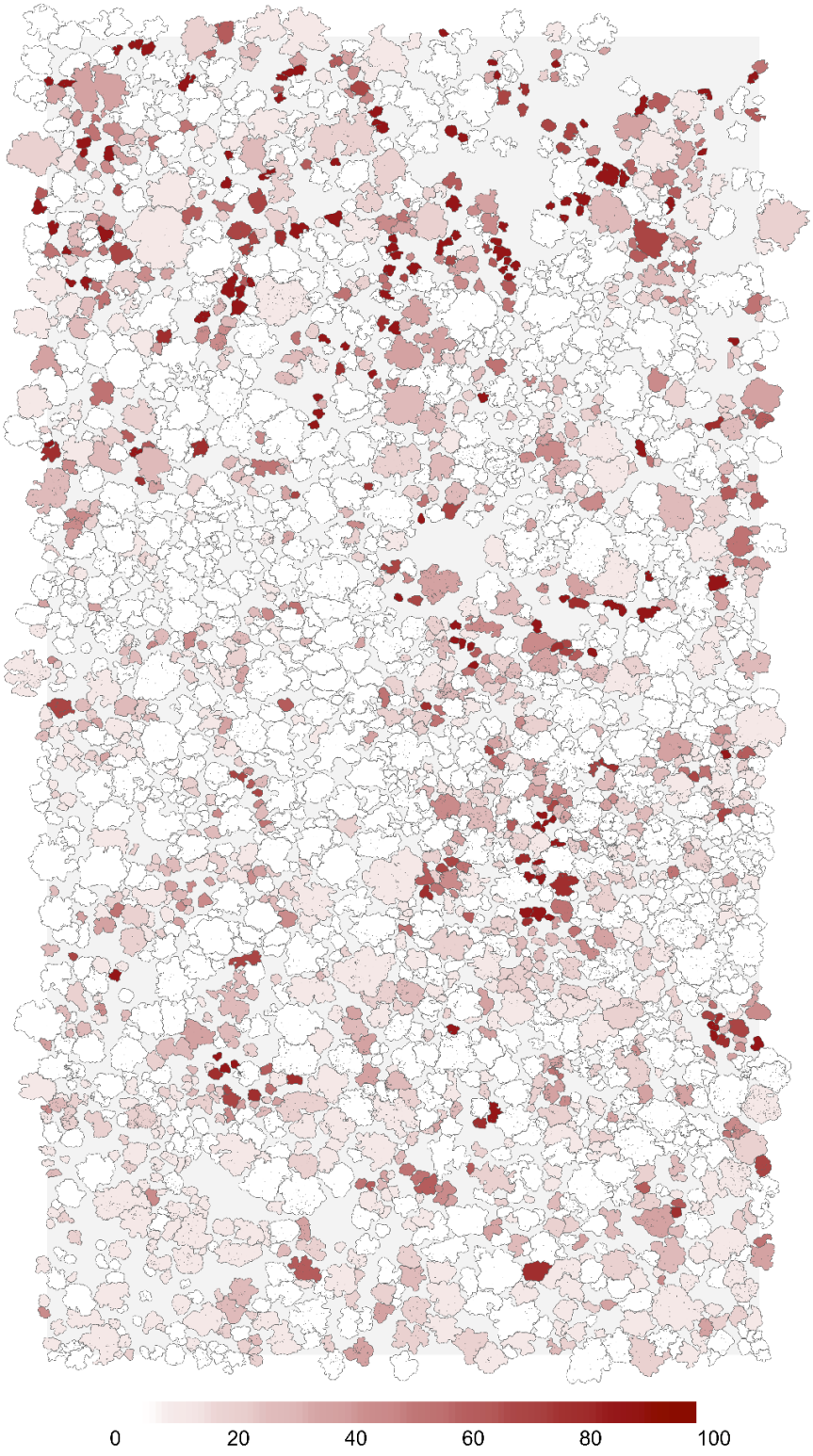


Figure 4-2: The location and liana infestation level of every tree crown surveyed (n = 2,428) within the 50 ha plot. The plot is indicated with grey shading. The red colour ramp indicates %liana infestation (darker = more heavily infested tree crowns).

Table 4-3: Boosted Regression Tree (BRT) model results across all liana infestation assessments (liana presence-absence (P/A), crown occupancy index (COI), and % liana canopy cover (%LC)) for the different predictor sets (LiDAR and ground data only, UAV and ground data only, UAV data only). The cross-validation (CV) correlation, self-statistics (SS), dominant variables (those with the greatest relative influence, values of which are given in brackets), and dominant model interactions from Boosted Regression Tree models are shown.

	LiDAR + Ground					**UAV + Ground**					**UAV**				
	CV	**SS**	**Predictor w. highest RI**	**Predictor w. 2nd highest RI**	**Dominant model interaction**	**CV**	**SS**	**Predictor w. highest RI**	**Predictor w. 2nd highest RI**	**Dominant model interaction**	**CV**	**SS**	**Predictor w. highest RI**	**Predictor w. 2nd highest RI**	**Dominant model interaction**
P/A	0.43	0.55	Tree height (42.36%)	Gaps 2m, <500m² (9.53%)	Gap 2m, <500m² * Tree height	0.45	0.60	Tree height (37.95%)	Distance to nearest infested neighbour (8.44)	Tree height * Gaps 5m, 100-500m²	0.44	0.58	Tree height (40.86%)	Distance to nearest infested neighbour (9.96%)	Tree height * Gaps 5m, 100-500m²
COI	0.52	0.69	Tree height (36.29%)	Gaps <2m, 100-500m² (6.96%)	Gaps 2m, 100-500m² * Tree height	0.53	0.68	Tree height (37.78%)	Gaps 10m, <500 (8.25%)	Tree height * Gaps 10m, 100-500m²	0.52	0.67	Tree height (39.90%)	Gaps 10m, <500 (8.91%)	Tree height * Gaps 10m, 100-500m²
%LC	0.54	0.70	Tree height (37.75%)	Gaps 2m <500m² (9.30%)	Gaps 2m, 100-500m² * Tree height	0.54	0.73	Tree height (32.0%)	Gaps 10m, <500 (9.17%)	Tree height * Gaps 10m, 100-500m²	0.52	0.66	Tree height (41.14%)	Gaps 10m, <500m² (10.05%)	Tree height * Gaps 10m, 100-500m²

Table 4-4: Boosted Regression Tree (BRT) model results across all liana infestation assessments (liana presence-absence (P/A), crown occupancy index (COI), and % liana canopy cover (%LC)) using different predictor sets (LiDAR and ground data only, UAV and ground data only, UAV data only) using model prediction validated with cross-validation (CV) correlation, and independent data. The percentage of deviance explained by each model, along with the area under the receiver operating characteristic curve (AUC) is given.

	Cross-validation									**Independent**								
	P/A			**COI**			**%LC**			**P/A**			**COI**			**%LC**		
	L&G	**U&G**	**UAV**	**L&G**	**U&G**	**UAV**	**L&G**	**U&G**	**UAV**	**L&G**	**U&G**	**UAV**	**L&G**	**U&G**	**UAV**	**L&G**	**U&G**	**UAV**
Percentage deviance explained	0.43	0.45	0.44	0.52	0.53	0.52	0.54	0.54	0.52	0.40	0.42	0.42	0.42	0.44	0.43	0.43	0.44	0.43
Area under the receiver operating characteristic curve	0.75	0.74	0.75	0.72	0.73	0.74	0.72	0.72	0.72	0.73	0.74	0.74	0.73	0.72	0.73	0.72	0.71	0.71

Other variables with high relative influence values across all BRT models were gap variables, particularly those for the largest gap areas (Tables 4-3 and 4-5). Crown area and distance to the nearest infested neighbour were important when UAV-derived data were included in the model (Tables 4-3 and 4-5). All these variables displayed negative relationships with liana infestation, indicating that as distance from gaps and infested neighbours increased, trees had less liana infestation, and trees with larger crown areas had less liana infestation. The LiDAR-derived gap variable with the highest relative influence for all liana assessment methods was 2 m gaps >500 m^2 (from -5.47% to -9.80%). For UAV-derived gap variables, however, 10 m gaps >500 m^2 were the strongest predictors, but only for COI and %LC (UAV and Ground: -8.25%; UAV only: -8.91% and UAV and Ground: -9.17%; UAV only: -10.05%, respectively) (Table 4-5). The most frequent and dominant model interactions were between canopy height (UAV- or LiDAR-derived depending on which predictor sets were used in the model) and distance to gap variables (Table 4-3). Of these gap variables, gaps of medium size (100-500 m^2) with varying depths were generally the most important.

The model contributions of slope variables from LiDAR, Ground and UAV were all relatively low (<5/-5%) with the exception of LiDAR-derived slope in the COI model built on the combined LiDAR and Ground data (-5.28%), and the UAV-derived slope in the COI model built on the UAV only predictor set (-5.40%) (Table 4-5). Model influences from soil variables were also typically low (<5/-5% model contribution) with the possible exception of Copper exhibiting a relative influence value of 5.77% for liana presence–absence in the LiDAR and ground combined model, and pH showing a relative influence value of 5.20% for %LC in the UAV and ground combined model (Table 4-5).

Table 4-5: Boosted Regression Tree (BRT) model results across all liana infestation assessments (liana presence-absence (P/A), crown occupancy index (COI), and % liana canopy cover (%LC)) for the different predictor sets (LiDAR and ground data only, UAV and ground data only, UAV data only). The relative influence (RI) of each predictor is shown, as well as the direction of this influence: the darkest shades indicate values over 10% and lighter shades between 5% and 10%.

	Relative influence (%) of each predictor																										
	LiDAR											Ground					UAV										
	Gaps									Height	Slope	Slope	Soil				Gaps								Height	Area	Slope	Env
	<2m height, 25 – 100m²	<2m height, 100 – 500m²	<2m height, >500m²	<5m height, 25 – 100m²	<5m height, 100 – 500m²	<5m height, >500m²	<10m height, 25 – 100m²	<10m height, 100 – 500m²	<10m height, >500m²				pH	Cu	Ph	ECEC	<2m height, 25 – 100m²	<2m height, 100 – 500m²	<2m height, >500m²	<5m height, 25 – 100m²	<5m height, 100 – 500m²	<5m height, >500m²	<10m height, 25 – 100m²	<10m height, 100 – 500m²	<10m height, >500m²				
P/A																											
L&G	-2.31	-5.22	-9.80	-3.40	-1.87	-5.18	-3.19	-2.97	-3.01	-42.36	2.94	-2.39	2.61	5.77	-2.61	2.44											
U&G												-2.61	2.40	3.55	-3.17	3.22	-4.61	-2.47	-4.76	-1.91	-2.38	-2.26	-3.43	-2.98	-3.54	-37.95	-7.62	-2.70	-8.44
UAV																	-5.63	-3.58	-5.91	-2.52	-3.49	-3.22	-4.21	-3.93	-4.17	-40.86	-9.00	-3.53	-9.96
COI																											
L&G	-3.27	-6.96	-6.59	-3.55	-3.54	-4.73	-4.36	-4.28	-4.93	-36.29	-5.28	-2.05	3.70	3.67	-3.73	3.07											
U&G												-2.00	4.04	2.69	-3.25	1.98	-3.82	-2.77	-5.35	-2.42	-2.58	-2.71	-2.65	-6.02	-8.25	-37.78	-3.49	-3.82	-4.38
UAV																	-4.65	-3.54	-6.49	-3.05	-3.57	-3.48	-3.39	-7.57	-8.91	-39.90	-4.79	-5.40	-5.25
%LC																											
L&G	-3.21	-7.73	-5.47	-3.55	-3.24	-3.69	-4.38	-4.79	-5.47	-37.75	-2.60	-1.76	3.34	3.25	-3.08	2.85											
U&G												-2.34	5.20	2.99	-3.62	2.19	-2.96	-3.97	-6.66	-2.02	-3.32	-3.64	-2.82	-5.80	-9.17	-32.00	-4.36	-3.44	-3.51
UAV																	-3.20	-4.56	-7.10	-2.48	-3.75	-4.46	-3.44	-6.74	-10.05	-41.14	-4.28	-4.60	-4.20

4.5 Discussion

Here we present the first landscape-level liana canopy distribution data for the Palaeotropics and analysis of what environmental variables may affect liana spatial distributions at this scale. Significant aggregation of liana infestation was observed (Moran's I = 0.036, $p \leq 0.001$; Figure 4-2), as expected. This is in line with other studies conducted in other tropical forests around the world which have found similar patterns in plot-level liana studies (Pérez-Salicrup & De Meijere, 2005; Schnitzer et al., 2012; Ledo & Schnitzer, 2014). Canopy height was shown to be the most important variable influencing this spatial patterning, with gap variables also being important (Tables 4-3 and 4-5). UAV-derived data were shown to be just as good as equivalent LiDAR-derived data for predicting liana spatial distributions.

The BRT models unanimously showed that the variable with the highest contribution was canopy height (either UAV- or LiDAR-derived) (Tables 4-3 and 4-5). This indicates that, for all liana load classifications, the presence and/or degree of liana infestation was determined primarily by tree crown height, with a higher degree of liana presence in shorter trees. This is in disagreement with previous research which has found that lianas most commonly affect taller trees (e.g. Pérez-Salicrup et al., 2001; Pérez-Salicrup & De Meijere, 2005; van der Heijden et al., 2008; Addo-Fordjour et al., 2009). This contradicts hypothesis H2 (that taller trees will have a higher incidence and degree of liana infestation). This inconsistency with previous research may reflect the differences in forest structure and composition of Southeast Asian forests to the Neotropical and African forests previously studied. In particular, Southeast Asian forests are characterised by emergent dipterocarps (Corlett & Primack, 2006) and recent research has suggested that lianas may have difficulties in infesting these trees (Wright et al., 2015). One hypothesis is that dipterocarps are able to avoid lianas

by shedding lower branches (and presumably lianas) ontogenetically as they shift from monopodial growth to sympodial growth during their transition from juveniles to adults. Further, as adults, dipterocarps have tall branch-free boles lacking trellises to support climbing lianas (Hallé & Ng, 1981; Campbell & Newbery, 1993).

It is also important to consider that tree crown height may be a proxy for disturbance. Areas with lower tree crown height potentially indicate younger trees that may indicate recent or ongoing potential canopy gaps, and vice versa. This tallies with our finding that the predictor with the second highest relative influence in our models is generally a gap variable (Table 4-3 and 4-5), and that canopy height and gap variables consistently present the dominant model interactions (Table 4-3). This finding is consistent with the disturbance hypothesis (Schnitzer & Carson, 2001; Schnitzer, 2005; Dalling et al., 2012; Schnitzer et al., 2012) and with our hypothesis H1 – that liana presence and degree of infestation will increase in proximity to disturbance (gaps).

Crown area had a relatively high (negative) RI value when UAV data were included in the model (Table 4-5) indicating that, with increasing crown area, liana infestation decreases. This is inconsistent with our hypothesis H3 (that larger crown areas have higher likelihood and level of liana infestation). When considering the same rationale as outlined above, however, that lianas may have difficulty infesting dipterocarps (Wright et al., 2015) this result is unsurprising. In Palaeotropical forests, dipterocarps are not only the tallest trees, but also the trees with the largest crowns. Therefore, the inconsistency between our results and hypothesis H3 may reflect the differences in forest structure and composition of Southeast Asian forests compared with their Neotropical counterparts, where the majority of the research underpinning the existing hypotheses on liana distributions and relationships to environmental variables has been done. A

potential limitation of this study is that only the trees with the whole or majority of their canopy exposed were included. This means that all adult dipterocarps were included but some understorey trees (which may have a higher rate of liana infestation) were not considered. We do not think that this limitation invalidates our findings, however, as a previous study of the forest at Danum Valley using a ground survey alongside a UAV survey to take into account these understorey trees revealed similar tree infestation rates across multiple plots, and exhibited the same negative relationship between increasing tree height and liana infestation (Waite et al., 2019). We therefore suggest that the benefits of using UAV images to assess liana tree crown infestation are not severely limited by the necessary omission of a limited number of understorey tree crowns.

The benefits of UAV data collection are further exemplified by the results of our BRT models. The BRT models built using LiDAR-derived data and those using UAV-derived data performed similarly to one another (Table 4-3). Calibration of the UAV data in this environment is very difficult, due to the complex terrain and vegetation cover, so exact values may not be as accurate as the LiDAR data. Nonetheless, uncalibrated UAV data were able to explain comparable amounts of variance in liana infestation as the LiDAR data, and performed similarly in predicting liana infestation (Table 4-4). Although all of our models had lowered predictive performance on independent data, the models built solely on UAV data accounted for ~42–43% of the variation in liana infestation measures (Table 4-4). Therefore, while such models built using UAV data will not be able to produce precise maps of liana infestation, they may assist in indicating areas where lianas are likely to be found. This may, in turn, assist in practices involved in liana cutting aiming to improve timber and fruit production (Kainer et al., 2014; Sist et al., 2003; Verwer et al., 2008) or for carbon restoration projects (Marshall et al., 2017).

The results of this study indicate that UAVs can be used as accurate, accessible, agile, cost-effective, and time-efficient new tool for collecting data not only on liana infestation (see Waite et al., 2019), but also on the variables that may determine liana spatial patterns. UAVs may, therefore, make such data collection more accessible to a wider variety of users and enable faster and cheaper mapping of variables that may be related to liana presence than possible with either Ground- or LiDAR-derived data. Thus, the use of UAVs would allow the extrapolation and implementation of the analyses presented here in other locations and/or forest types (e.g. logged forest). This would increase our knowledge of liana spatial distributions and their relationships to environmental variables and may assist in providing a more comprehensive understanding of the maintenance of plant species diversity and the factors that control plant species distributions. This may prove invaluable as lianas may continue to increase with future climate change, altering our tropical forest functioning with serious implications for tropical forest carbon storage.

Chapter 5: Increase in liana infestation in Malaysian tropical forest tree crowns and concurrent canopy changes in the aftermath of the 2015/16 El Niño Event

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5.1 Abstract

Tropical forests store and sequester large quantities of carbon, mitigating climate change. Lianas (woody vines) are important tropical forest components, most conspicuous in the canopy. Lianas reduce forest carbon uptake and have been increasing in recent years with global implications for climate change. Recent liana increases are hypothesised to be due to increases in the length and severity of droughts, which are predicted to continue in the coming decades. It is therefore important to know whether ENSO-related droughts can be linked to increasing liana infestation, and any potential impacts this may have on the forest canopy. A method to facilitate short-term monitoring of tropical forest canopy response, including changes in liana infestation, to such droughts is needed.

We used a lightweight, commercially available unmanned aerial vehicle (UAV) to collect image data of the forest canopy during and after the 2015/16 El Niño drought in the primary tropical forest of Sabah, Malaysia. By visually interpreting the images, we assessed the degree of liana infestation in 2016 and 2017, and the changes during that time period, for 50 ha of forest. We also assessed canopy metrics, tree leaf cover, area and greenness, and examined change in these between the years, and whether this related to liana load.

Tree-level liana infestation and crown area showed significant increase, whereas crown greenness and tree leaf cover showed a significant decrease, between years. Percentage liana cover is significantly higher for trees that experienced mortality between the surveys than for those that did not. Changing climatic conditions, and the associated increases in length and severity of droughts may, therefore, alter liana infestation and impacts on tropical tree canopies. This has important implications for tropical forest carbon storage. The use of UAVs provides an effective, reproducible method to assess changes in tropical forest canopies in response to events such as El Niño droughts. This can facilitate short-term

monitoring as well as provide an archive of image data for multi-temporal studies which can be built upon in future. Such data may provide a means to derive information on what the impacts of changing climatic conditions and increasing liana abundance may be on forest canopies and, by extension, on the carbon storage potential of tropical forests, now and into the future.

5.2 Introduction

Lianas (woody vines) peak in abundance, species richness and species diversity in tropical forests (Gentry, 1991, Schnitzer & Bongers, 2002), commonly contributing up to 40% of woody stems, and more than 25% of woody species (Schnitzer & Bongers, 2002; 2011; van der Heijden et al., 2015). Lianas are an important agent in changing carbon cycling in tropical forests. They can decrease the amount of carbon fixed by a given area of tropical forest by reducing the productivity of, and increasing the mortality of, host trees (Phillips et al., 2005; Kainer et al., 2006; Nabe-Nielsen et al., 2009; van der Heijden & Phillips, 2009; Ingwell et al., 2010; Schnitzer et al., 2014). This occurs through above- and below-ground competition for resources, such as essential nutrients, water and light (Perez-Salicrup & Barker, 2000; Schnitzer et al., 2005; van der Heijden & Phillips, 2009; Tobin et al., 2012; Johnson et al., 2013). Lianas may also increase the mortality of neighbouring trees by connecting tree canopies, increasing the number and size of trees pulled down when liana-infested trees fall. Furthermore, lianas not only decrease tree growth and increase tree mortality, but further reduce carbon uptake by failing to replace the biomass lost, and therefore further constrain above-ground forest primary productivity (van der Heijden et al., 2013). Lianas contribute relatively little to forest-level biomass as they rely on trees for structural support to deploy leaves in the canopy, and so are able to allocate a higher proportion of biomass to foliage production over carbon-dense stem production. Indeed, a 3-year liana removal experiment found that lianas reduced

net carbon uptake by ~76%/year (van der Heijden et al., 2015), mostly attributed to a reduction in tree growth, due to competition by lianas.

This reduction in carbon uptake and storage may be exacerbated by lianas increasing in abundance, richness, and biomass in tropical forests (Phillips et al., 2002; Schnitzer & Bongers, 2011). Although the mechanism(s) behind this increase are largely unknown, one proposed putative mechanism is a decrease in rainfall or an increase in length and severity of droughts (Schnitzer & Bongers, 2011). Multiple studies (including Schnitzer, 2005; Swaine & Grace, 2007; Cai et al., 2009; Sánchez-Azofeifa et al., 2009; Zhu & Cao, 2009; DeWalt et al., 2010; Chen et al., 2015; Schnitzer & van der Heijden, 2019) posit that lianas have a growth advantage over trees during dry conditions. This is due, in part, to their foliar traits: lianas have higher specific leaf area, photosynthetic rates and leaf nutrient levels, and lower leaf life span (Sanchez-Azofeifa et al., 2009; Zhu & Cao, 2010; Asner & Martin, 2012). These traits allow more efficient resource allocation during drought, which can amplify carbon fixation (Cai et al., 2009). Lianas also have long roots (Schnitzer, 2005), allowing them to uptake water from deeper soil layers (Andrade et al., 2005; Chen et al., 2015) than trees, and potentially extending the availability of water during drought periods. This, coupled with the strong stomatal control of lianas, which may allow them to limit water loss, means lianas can efficiently use water during droughts and may contribute to their ability to continue to grow even when many of their competitors, such as trees, are dormant (Cai et al., 2009). This is particularly advantageous: lianas can exploit the abundance of resources that would usually be limited during wet periods, including higher light levels, due to the reduced cloud cover (Condit et al., 2000; Graham et al., 2003).

This advantage of lianas to grow in droughts may help to explain their increasing dominance in tropical forests (Schnitzer, 2005): research has indicated that, on

average, the temperature and severity of drought has increased, while rainfall has decreased, in recent decades (Malhi & Wright, 2004; 2005; Li et al., 2008). This may have promoted liana proliferation, and if so, can be expected to increase into the future. This is because it is predicted that many tropical forests are likely to undergo heightened incidence and severity of droughts under climate change (Stork et al., 2009; Phillips et al., 2009; Lee & McPhaden, 2010; Lowman et al., 2013; Mora et al., 2013; Corlett, 2016). Perhaps of particular importance is the fact that many tropical forests are suffering from increased frequency and severity of ENSO-related droughts (Phillips et al., 2009; Allen et al., 2010; Enquist & Enquist, 2011; Cai et al., 2014). This is predicted to increase further in future, which will increase water stress (Lee & McPhaden, 2010) and may increase liana abundance and biomass, as well as associated liana-induced reduction in the carbon sink function of these forests (Schnitzer, 2005; Schnitzer & Bongers, 2011; Schnitzer et al., 2012).

Research on whether ENSO-related droughts result in an increase of liana infestation, and any potential impacts this may have on the forest canopy is particularly important as tropical forests are critical components of the global carbon cycle (Beer et al., 2008; Marvin et al., 2016). They account for a third of carbon fixed by photosynthesis (Beer et al., 2010; Schnitzer & Bongers, 2011; van der Heijden et al., 2015), taking in ~1.19 ± 0.41 Pg carbon yr^{-1} from the atmosphere (Pan et al., 2011) and storing ~285 Pg carbon in aboveground biomass (Feldpausch et al., 2012). Increasing our understanding of potential impacts of ENSO-related drought on lianas and tree canopies will provide us with much-needed information on what the impact of changing climatic conditions and increasing liana abundance and biomass may be on tropical forest canopies and the carbon storage potential of tropical forests, now and into the future.

Study of the influence of El Niño drought on lianas so far, however, has focused mainly on the Neotropics. Very little research on this topic has been conducted in Palaeotropical forests despite their clear ecological differences (Corlett & Primack, 2006; 2011), as well as the differences in the impact of El Niño events in these areas (Diaz, 2000). Furthermore, studies of drought impacts on lianas have focused on ground-based measurements of liana growth, such as stem diameter assessments (Schnitzer & van der Heijden, 2019; van der Heijden et al., 2019). Such ground-assessments are not able to characterise changes in tree crowns, such as alterations in tree leaf cover, crown area, and crown greenness. Our knowledge of the potential effects in the canopy layer is, therefore, extremely limited. UAVs have proven to be an accessible, cost-effective, time-efficient, and easily deployable tool to provide accurate data for liana load assessment in tropical forest canopies (Waite et al., 2019), and for study of factors affecting liana distribution in the canopy (Chapter 4). Their potential for temporal monitoring of lianas, however, has not yet been explored.

Here we aim to assess, for the first time, the potential for the use of Unmanned Aerial Vehicles (UAVs) to assess short-term change in tropical forest canopies. Based on existing research (reviewed above), we hypothesise that: (i) liana infestation will increase in tropical forest tree crowns in association with drought events such as El Niños; and (ii) it is likely that lianas will have negative impacts on trees. Hypothesis (ii) predicts that changes through time (specifically between 2016 and 2017) in forest canopy tree leaf cover, crown area and crown greenness may be more pronounced at higher levels of liana infestation (in 2016). We test these expectations in a globally important study area in Southeast Asia, following the El Niño event of 2015/2016.

5.3 Methods

5.3.1 Study site

UAV flights were conducted over the Center for Tropical Forest Science 50 ha permanent research plot in the lowland, evergreen mixed dipterocarp forest in the Danum Valley Conservation Area (hereafter 'Danum') (4°57' N, 117°42' E) in Sabah, Malaysia (Figure 5-1). The climate at Danum is equatorial but subject to occasional drought (Walsh & Newbery, 1999). Daily temperature, rainfall, humidity and sunshine duration are recorded at a weather station on site and are freely available from the Southeast Asian Rainforest Research Partnership (www.searrp.org/scientists/available-data/).

Mean maximum annual temperature is 31.5°C and mean annual rainfall is 2844.1 mm. Climate at Danum is mildly influenced by the edge effects of two monsoons: the wettest months fall between November to March due to a north-eastern monsoon while drier, more consistent conditions occur due to a southwestern monsoon in June and July (Marsh & Greer, 1992; Walsh & Newbery, 1999; Clark & Walsh, 2006). Danum also is impacted by ENSO, with El Niño events occurring roughly every two to seven years (Chen et al., 2016). These El Niño events can cause considerable variation in the rainfall of the area, altering it from 3294.1 mm in 1995 to 1918.4 mm in the El Niño of 1997/98 and from 3210.7 mm in 2013 to 2181.2 mm in the El Niño year of 2015/16.

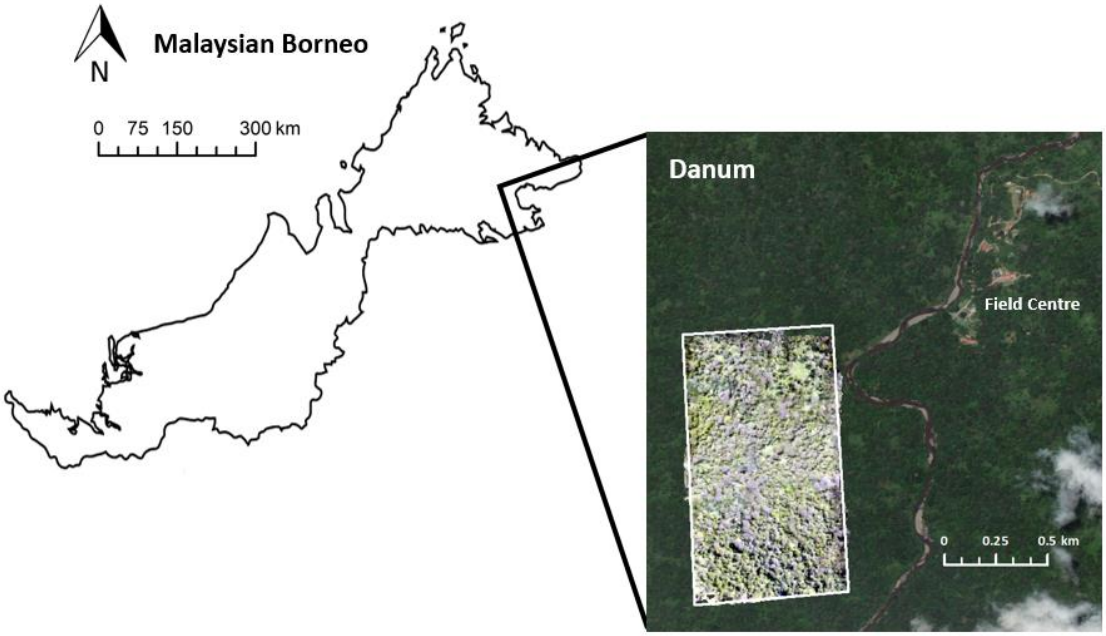


Figure 5-1: Location of the study site and 50 ha plot, which are located in the state of Sabah, Malaysia, on the island of Borneo, Southeast Asia. The orthomosaic created from our UAV survey of the 50 ha plot is shown outlined in white on top of satellite imagery of the Danum Valley Conservation Area. Satellite imagery source: DigitalGlobe WorldView2 RGB imagery.

5.3.2 Data collection

Images of the study area were captured using a DJI Phantom 3 Advanced UAV with an integrated three-waveband (RGB) 12-megapixel camera, on 14th–16th June 2016 and the 20th–23rd February 2017. The images have a spatial resolution of ~12.4 mm/pixel and cover both the 50 ha plot and a ~50 ha of buffer of surrounding forest. The images were then processed to form two orthomosaics, one for the 2016 data, and one for the 2017 data, geo-referenced to the WGS84 UTM Zone 50N projected coordinate system, using Agisoft-Photoscan version 1.3.0. Full details of the UAV, flight characteristics and processing method are found in Waite et al. (2019). The orthomosaics were exported to ERDAS IMAGINE version 16.5.0 where all tree crowns within the 50 ha plot, for which the whole (or majority) of the crown was visible, were visually identified and manually delineated to produce individual raster layers and a shapefile for each tree crown.

Any tree crowns <25 m^2 in area or too shaded to accurately determine the edge of the tree crown and/or assess visually for liana infestation were excluded from further analysis.

For each identified tree crown, the liana load was classified from the orthomosaics using a detailed measure: percentage liana cover (%LC) (Waite et al., 2019). The crown is visually spilt into four quadrants (the north-east, north-west, south-east, and south-west), and the % crown cover of lianas for each estimated to the nearest 5%, with the average of the four quadrants taken as the % liana cover of the tree crown (Marvin et al., 2016; Waite et al., 2019). The increase in %LC between the two years (where negative values represent decreases) was then calculated for each tree, as follows:

$$\boldsymbol{\Delta} \text{ in } \%\text{LC} = \%\text{LC in } 2017 - \%\text{LC in } 2016 \quad [1]$$

Tree crown leaf cover was calculated for a subset of tree crowns crown by visually determining the percentage of the crown covered by tree leaves (%TC). This does not include any areas where bare branches were visible, or areas consisting of liana leaves so the total potential %TC is always 100%. The increase in %TC between years (where negative values represent decreases) was then calculated for each tree as follows:

$$\boldsymbol{\Delta} \text{ in } \%\text{TC} = \%\text{TC in } 2017 - \%\text{TC in } 2016 \quad [2]$$

Tree crown area was calculated for each individual crown by determining the pixel size of the orthomosaics, and multiplying this by the number of pixels comprising the crown. The % increase in area between years (where negative values represent decreases) was then calculated as follows:

$$\%\boldsymbol{\Delta} \text{ in tree crown area} = \frac{2017 \text{ area} - 2016 \text{ area}}{2016 \text{ area}} \times 100 \quad [3]$$

To determine tree crown greenness, the values for each of the three wavebands (red, green and blue: RGB) for each pixel in each tree crown raster were extracted, and the sum of values for each channel calculated. The greenness of the tree crown was then calculated with the equation:

$$\text{greenness} = \frac{g}{r + g + b} \quad [4]$$

Where: *g, r,* and *b* represent the raw sum green, red and blue values for each pixel.

This gives the proportion of the pixel's overall intensity that is on the green channel and is, therefore, invariant to the overall brightness of the pixel (Richardson et al., 2007; Morris et al., 2013). This means that changes in illumination in the images between years due to differences in cloud cover, for example, should not affect the greenness value of each pixel. The increase in greenness between years (where negative values represent decreases) was then calculated as follows:

$$\boldsymbol{\Delta} \text{ in greenness} = 2017 \text{ greenness} - 2016 \text{ greenness} \quad [5]$$

We have previously shown the UAV-derived measure of liana infestation to accurately measure liana loads across forest types and at different spatial resolutions, with little inter-observer bias (Waite et al., 2019). As we are assessing change through time, however, and two observers classified liana load from the UAV image data across the contiguous 50 ha plot area, we performed additional testing to assess possible inter-observer bias, to check it was not causing systematic differences in liana load between the two halves of the plot. We also tested for inter-observer bias in crown delineation and, therefore, resultant crown greenness and area values. The two observers independently classified the tree crown liana load, delineated the tree crown and extracted greenness and area

values, for ~400 random trees (~100 random trees each for each year, from the other observer's initial half of the plot).

5.3.3 Analysis

Paired-samples t-tests were used to assess differences between observers in tree crown %LC, greenness, or area as well as to assess potential differences in tree crown %LC, %TC, greenness, and area between the years. Furthermore, an independent samples t-test was used to assess whether the liana infestation level in 2016 was significantly different for trees that died between the years than trees that survived.

5.4 Results

No significant differences between observers were found in %LC, greenness, or area, using paired-samples t-tests (Table 5-1). In total, 2,424 tree crowns were delineated in 2016 (Figure 5-2). Of these, 43 (1.77%) individuals died between surveys leaving 2,381 tree crowns in 2017 (there was no recruitment of tree crowns into the canopy during this period). Overall, the percentage of tree crowns infested by lianas remained nearly constant from 2016 (51.16%) to 2017 (51.36%). However, this disguises tree-level change between the years: quite a few (given the short time period) previously uninfested trees became infested, and most trees that died had been heavily infested. In total, 54 trees (2.23% of all trees recorded in 2016) gained liana infestation in 2017 (having been uninfested in 2016) and 43 trees (1.77% of those recorded in 2016) died between the years.

There was a statistically significant increase in %LC of individual trees (excluding those trees that experienced mortality) between the two years (Figures 5-2 and 5-3, Table 5-2). Of the individual trees, 11.3% had reduced liana cover, 27.4% had increased liana cover, 47.17% were uninfested in both years and 14.15% were infested to the same degree in both years (identical %LC). There was a statistically

significant decrease in greenness and %TC from 2016 to 2017 and a statistically significant increase in crown area of individual trees from 2016 to 2017 (Figure 5-4, Table 5-2).

Of the 43 trees that died between 2016 and 2017, 34 crowns were infested by lianas in 2016 (79%), with all but one of these crowns highly or very highly infested by lianas: 19 crowns highly (>50%LC) infested and 14 very highly (>75%LC) infested. The liana infestation level in 2016 of trees that died between years (mean %LC = 43.401, SD = 40.343) was significantly higher than for those trees which remained alive (mean = 15.595, SD = 26.020) (independent samples t-test assuming unequal variances: $t = 4.50$, $df = 42.63$, $p \leq 0.001$). Small trees were disproportionately affected by mortality; when split into four size classes, 27 of the 43 crowns in the small category and 13 in the second smallest size class.

Table 5-1: Test of differences between observers presented for the 2016 and 2017 test sets together (All) as well as the test sets separately. Differences are assessed with paired-samples t-tests and shown between observers in independently assessing liana infestation of tree crowns in UAV image data using percentage liana cover (%LC), as well as independently assessing tree crown delineation to derive greenness and area values.

	%LC			**Greenness**			**Area**		
	df	**t**	**p**	**df**	**t**	**p**	**n**	**t**	**P**
All	396	-1.802	0.072	390	0.431	0.667	390	-1.610	0.108
2016	199	-1.181	0.147	196	0.046	0.963	196	-1.177	0.241
2017	196	-1.096	0.274	193	0.579	0.564	193	-1.102	0.272

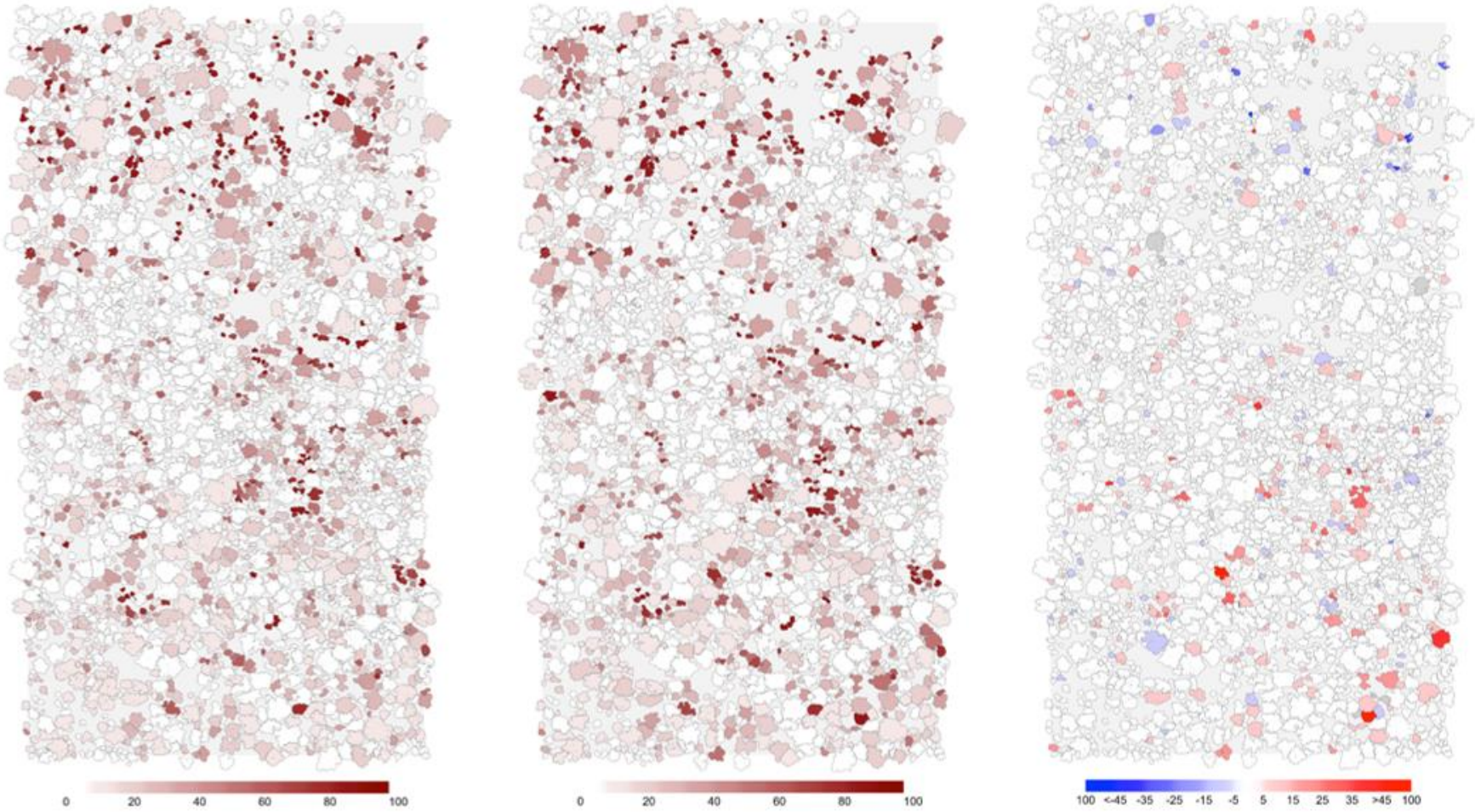


Figure 5-2: The location and liana infestation level of every tree crown surveyed within the 50 ha plot in (a) 2016, (b) 2017, and (c) the change in liana infestation level between the two years. The plot is indicated with grey shading. In (a) and (b), the red colour ramp indicates %liana infestation (darker = more heavily infested). In (c), blue shows reduced liana infestation, and red shows increased liana infestation; darker colours indicate greater change.

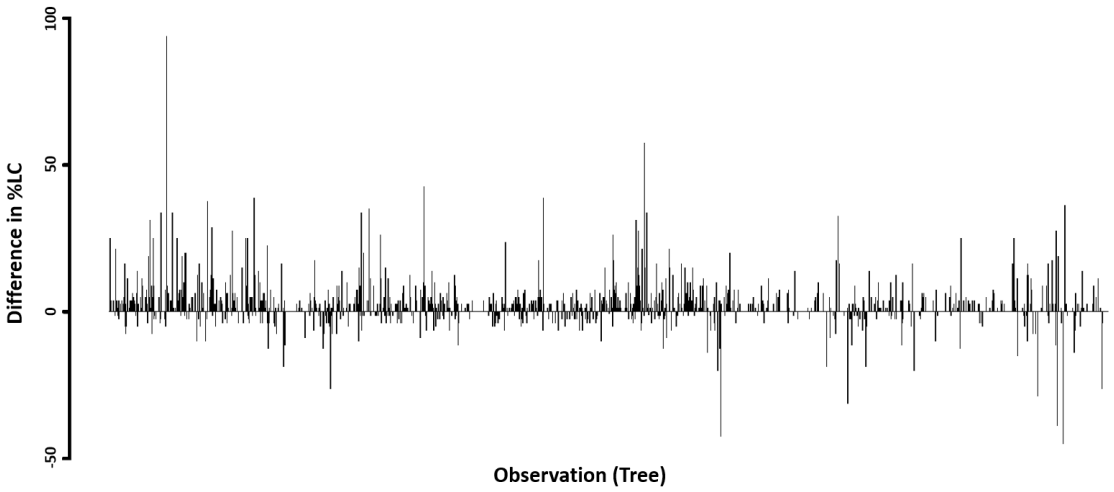


Figure 5-3: Differences in % liana canopy cover (%LC) between 2016 and 2017 (n = 2,381). Each bar represents an individual tree and the length of the bar represents the size of the difference (above the line = increase in liana cover; below the line = decrease in liana cover).

Table 5-2: Test of differences between 2016 and 2017 (excluding trees that experienced mortality in this timeframe) for tree crown variables: percentage liana cover (%LC), percentage tree leaf cover (%TC), crown area and crown greenness. Differences are assessed with paired-samples t-tests, and the mean pairwise difference (2017–2016) and standard error (SE) are given for each test.

	df	p	t	2016		2017		Pairwise difference	
				Mean	SD	Mean	SD	Mean	SE
%LC	2380	<0.001	-10.167	15.595	26.020	16.790	27.022	1.195	0.118
%TC	1422	<0.001	6.458	83.744	21.688	81.809	24.012	-1.935	0.230
Area	2380	<0.001	-22.137	134.160	154.748	141.956	164.353	7.796	0.352
Greenness	2380	<0.001	21.898	0.378	0.017	0.370	0.015	-0.007	<0.001

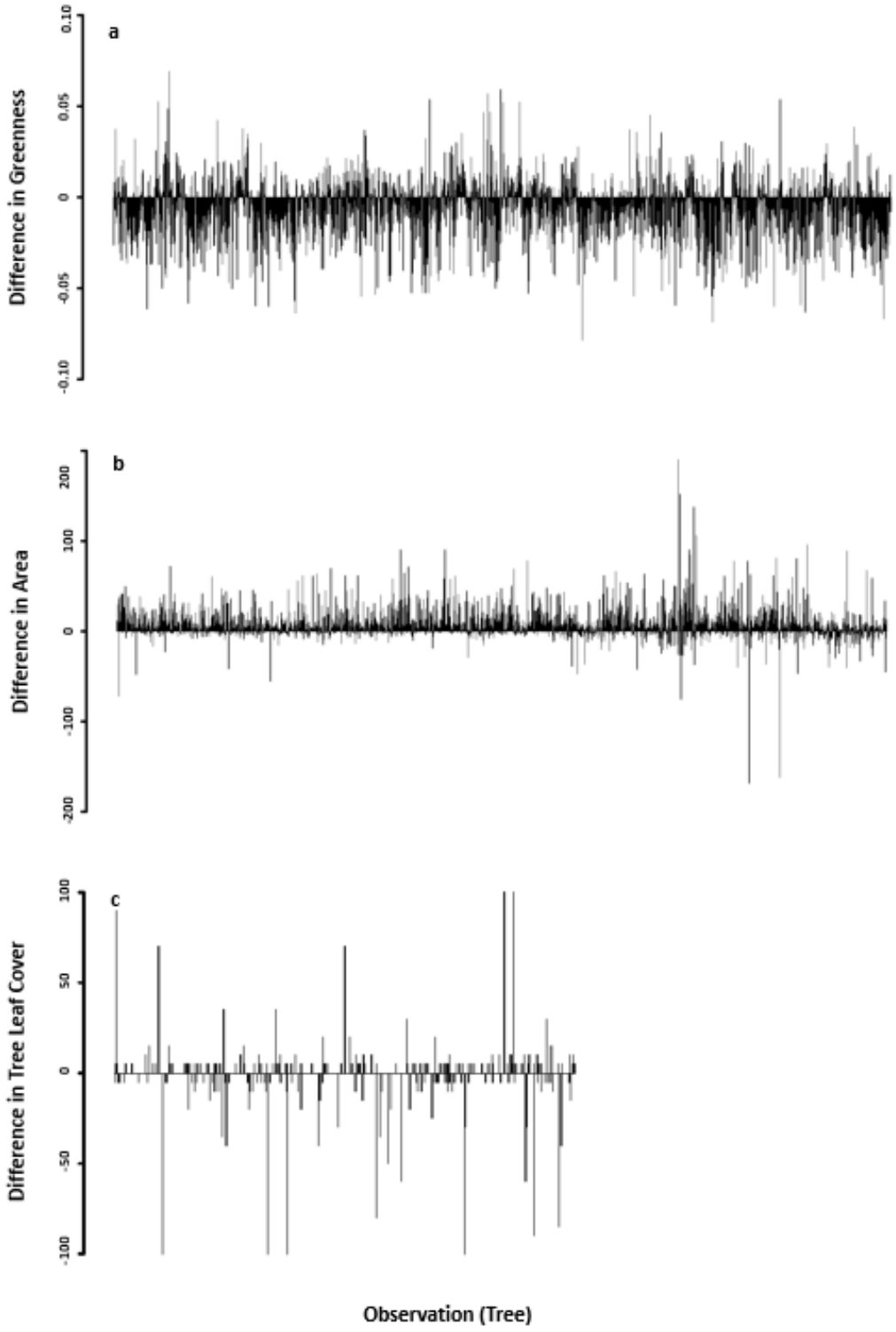


Figure 5-4: Bar chart of the differences in (a) tree crown greenness, (b) area, and (c) tree leaf cover (%TC) between 2016 and 2017. Change in tree leaf cover was only assessed for a subset of trees (area and greenness: n = 2,381, %TC: n = 1,423). Each bar represents an individual tree and bar length represents the magnitude of change (calculated as 2017-2016).

5.5 Discussion

Here we demonstrate, for the first time, that UAVs can be used as a tool to assess small-scale, rapid changes in tropical forest tree canopies. Significant increases in individual tree crown liana load were observed between the 2016 and 2017 surveys (Figures 5-2 and 5-3; Table 5-2), as well as a significant increase in tree crown area, and significant decreases in tree canopy greenness and tree leaf cover (Figure 5-4; Table 5-2). Furthermore, a significantly higher percentage liana canopy cover (%LC) was found for trees that died between the years compared with those that survived. The increase in %LC between years, as well as greater tree mortality in trees with higher %LC, provides evidence consistent with our expectation that %LC will increase and this will have negative impacts on the host tree.

Across the plot, individual tree-level liana infestation increased between years (Figures 5-2 and 5-3; Table 5-2). Research conducted in other parts of the world suggests that lianas have a growth advantage over trees in dry conditions, allowing them to proliferate both during, and in the aftermath of, drought periods (Schnitzer, 2005; Swaine & Grace, 2007; Cai et al., 2009; Sánchez-Azofeifa et al., 2009; Zhu & Cao, 2009; Chen et al., 2015). The dry conditions associated with the El Niño in our study site may, therefore, have contributed towards the observed increase in liana infestation. With our data, we cannot be sure whether the El Niño caused the observed increase in liana infestation, or not. Variability in liana infestation, with a trend towards year-on-year increase in lianas, has been noted by studies in areas and in years unaffected by drought episodes (Schnitzer & Bongers, 2011). The increase we observed could represent natural variability of increase in liana infestation. A longer time-series taking into account 'normal' years without drought occurrence would help us to determine whether the

changes we observed are natural variability or of greater magnitude than occurring in most years.

Significant reductions in tree crown greenness and tree leaf cover were observed between the two surveys (Figure 5-4; Table 5-2). Again we cannot be sure whether these changes are a result of the El Niño, but if the drought is assumed to have contributed to them, the reduction may seem counter-intuitive. Typically, it may be assumed that tree leaf cover and canopy greenness would be lower during drought periods, when trees are under water-stress, and these variables would increase with the return of rain (Samanta et al., 2010; Xu et al., 2011; Morton et al., 2014). However, some studies have indicated a 'green-up' of tropical forest canopies during dry conditions (Maeda et al., 2014), such as those observed during the dry season of 2000 – 2005 in Amazonia (Huete et al., 2006; Saleska et al., 2007). Such green-up is interpreted as the emergence of new leaves at the onset of, and during, dry conditions due to the increase in solar radiation as a result of low or absent cloud cover (Bonal et al., 2016). Such increases in leaf cover in tropical forest tree canopies during the 2015/16 El Niño drought were observed in Amazonian forests (Smith et al., 2019). It is thought that such canopy green-up during dry conditions may depend on whether the trees have access to deep soil water (Hilker et al., 2014). We know that the El Niño drought of 2015/16 was not particularly strong in Danum (Whitfield et al., 2019). This may mean that trees could take advantage of the higher light levels, without the drought being severe enough to seriously deplete deep soil water. This may contribute to the higher canopy greenness and tree leaf cover that we observed in 2016, near the end of the El Niño drought, than during the rainier period that followed (our 2017 data).

Tree mortality was detected by the UAV image data, with 43 trees dying between the surveys. A previous study examining the effect of the 2015/16 El Niño using WorldView-3 satellite images indicated very little evidence of short-term tree

mortality in the region, but they acknowledged the difficulties and limitations in doing so with relatively coarse spatial resolution (Whitfield et al., 2019). This highlights the usefulness of UAVs, with the higher resolution data capture that they offer, as a tool to monitor short-term change in tropical forest canopies. We observed significantly higher levels of liana infestation in trees that died between the years, than in those that survived. This agrees with the literature that indicates tree mortality is increased when trees are infested by lianas (e.g. Putz & Chai, 1987; Phillips et al., 2002; 2005; Ingwell et al., 2010; Schnitzer et al., 2011). If tree mortality was related to the drought (which it might not have been), this result may indicate that the detrimental effect of the drought on the trees was exacerbated by liana infestation. A possible mechanism for the higher mortality rates in more heavily infested trees would be intense competition that lianas exert on trees, for essential nutrients and, importantly in droughts, water (Tobin et al., 2012).

Of course, with only two time-points, we cannot be sure whether any observed alterations in the forest canopy are a result of the drought or merely normal canopy variability. The collection of UAV data in multiple subsequent years to develop a longer time-series is essential. This will enable us to analyse whether the changes we present here are of the same magnitude as 'normal' levels of canopy variable change in non-El Niño years or whether the magnitude of these changes are anomalous, and the canopy will revert back to a more stable state in subsequent years. Of course, we may be detecting significant change over short timescales because the canopy responds faster to short-term perturbations than the woody tissue (Meir et al., 2008). These changes in the canopy may, therefore, be decoupled from changes in the understorey (such as an increase in tree or liana stem diameter) which could potentially present a more lagged effect (Meir et al., 2018). Future studies may consider examining the forest canopy and understorey

concurrently to increase our understanding of the relationship between changes in the forest canopy and changes in other forest layers.

UAV imagery will be valuable for such studies. The top-of-the-canopy view afforded by UAV platforms enables small-scale changes in tropical forest tree crowns over short timescales to be discerned. UAV surveys also result in an archive of imagery that facilitates: (i) reproducibility, as it is possible to check previous results; and (ii) the derivation of additional variables that were not measured at the time but are later deemed important. The reproducibility of the UAV data is demonstrated here as we found little inter-observer bias in visual classifications of liana load from the UAV images, or delineation of tree crowns to produce tree canopy greenness and area values (Table 5-1), indicating that any observed changes are a result of temporal fluctuation and not observer bias. The data we provide herein have value for future studies; we have created two datasets for a globally important study site. The Center for Tropical Forest Science 50 ha plot surveyed here was established in 2010 to provide a baseline for on-going studies of forest regeneration, carbon dynamics and biodiversity. The datasets presented here will add to this, setting the baseline data on canopy change for a longer time-series to develop.

Chapter 6: Future Directions and Conclusions

This chapter begins with an overview of the advances made by this thesis in relation to the initial research aims, as identified in Chapter 1. Summaries of the rationale and aims of the three research papers (Chapters 3–5) are presented along with the key findings associated with each. This chapter then moves on to highlight broad directions and questions for future research in liana ecology. Key methodological questions are also presented that were brought to light by the research undertaken in this thesis. This chapter closes with the final conclusions of the thesis.

6.1 Overview of research aims

As outlined in Chapter 1, this thesis aimed to enhance our ecological understanding of lianas in tropical forest tree crowns, focusing on the lesser studied Palaeotropics. Integral to this was the development of a novel method to enable faster, cheaper and more canopy-centred assessment of liana infestation in tropical forest trees than possible with traditional assessment methods. In this way, this thesis aimed to provide a methodological and substantive contribution to liana studies; developing and testing a new method to study liana infestation (Chapter 3, Waite et al., 2019) and using it to enhance our ecological understanding of lianas (Chapters 4 and 5).

This thesis has developed and demonstrated the usefulness of a novel UAV-based method for collecting data on liana tree crown infestation (Waite et al., 2019; Chapter 3) and for enhancing our ecological knowledge of lianas through spatial mapping (Chapter 4) and temporal monitoring (Chapter 5). The data collected by the novel UAV-based method is reproducible between observers and at least as accurate as traditional ground-derived data. It is considered superior at assessing liana infestation in tree crowns in upper canopy layers (Waite et al., 2019; Chapter

3), and can be used for spatial mapping of liana infestation (Chapter 4) and monitoring of temporal changes (Chapter 5).

Furthermore, the novel UAV method developed in this thesis promotes reproducibility of results and quality control and enables additional variables to be derived from the image data. It is more time-efficient, cost-effective and covers larger geographical extents than traditional ground surveys. This is important for assessing the influence of (a)biotic variables on liana distributions, and the impact of short-term changes such as drought on lianas in tropical forest tree crowns. The method is particularly useful for tailored, targeted, and effective management of tropical forests for enhanced carbon sequestration. A summary of the three papers, including their rationales, aims and key findings, is given in Table 6-1.

6.2 Summary of the research papers

Table 6-1: A summary of the three papers comprising Chapters 3, 4, and 5 of this thesis. The rationale and main aim(s) of each paper are given, as well as an overview of the key findings.

Paper	Title	Rationale, main aim(s), and key findings
I	A view from above: Unmanned aerial vehicles (UAVs) provide a new tool for assessing liana infestation in tropical forest canopies	**Rationale and aim(s):** Lianas reduce forest carbon uptake and are increasing in tropical forests. Current methods to assess liana infestation are labour- and time-intensive, particularly for upper canopy layers. We need a new way to accurately, efficiently and reproducibly map and monitor lianas to increase our knowledge of their location and enhance applications to increase effective management of tropical forests for carbon storage (e.g. liana cutting). The aim was to assess the validity of using a consumer-grade UAV as a new method for collecting liana infestation data, by: (i) assessing inter-observer bias in classifying liana infestation from UAV images; (ii) evaluating the strength of the correlation between UAV- and ground-derived measures of liana infestation on individual tree- and plot levels, and for different canopy strata; and (iii) comparing input time and costs between ground and UAV surveys of liana infestation. **Key findings:** Liana infestation data derived from UAV image data are at least as accurate as traditional ground-derived data, and superior at assessing liana infestation in tree crowns in upper canopy layers. These findings are reproducible between observers and hold at individual tree and plot level, and across multiple forest types and spatial resolutions. The novel UAV method promotes reproducibility of results and quality control and enables additional variables to be derived from the image data. It is more time-efficient, cost-effective and covers larger geographical extents than traditional ground surveys, enabling more comprehensive monitoring of changes in liana infestation over space and time. This is important for assessing liana impacts on the global carbon balance and particularly useful for tailored, targeted and effective management of tropical forests for enhanced carbon sequestration.
II	A ladder to the sky: the roles of tree size and canopy gaps in liana infestation patterns of tropical forest canopy in Sabah, Malaysia	**Rationale and aim(s):** Lianas are key components in tropical forests where they are increasing in abundance. Relatively little is known about landscape-level liana distributions in tropical forest tree crowns, especially in the Palaeotropics. The new method developed in Paper 1 has increased the speed at which reliable, accurate, reproducible, liana data can be collected, as well as reducing the cost of such data collection. Now we have the opportunity to determine, for the first time, landscape-level distributions and spatial patterns of liana canopy cover and test the main hypotheses and ideas about what determines liana occurrence and abundance in tree crowns. Our aims were to: (i) test our expectation that liana infestation will be spatially aggregated across a 50 ha plot; (ii) evaluate the

		relative strengths of environmental variables to predict liana distributions and test our hypotheses concerning each; and (iii) evaluate how well UAV data are able to explain and predict liana distributions in comparison to traditional data (i.e. occupied airborne LiDAR and ground-collected data). **Key findings:** This study represents the largest and most comprehensive assessment of Palaeotropical tree crown liana infestation, and analysis of environmental variables that may influence this, to date. Liana infestation was significantly aggregated across the 50 ha plot. Tree canopy height was the most important variable influencing liana spatial distribution, with taller trees being less often and less heavily infested by lianas. The second most important variable was the presence of canopy gaps. Liana infestation occurred more often, and to greater extents in close proximity to canopy gaps. UAV-derived environmental variables were comparable to equivalent LiDAR-derived measures, demonstrating that UAVs can be used to derive environmental variables data for examining how and why lianas are distributed in the forest canopy at landscape-scales. Examining this may help us to determine what variables may determine increases in lianas with environmental change in the future and provide a step towards more comprehensive testing of ecological theory in tropical forests.
III	Increase in liana infestation in Malaysian tropical forest tree crowns and concurrent canopy changes in the aftermath of the 2015/16 El Niño Event	**Rationale and aim(s):** Lianas are increasing in tropical forests, reducing forest carbon uptake. Their increase is thought to be due to increases in the length and severity of droughts, which are predicted to continue in the coming decades. It is therefore important to know whether droughts can be linked to increasing liana infestation, and any potential impacts this may have on the forest canopy. Our aim was to use the potential for UAVs to assess short-term change in tropical forest canopies to: examine (i) change in liana infestation; and (ii) associated changes in tree crown characteristics following the El Niño event of 2015/16. **Key findings:** Tree-level liana infestation and tree crown area showed significant increases between surveys in 2016 and 2017, whereas tree crown greenness and tree leaf cover showed a significant decrease. Percentage crown cover of lianas is significantly higher for trees that experienced mortality between the surveys than for those that didn't, and percentage crown cover of lianas is significantly negatively correlated with percentage increase in tree crown area. Changing climatic conditions, and the associated increases in length and severity of droughts may, therefore, alter liana infestation and liana impacts on tree canopies. This has important implications for tropical forest carbon storage and sequestration. The use of UAVs provides an effective, reproducible method to monitor changes in tropical forest canopies, providing an archive of imagery that can be built upon to develop time-series data for on-going research.

6.3 Directions for future research

As outlined above, this thesis enhances our ecological understanding of lianas in Palaeotropical forest tree crowns through the development of a novel method to collect liana infestation data and its application through space and time. Thus, this thesis presents a clear substantive and methodological contribution to liana research. In addition to this contribution, the work presented herein raises questions for future tropical forest ecology research. A number of specific ecological questions are addressed in the relevant research papers where they arose (Chapters 4–5) and more general ecological questions are outlined below.

This work has demonstrated that lianas are dynamic and characteristic components of tropical forests, in line with previous research (Schnitzer & Bongers, 2002). The ability of a UAV-based method to assess liana infestation patterns, and small-scale changes in them over short timescales, highlights the dynamic nature of our tropical forest canopies, and the need for measurement and monitoring tools that can detect this. Such small-scale changes are not observable from traditional canopy assessment methods, however, and this highlights a concern:

> How wrong are satellite-derived maps of carbon if they do not take into account liana infestation and spatial distributions?

There is already uncertainty in carbon maps of tropical forests, and concern over whether our tropical forests are switching from a net carbon sink to a net carbon source (Mitchard, 2018). Lianas have been shown to have significant impacts on carbon cycling in tropical forests (Laurance, 1997; Gerwing & Farias, 2000; Durán & Gianoli, 2013; van der Heijden et al., 2013; van der Heijden et al., 2015) and yet are conspicuously absent from most global tropical forest carbon maps. In the light of the key role that lianas play in forest dynamics, I would encourage their

inclusion in future models. This leads to the second broad question arising from this thesis:

How can liana data be used to improve ecological forecasting under climate change?

Tropical forests are among the most complex ecosystems on Earth, playing a crucial role in the maintenance of biodiversity and providing unique local and global ecosystem services to all life on Earth (Ozanne et al., 2003; Lowman et al., 2013; Nakamura et al., 2017). As such, any alteration to tropical forests may reduce their ability to mediate climatic changes (Lewis et al., 2015; Mitchard, 2018) and bring broad and important ramifications for species diversity and productivity, as well as the global climate and carbon cycles (Schnitzer & Bongers, 2011). Forest canopies may provide early-warning indicators of environmental changes, however, as their declining health is a harbinger of environmental changes on a global scale, as well as a driver of further change (Foley et al., 2003; Janssen et al., 2008). Thus, improved understanding of global change impacts on forest ecosystems and improved monitoring of forest canopies is essential (Mori et al., 2017). UAVs may provide us with the means to study and monitor our forest canopies. The integration of the data that UAV platforms will offer with existing knowledge and models of environmental change should help us understand the impacts of global change on our tropical forests and how this may change into the future.

6.4 Key methodological questions arising

There are many pathways to follow as we move forward with liana research, particularly in relation to the new possibility for UAV-enhanced liana research resulting from this thesis. Key questions arising are:

(1) What are the limits for the success of the novel UAV-based method for assessing liana infestation in tropical forests?

(2) Is automation of liana infestation assessment from UAV images possible, and will it further improve the cost- and time-efficiency of the method?

(3) Can UAV data be integrated with occupied airborne and/or satellite data to enhance liana detection and mapping over larger geographical extents?

(4) Will the use of UAVs, and the catalogue of image data created now remain useful with the advent of new technologies?

6.4.1 What are the limits for the success of the novel UAV-based method for assessing liana infestation in tropical forest canopies?

In Chapter 3, the accuracy and reproducibility of the UAV method to assess liana tree crown infestation were examined across individual tree- and plot-levels, for different canopy strata, and across multiple forest types. The data included a range of visual presentations of liana infestation, varying in terms of level of infestation, as well as between species – with both tree and liana species varying – resulting in a wide variety of colours and textures of both liana and tree leaves (Figure 6-1). These analyses were designed to provide a rigorous test for the UAV method, which proved successful for all. The UAV method appears reproducible, therefore,

and able to be extrapolated successfully, at least within different forest types of Southeast Asia. It should be appreciated, however, that the geographical area used for the testing of the UAV method is relatively small, and that different tropical forests across the world are distinct ecological entities, with key differences (Corlett & Primack, 2006; 2011). Although the success of the method across multiple forest types in Sabah, Malaysia may indicate that similar successful performance may be expected in other tropical forests around the world, we cannot extrapolate our findings directly or state the limits of what forests this method will prove successful in. Future research could further test this method in other tropical forests around the world to delimit the forest types where the method can be used successfully to provide data comparable with traditional ground-derived data. In some cases, an integrated UAV-based and ground-based approach may work best to most accurately assess liana infestation.

A second question remains for determining limits for the successful use of the UAV method: at what spatial resolution do the data provided by the UAV platforms become too coarse to successfully identify liana infestation? An analysis of the success of the UAV-method at different spatial resolutions is included within Chapter 3 (Supplementary Information, Appendix S3-3.3). Liana infestation was still clearly identifiable when using the coarsest (~20 mm/pixel) spatial resolution data available, however. The lack of additional, coarser, spatial resolution data from the UAV platform means that we cannot specify what the spatial resolution limit of data is to still be able to discern presence and degree of liana infestation in tropical forest tree crowns. Future work, therefore, could determine at what spatial resolution data become too coarse to successfully identify liana infestation. This knowledge will enable us to pinpoint what altitude is the highest possible to undertake flights in order to receive appropriate data for the intended application.



Figure 6-1: Six images taken using the DJI Phantom 3 Advanced, each cropped to show a tree crown with liana infestation. Different levels of infestation are shown, across different liana and tree species, presenting an array of different colours and textures in the images.

Although lianas were still identifiable in the coarsest resolution data collected in the field in this thesis, some idea of how reduced spatial resolution of the data may affect liana identification is given in Figure 6-2. Here, the resolution of the UAV images has been artificially reduced, rather than being reduced naturally as would occur from conducting UAV surveys at greater altitudes. It is clear that the ability to discern liana presence and degree of infestation degrades with reduced resolution, to different extents for different liana and tree sizes and species. Distinction of liana and tree leaves at lowered resolutions is possible to a greater extent in those tree crowns with the most differently coloured and textured liana and tree leaves, and harder for those trees where the liana leaf colour and/or texture was more similar.

Although these data are artificially reduced in resolution and therefore not entirely representative of real-world flights at different elevations (with associated changes in weather conditions such as wind speed and light levels), the fact that it is often still possible to discern liana cover at greatly reduced resolutions (in some cases up to 90-95% reduced resolution, although this would not be true for all cases) makes it likely that flights with greater altitudes than those used in this thesis will still result in images of sufficient quality to assess liana infestation. This will be especially useful in studies with time-restrictions (as flying higher enables surveys to be accomplished more quickly), for example those looking at the response of tropical forest canopies to short-term events such as droughts. It would also prove helpful for studies aiming to cover large areas, for example those that may be mapping liana infestation to determine areas of forest most suitable for targeted management practices.

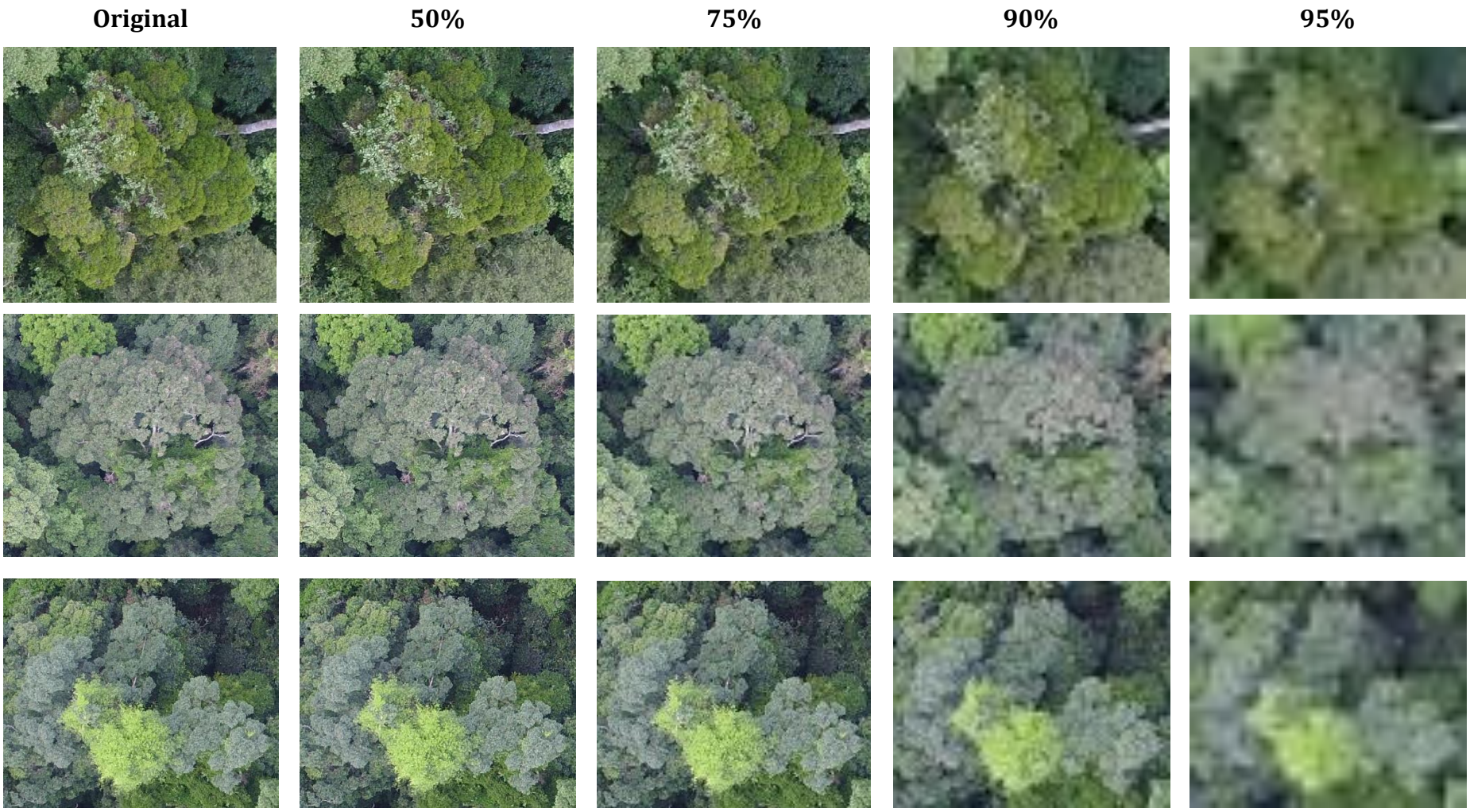


Figure 6-2: Three images taken using the DJI Phantom 3 Advanced, cropped to show a single liana-infested tree crown, with the spatial resolution reduced to different extents. The original cropped image is given on the far left, and the same image with the resolution reduced by 50%, 75%, 90% and 95% (i.e. 50%, 25%, 10% and 5% of the original pixels remaining, respectively) moving from left to right.

Naturally, different UAV platforms will also result in differing limits for the success of UAV-based methods. A rotor-based UAV was used in this research, as it allowed for more precise user-control, less in-flight vibration and vertical take-off and landing (Wallace et al., 2011; Kumar & Michael, 2012) enabling manoeuvrability through canopy gaps. These were important considerations for the research presented here, where the potential for UAVs to identify liana coverage through space and time was tested. Having established that this is possible, and that there is potential for flights to take place at higher altitudes than those presented here and still identify lianas (as described above), the use of fixed-wing platforms can also be considered. The longer battery life of these platforms will enable flights at greater altitudes than rotary platforms, allowing for the potential for launch and landing at sites at a further distance from the field plots (such as a research station). This, coupled with the faster flight times of fixed-wing systems, may further reduce the time (and therefore cost) input required for UAV surveys. Importantly, this will also allow for greater spatial coverage of the UAV data. From this, more potential ecological insights may be gained at larger landscape scales than those presented here.

6.4.2 Is automation of liana infestation assessment from UAV images possible, and will it further improve the cost- and time-efficiency of the method?

Perhaps the key limiting factor in the novel method of utilising UAV data to assess liana infestations through space and time is the time input required to visually identify lianas in the UAV images. As shown in Figure 6-1, lianas can appear differently in different tree crowns. The level of liana infestation can vary, as well as the colour and texture of the liana and tree leaves. This increases the time taken to visually identify lianas. Although the UAV method is more time-efficient than the traditional ground-based method, which require 12.5 hours/ha and 45 hours/ha, respectively (Waite et al., 2019), visual assessment of the UAV images is

very time- and labour-intensive. The ability to automate or semi-automate this so that the process of: (i) collecting UAV image data; (ii) image processing; and (iii) identification of liana cover within the images can be achieved with reduced manual input, would further increase the time- and cost-efficiency of the novel UAV method. Although automated processes can introduce more error than fully manual classification (Pal & Mather, 2003), they are better able to cope with the vast quantities of data that are produced via UAV surveying. In this case they would facilitate the use of the UAV method over larger geographical extents and increase the temporal resolution at which lianas (and other ecological phenomena) can be studied.

Potential avenues to explore for developing such automation techniques include textural and spectral analysis, likely to be assisted by machine learning algorithms. Texture is the visual effect in image data caused by spatial variation in tonal quality of pixels over relatively small areas (Anys & He, 1995) and textural analysis is achieved by computing local variance in pixel brightness by passing a texture filter, of a specific window size, over the image (e.g. Anys et al., 1994). It is, therefore, a common method for delineating features that cause localised variation in pixel brightness, such as changes in biophysical properties of the forest canopy (Asner et al., 2002), and has been widely used in conjunction with remotely sensed data, including that from UAV platforms (e.g. Laliberte & Rango, 2009; Malek et al., 2014; Feng et al., 2015).

Indeed, the ability of texture to represent patterns that cannot be described by spectral values and individual pixels alone means that it can assist in analyses where spectral resolution is limited (Feng et al., 2015). This is often the case for research utilising consumer-grade UAVs, aiming to make data collection cost-effective and accessible, as exemplified in Chapter 3 of this thesis. In such studies, textural analyses enable the detection of small-scale canopy features. For example,

the ability of texture analysis to assist in quantifying leaf phenology of individual trees in a tropical forest from UAV image data was recently demonstrated (Park et al., 2019).

So far, however, the use of textural analysis has not extended to the identification of lianas and this presents a potential avenue for future research. Part of this research should consider the testing of multiple window sizes in order to ascertain which is best able to differentiate liana leaves from tree leaves. Window size is a key parameter in texture analysis, and is often selected by trial and error (Pesaresi, 2000; Franklin et al., 2001) as, in general, larger windows may lose sensitivity to highly localised features (of which lianas may be considered) and result in coarser information provided by the texture features (Kayitakire et al., 2006). Also, textural analysis is likely to have the greatest success when used in conjunction with higher spatial resolution images as opposed to lower spatial resolution images. This is because, as Figure 6-2 shows, as spatial resolution is reduced, the clarity of the definition between the liana and tree leaves is reduced, with fewer pixels comprising this boundary. This may limit the ability of the textural window to detect the boundary between liana and tree leaves. Future research could focus on running texture analysis on UAV images of varying resolutions to determine the limits of success for this automation technique.

Another potential avenue for automating such liana detection from UAVs is the use of spectral data. Recent advances in the miniaturisation of sensor technology now allow multi- and hyper-spectral sensors to be mounted on UAV platforms (Sankey et al., 2017). Such sensors collect data in many more spectral bands than possible with consumer-grade UAVs such as the one used in this thesis. The spectral data provided by these sensors may enable automation of liana identification due to the difference that has been observed between liana and tree spectral signatures using ground-based field spectrometer measurements (Castro-Esau et al., 2004;

Sánchez-Azofeifa et al., 2009; Hesketh & Sánchez-Azofeifa, 2012). Indeed, research using an occupied airborne platform to collect hyperspectral data was successful in identifying liana presence–absence and classifying percentage liana cover into four categories: 0-25%, 25-50%, 50-75% and 75-100% (Marvin et al., 2016). A limitation of this study in addition to the high cost, however, was the difficulties encountered in differentiating between uninfested tree crowns, and those with low levels (<25% canopy cover) of liana infestation. Continued investigation into liana detection in this lowest threshold is valuable because even low levels of liana infestation can have a detrimental impact on tree growth (Schnitzer & Carson, 2010). The higher spatial resolution that UAV platforms provide, if coupled with hyperspectral sensors, may help to detect these low levels of liana infestation. Although hyperspectral sensors for UAVs are currently cost-prohibitive to many studies (Buters et al., 2019), predicted future technological advances and associated reductions in cost will make them more widely available. This will improve accessibility of these data and open the door for future work utilising such sensors, improving their utility for automating liana detection into the future.

If automation methods, such as those outlined above, could be developed, arguably the next key question to be answered would be:

Are automatically (or semi-automatically) derived liana data from UAV images comparable to expert visual identification of liana infestation in terms of: (i) how well they match the traditional ground-collected data; and (ii) how much they cost to produce, in terms of both time and money?

Thus, the potential for automation of liana identification from UAV imagery poses an array of possible research questions for future studies to examine. This thesis has provided a basis for liana identification using UAV image data, and the possibilities to build on this in the future are very exciting.

6.4.3 Can UAV data be integrated with occupied airborne and/or satellite data to enhance liana detection and mapping over larger geographical extents?

If automation of liana identification in UAV images can be achieved, perhaps using one of the potential solutions outlined above, it solves one of the key questions raised by the novel method: how can we make it even faster and easier to use? However, there are other potential challenges facing the use of the UAV method to gather data on liana infestation. One of these is the relatively small spatial extents covered. Of course, the areas covered by UAV surveys are still larger than those achieved with traditional ground-based methods, but do not compare to spatial coverage achievable with occupied aircraft or satellite platforms. A trade-off is necessary with the use of occupied aircraft or satellite platforms, however: they provide a larger spatial extent, but with the limitations of reduced spatial resolution of the data and obscuration by clouds. As outlined previously, this means that these platforms lack the ability to provide detailed assessments of liana canopy cover, especially at low levels (Marvin et al., 2016).

Until recently, methods to assess percentage liana canopy cover in occupied airborne imagery have been performed at the tree-level and are, therefore, object-based. This assumes accurate tree crown segmentation, as errors caused by over- and under-segmentation can affect the accuracy of object-based classification (Chen et al., 2018). An alternative to this would be the estimation of percentage liana canopy cover at an individual pixel level. This is not possible with traditional ground-based methods of assessing liana canopy cover. Co-registering UAV-derived image data with occupied airborne-derived image data, however, may provide a means to estimate liana infestation for individual pixels of the airborne remotely sensed imagery. This may, in turn, enable more precise estimates of liana canopy cover in the occupied airborne imagery, which can be extrapolated over much larger areas than those covered by the UAV image data.

6.4.4 Will the use of UAVs, and the catalogue of image data created now remain useful with the advent of new technologies?

This thesis has developed and demonstrated the usefulness of a novel UAV-based method for collecting data on liana tree crown infestation. The method enables reproducible results and enables the compilation of a catalogue of image data to facilitate future research and was shown to overcome the limitations surrounding existing ground-based and satellite/occupied aircraft-based methods to collect data on tropical forest tree crowns. These limitations include the time-consuming nature and limited spatial extent of ground-based methods, as well as the issues of cloud obscuration, high expense and relatively coarse spatial and temporal resolutions of satellite and occupied airborne data.

The question remains, however: with the continual technological advancements, will image data collected by UAVs remain useful? Current satellite sensors can provide optical imagery with <1 m spatial resolution, for example Digital Globe's WorldView-3 30 cm spatial resolution. As sensor technology develops further, this spatial resolution could continue to increase. As UAV sensor technology will be developing in tandem, I do not believe that satellites will ever achieve the same spatial resolution as available with UAV platforms, but satellite data present additional advantages. The fixed revisit period of satellites, and satellite constellations, now provide near constant monitoring of the Earth's surface. This potentially increases the availability of satellite data in the immediate aftermath of a short-term event that may affect the forest canopy, such as a fire or drought, compared to UAV data. Although UAV data offer flexibility and user-specified choice in flight dates, as well as little to no risk of atmospheric interference such as clouds, we cannot always predict in advance when a short-term event may occur and may therefore experience some time-delay before being able to carry out UAV surveys. The trade-off for high resolution satellite data, however, is the high cost associated with obtaining the images. Although this may reduce in the

future, the projected decrease in the cost of UAV technology is likely to be faster (Sankey et al., 2017). Therefore, UAVs are likely to continue to provide a relatively low-cost method to collect high spatial and temporal resolution data, improving accessibility and flexibility to researchers in the future (Pajares, 2015).

The question may also be raised as to how useful UAV image data may be in the future to produce DTMs derived through Structure from Motion (SfM) compared to more traditional DTMs from active sensors such as satellite or manned-airborne LiDAR. Currently, UAVs are being used to successfully create DTMs and CHMs in tropical forests, in leaf-off and leaf-on conditions (Zahawi et al., 2015; Wallace et al., 2016; Aguilar et al., 2019). Research by Zahawi et al. (2015) demonstrated that UAV measurements were highly correlated with field-based measurements ($r \geq 0.92$), a result comparable in precision to LiDAR-based remote sensing measurements, while Aguilar et al. (2019) showed that UAV-derived DTMs had low vertical bias and random error. Therefore, SfM has been found to be a viable low-cost alternative for surveying of forest stands (Wallace et al., 2016).

With potential reductions in the price of LiDAR sensors mounted on satellite and manned airborne platforms, however, this UAV-based low-cost alternative may start to seem obsolete. Rapid advances in the miniaturisation of LiDAR sensors increasingly enable them to be mounted on UAVs (Sankey et al., 2017), however, and predicted future price drops will increase their accessibility. UAVs, therefore, are unlikely to be outpriced by alternative platforms, and the reduced distance from UAV to canopy compared to other platforms types may well result in more accurate and detailed LiDAR point clouds. It may mean, therefore, a change in the usefulness of UAVs from using the image data for SfM techniques to produce point clouds and DTMs to mounting LiDAR sensors on the UAVs, but the platform itself is likely to remain useful. Therefore, with the emergence of new platform and

sensor capabilities, it is probable that the opportunities for using UAVs in both liana, and canopy research more generally, will increase.

Rapid growth in the use of UAVs for ecological research has already occurred, and difficulties in comparing data between studies due to lack of standardisation or comparability in methodological approaches has become apparent as a limitation (Buters et al., 2019). With the advent of increasingly complex sensors and platforms, this issue is likely to increase. Taking steps to help ensure comparability of data between studies would be beneficial. These could include: developing (i) consistency in the application of particular platforms and sensors to the monitoring of target landforms, organisms and ecosystems; and (ii) optimisation of data analysis techniques and consistency in the manner in which they are reported. If this is implemented, UAV data could be of use to ecological research questions requiring the integration of multiple studies and continue to revolutionise and improve ecological research into the future.

6.5 Conclusions

The recent proliferation of lianas, coupled with their large impacts on the carbon balance and cycle of tropical forests, has made it important to study liana infestation of tropical forest tree canopies. Most previous work on liana ecology has been biased towards the Neotropics, however, with the Palaeotropics receiving less attention. This is particularly true of the forests of Southeast Asia. Furthermore, existing liana studies have predominantly focused on liana stem measurements, due to the difficulties in assessing liana canopy cover from the ground (Marvin et al., 2016; Waite et al., 2019). Liana canopy cover is more directly related to liana–tree competition, however, rendering it important to develop a method that is capable of collecting data on this.

This thesis shows, for the first time, how capturing RGB images of tree canopies via an inexpensive, lightweight UAV can be used accurately and efficiently to assess liana infestation and help make such data collection more accessible. Liana infestation data derived from UAV image data are at least as accurate as traditional ground data, and superior in assessing liana infestation of tree crowns in upper canopy layers, enabling future advances in liana and tropical forest ecology research. The novel UAV method is more time-efficient, cost-effective and covers larger geographical extents than traditional ground surveys, while promoting reproducibility of results and quality control, allowing more comprehensive monitoring of changes in liana infestation over space and time. The UAV method also enables other environmental data to be collected. This includes canopy variables such as tree crown area, leaf cover, and greenness, as well as structural variables such as tree height and canopy gap height and area. Such data enables additional ecological questions to be addressed and, coupled with the UAV-derived liana data, has the potential to revolutionize both liana ecology and tropical forest canopy research.

By utilising the new UAV method, this thesis presents the largest and most comprehensive continuous assessment of Palaeotropical tree crown liana infestation, and analysis of environmental variables that may influence this, to date. Liana infestation was significantly aggregated at the landscape scale, with tree canopy height being the most important variable influencing this; taller trees were less often and less heavily infested by lianas. Presence of canopy gaps which are an indicator of disturbance was also important in influencing liana distributions, with liana infestation occurring more often and to greater extents in close proximity to canopy gaps. Examining how and why lianas are distributed in the forest canopy at landscape-scales may help us to determine what variables may determine increases in lianas with environmental change in the future and

provide a step towards more comprehensive testing of ecological theory in tropical forests.

As well as this, the thesis presents the first study assessing short-term temporal change in liana canopy cover and associated alterations in the forest canopy using UAV image data. Tree-level liana infestation showed a significant increase between surveys in the aftermath of the 2015/16 El Niño. In addition, percentage crown cover of lianas was significantly higher for trees that experienced mortality between surveys demonstrating a potential negative impact of lianas on tree crowns. Changing climatic conditions, and the associated increases in length and severity of droughts may, therefore, alter liana infestation and increase liana impacts on tree canopies. This has implications for tropical forest carbon storage and sequestration.

The use of UAVs provides an effective, reproducible method to monitor such changes in tropical forest canopies and provide an archive of imagery that can be built upon to develop time-series data for on-going research. Furthermore, the continued use of UAVs will enable tailored and targeted liana management protocols to effectively control liana infestation to aid restoration of degraded forests, silvicultural systems, and projects designed to increase carbon storage and sequestration in tropical forests. These advantages of UAV-derived data for liana and canopy research will be enhanced by rapidly developing protocols for UAV use in science and technological advancements in sensors and platforms. UAVs, therefore, provide us with a method to collect information on tropical forest canopies and assess what the impacts of changing climatic conditions and increasing liana abundance may be on the carbon storage potential of tropical forests, now and into the future.

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RESEARCH ARTICLE

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A view from above: Unmanned aerial vehicles (UAVs) provide a new tool for assessing liana infestation in tropical forest canopies

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Abstract

1. Tropical forests store and sequester large quantities of carbon, mitigating climate change. Lianas (woody vines) are important tropical forest components, most conspicuous in the canopy. Lianas reduce forest carbon uptake and their recent increase may, therefore, limit forest carbon storage with global consequences for climate change. Liana infestation of tree crowns is traditionally assessed from the ground, which is labour intensive and difficult, particularly for upper canopy layers.
2. We used a lightweight unmanned aerial vehicle (UAV) to assess liana infestation of tree canopies from above. It was a commercially available quadcopter UAV with an integrated, standard three-waveband camera to collect aerial image data for 150 ha of tropical forest canopy. By visually interpreting the images, we assessed the degree of liana infestation for 14.15 ha of forest for which ground-based estimates were collected simultaneously. We compared the UAV liana infestation estimates with those from the ground to determine the validity, strengths, and weaknesses of using UAVs as a new method for assessing liana infestation of tree canopies.
3. Estimates of liana infestation from the UAV correlated strongly with ground-based surveys at individual tree and plot level, and across multiple forest types and spatial resolutions, improving liana infestation assessment for upper canopy layers. Importantly, UAV-based surveys, including the image collection, processing, and visual interpretation, were considerably faster and more cost-efficient than ground-based surveys.
4. *Synthesis and applications.* Unmanned aerial vehicle (UAV) image data of tree canopies can be easily captured and used to assess liana infestation at least as accurately as traditional ground data. This novel method promotes reproducibility of results and quality control, and enables additional variables to be derived from the image data. It is more cost-effective, time-efficient and covers larger geographical extents than traditional ground surveys, enabling more comprehensive monitoring of changes in liana infestation over space and time. This is important for assessing liana impacts on the global carbon balance, and particularly useful for

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forest management where knowledge of the location and change in liana infestation can be used for tailored, targeted, and effective management of tropical forests for enhanced carbon sequestration (e.g., REDD+ projects), timber concessions, and forest restoration.

KEYWORDS
drone, drone ecology, liana infestation, lianas, remote sensing, tropical forest canopy, unmanned aerial vehicles, visual image interpretation

1 | INTRODUCTION

Tropical forests and their canopies play a crucial role in the maintenance and provision of unique biodiversity and essential ecosystem services to all life on Earth (Lowman & Schowalter, 2012; Ozanne et al., 2003). One of the most important ecosystem services that tropical forests provide is their ability to store and sequester carbon (Pan et al., 2011). Managing tropical forests for carbon sequestration, therefore, provides a key opportunity to mitigate some of the effects of climate change resulting from increasing atmospheric CO_2 concentrations (Canadell & Raupauch, 2008).

Lianas (woody vines) are conspicuous components of tropical forests, where they peak in abundance, biomass, and species richness (Schnitzer & Bongers, 2002). Lianas use the structural biomass of trees to deploy leaves in the canopy, thus investing relatively more resources in producing an extensive leaf canopy than in woody tissue. Lianas, therefore, disproportionately contribute to the forest canopy: liana leaves can comprise up to 30% of forest leaf area but only up to 5% woody stem biomass of tropical forests (van der Heijden, Schnitzer, Powers, & Phillips, 2013). Liana abundance and biomass have increased over the last few decades (Schnitzer & Bongers, 2011). Consequently, lianas have proliferated in the forest canopy, indicated by an increase in their contribution to leaf productivity as well as in the number of tree crowns infested (Ingwell, Wright, Becklund, Hubbell, & Schnitzer, 2010; Wright, Calderón, Hernandéz, & Paton, 2004). Partly due to their extensive canopies, lianas aggressively compete with trees, reducing tree growth (Ingwell et al., 2010; van der Heijden & Phillips, 2009), fecundity (e.g., Kainer, Wadt, & Staudhammer, 2014), survival (Ingwell et al., 2010; Phillips, Vásquez Martínez, Monteagudo Mendoza, Baker, & Núñez Vargas, 2005) and, consequently, forest biomass and net carbon uptake (van der Heijden, Powers, & Schnitzer, 2015). Lianas pose a particular problem for managed forests, where they can substantially hinder carbon sequestration and forest restoration (e.g., Marshall et al., 2017). Liana cutting is often used to enhance carbon uptake (Marshall et al., 2017; van der Heijden et al., 2015); however, this is expensive and labour intensive to perform over large extents. The ability to identify where liana management would be most beneficial would therefore help target management of tropical forests.

Being able to accurately monitor the presence and degree of liana infestation in forest canopies over time and space is, therefore, important for determining whether and where liana impacts are high and/or may be increasing, particularly in managed tropical forests. Due to practical difficulties in accessing tropical forest canopies (Nakamura et al., 2017), assessing liana canopy infestation is traditionally done by ground-based surveys (e.g., van der Heijden, Feldpausch, Herrero, van der Velden, & Phillips, 2010). These are labour- and time intensive, and consequently limited in their spatial and temporal coverage, and lianas, therefore, remain understudied in tropical forests (Marvin, Asner, & Schnitzer, 2016). Furthermore, the stratified nature of tropical forests often limits the visibility of canopy and emergent tree crowns, affecting the reliability of ground-based estimates for them. As these larger trees tend to store and sequester the most carbon and, due to high light conditions in their crown, often harbour lianas (van der Heijden, Healey, & Phillips, 2008), reliable assessment of liana infestation for top-of-the-canopy trees is especially important.

Assessing lianas from a vantage point above the canopy should be feasible using remote sensing platforms which offer views of the canopy with much less obscuration by vegetation than possible from the ground (Nadkarni, Parker, & Lowman, 2011). However, satellite and many airborne platforms generally provide data too coarse in temporal or spatial resolution for this task, too expensive at very fine resolutions, and frequently suffer from cloud obscuration, especially in moist forests. Workarounds exist: using hyperspectral and LiDAR sensors, the Carnegie Airborne Observatory was able to accurately map heavy liana infestation across the forests of Panama (Marvin et al., 2016). The use of such sensors is very expensive and restricted to specialists, however, prohibiting their accessibility to the majority of researchers and forest managers. Furthermore, such remote sensing campaigns are typically carried out as one-time operations, so frequent monitoring is difficult (Xue & Su, 2017).

Unmanned aerial vehicles (UAVs) with sensors overcome most of the aforementioned limitations of remote sensing platforms (Cunliffe, Brazier, & Anderson, 2016). They can acquire remotely sensed data from relatively inaccessible environments, and thus are useful for measuring and (long-term) monitoring of forest canopies (Kachamba, Ørka, Gobakken, Eid, & Mwase, 2016; Paneque-Gálvez, McCall, Napoletano, Wich, & Koh, 2014; Zahawi et al., 2015; Zhang et al., 2016). Additionally, UAVs can capture data at even finer temporal and spatial resolutions than satellite and manned-airborne remote sensing (Nakamura et al., 2017). This is especially important because visually distinguishing lianas from trees requires ultra-fine resolution (mm–cm) image data: liana leaves grow among the leaves

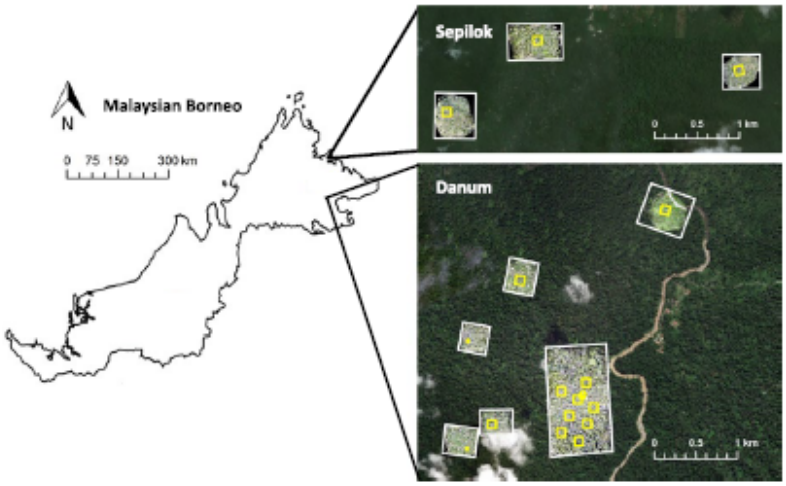


FIGURE 1 Location of the 2 study sites and 17 plots, which are in the state of Sabah, Malaysia, on the island of Borneo, Southeast Asia. The orthomosaics created from the UAV survey (150 ha) are shown outlined in white on top of satellite imagery, and the plots (14.15 ha) outlined in yellow. Satellite imagery source: DigitalGlobe WorldView2 RGB imagery

of the trees in which they are located, becoming embedded in the canopy, and are also heterogeneous in nature, as lianas are phylogenetically and functionally highly diverse (Burnham, 2004; Gentry, 1991). Because their physical traits vary, leaves of a given liana species may look very different or very similar to other liana species or the tree in which they are located. Additional textural context, such as leaf shape or arrangement, could allow improved discrimination of liana leaves from tree leaves in cases where spectral discrimination is unfeasible. Thus, UAVs and the enhanced spatial resolution they offer are potentially effective for assessing canopy-level liana infestation. However, even though UAVs have been used to study other canopy phenomena (e.g., Zahawi et al., 2015); thus far, they have not been used to study lianas.

Here, we examine, for the first time, the applicability of UAV-derived image data to assess the presence and degree of liana infestation in tropical tree canopies, using ground-based observations as a benchmark. Specifically, we aim to assess the validity of utilizing a consumer-grade UAV and camera as a new method for collecting data on liana infestation, by (a) assessing interobserver bias in classifying liana infestation from UAV images (*reproducibility between observers*); (b) evaluating the strength of the correlation between UAV- and ground-derived measures of liana infestation on individual tree- and plot levels, and for different canopy strata (*accuracy and reproducibility against benchmarked method*); and (c) comparing input time and costs between ground and UAV surveys of liana infestation (*efficiency against a benchmarked method*).

2 | MATERIALS AND METHODS

2.1 | Study sites

Ground and UAV-based surveys were conducted in two sites across eastern Sabah, Malaysia: Danum Valley Conservation Area (Danum) (4°57′N, 117°42′E) and Sepilok Forest Reserve (Sepilok) (5°52′N, 117°56′E) (Figure 1). Danum is characterized by lowland, evergreen dipterocarp forest, covering ~43,800 ha, and Sepilok by alluvial lowland dipterocarp, sandstone hill dipterocarp, and kerangas forests, covering ~4,300 ha. We surveyed 17 plots: eight 1-ha plots located in the Center for Tropical Forest Science (CTFS) 50-ha plot, three additional 10-ha plots (Berry, Phillips, Ong, & Hamer, 2008), and three 0.05-ha circular plots (Foody et al., 2001) in Danum and three 1-ha plots in Sepilok located in the alluvial, sandstone hill, and kerangas forests (Nilus, 2004).

2.2 | Ground-based data collection and liana assessments

We classified the liana load carried by each tree ≥10 cm DBH within the plots using two methods: (a) crown occupancy index (COI) and (b) percentage liana cover (%LC). The COI expresses liana load in the tree crown on a simple 5-point 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). This index is widely used in liana research and accurately measures liana loads at both the individual tree- and site level with little interobserver bias (van der Heijden et al., 2010). %LC is a more detailed estimate, expressed as the mean of four compass quadrants into which the tree crown is visually split and percentage of the crown covered by lianas estimated to the nearest 5% (cf. Marvin et al., 2016).

The plot corners (or midpoints for the 0.05-ha plots) and individual trees ≥10 cm DBH within each plot were georeferenced using a handheld GPS unit (Garmin eTrex Vista HCx), allowing individual tree crowns to be identified and cross-referenced in the UAV images. We also assigned each tree ≥10 cm DBH a value indicating the light level its crown received using the crown illumination index (CII) (Clark & Clark, 1992). This ordinal scale index is more-or-less equivalent to canopy stature (1 = understorey, 2 = lower canopy, 3 = mid canopy, 4 = upper canopy, 5 = emergent); it helped identify individual trees on the UAV image data and allowed comparison across different tree canopy statures.

The CII, COI, and %LC values were assigned by two independent observers, who discussed their estimates in the field and agreed final values for each tree. In one of the Danum plots %LC data were not collected, and in the Sepilok plots we only collected data for higher canopy-level trees.

2.3 | UAV data collection and liana assessments

We acquired images of the forest canopy using a lightweight, agile, inexpensive, commercially available quadcopter UAV: a DJI Phantom 3 Advanced equipped with an integrated three-waveband (RGB) camera, mounted on a three-axis, gyro-stabilized gimbal. The high-quality Sony EXMOR 1/2.3" 12-megapixel camera has a narrow 94° field of view lens (35 mm format equivalent: 20 mm) reducing "fish-eye" image distortion, and an f/2.8 aperture and 8s–1/8000s shutter speed reducing image blur. The UAV possesses GPS and GLONASS positioning to enable autonomous flights of up to ~23 min. Each image is geo-tagged with the GPS location and altitude of the UAV at the point of capture.

The plots were flown using the automatic mapping software Map Pilot, with predetermined flight plans with the same parameters (speed: 4 m/s; image overlap at ground-level: 90% forward, 90% side; altitude: 30 and 60 m above canopy surface) in parallel tracks that covered the plot and a "buffer" of surrounding vegetation to minimize edge-effects affecting the images of the plot in processing. High image overlap at ground-level was necessary to maintain adequate overlap for producing orthomosaics at canopy-level (for more information see Supporting Information Appendix S1.3). We identified canopy gaps large enough to allow the UAV to be launched/landed, and manually piloted it through, to ensure maximal pilot control and minimal risk of collisions. The flights were conducted during calm conditions to prevent wind effects on leaves (McNeil, 2016) and, where possible, when there was even cloud cover to ensure diffuse radiation and minimize shadowing in the canopy—improving clarity in the images and aiding liana identification. All flights took place concurrently with the ground assessments in May and June 2016. Additional details on the UAV surveys, and our experiences and recommendations for using UAVs for research, are in Supporting Information Appendix S1.

In total, 6,094 and 1,344 images taken 30 and 60 m above the canopy were captured with spatial resolutions of ~10 mm/pixel and ~20 mm/pixel, covering ~150 ha and ~50 ha of forest, respectively, within which the plots cover 14.15 ha. The images were assembled to form a single two-dimensional orthorectified image (orthomosaic) for each plot, geo-referenced to the WGS84 UTM Zone 50N projected coordinate system, using Agisoft PhotoScan version 1.3.0. An example Agisoft PhotoScan output is in Supporting Information Appendix S2. The orthomosaics were exported into ArcGIS to identify individual trees (supplemented by the original images, to provide multiple views from different angles, where necessary). The 30 m data were used for all analyses; the 60 m data were used to compare different spatial resolutions.

For each individual tree, COI and %LC values were determined by visual image interpretation using the same method used on the ground but applied from above. Interpreting the images in this way is beneficial because it (a) matches the visual assessment used on the ground and (b) harnesses the power of human interpretation skills, which is especially important as no algorithm has been developed



FIGURE 2 An example image taken using the DJI Phantom 3 Advanced. Two sections of the image have been selected to show a (a) liana-free and (b) liana-infested tree crown (indicated by a white border). The yellow border in (b) indicates the liana leaves

to automate liana infestation identification in tree canopies from RGB image data. Any trees for which ground data were collected, but which were obscured by larger trees and not visible on the UAV image data, were excluded from further analysis on individual tree levels but retained for plot-level comparisons of UAV and ground surveys.

3 | RESULTS

Liana load data were collected in 17 plots across 4 forest types, via both ground- and UAV-based methods, for more than 3,500 trees. The ultra-fine spatial resolution (10 mm/pixel) of the UAV data rendered each tree crown recognizable and individual leaves clearly identifiable (Figure 2). Liana load could, therefore, be assessed: trees without liana infestation (Figure 2a) could be distinguished from liana-infested trees (Figure 2b). This remained true when using the coarser ~20 mm/pixel spatial resolution.

3.1 | Reproducibility (between observers)

We assessed interobserver bias in classifying liana load from the UAV image data; bias in ground-based surveys was examined previously by van der Heijden et al. (2010) and therefore not assessed here. Three independent observers with differing levels of experience in liana identification classified the COI and %LC for 200 randomly selected trees. We used Kendall's coefficient of concordance (Kendall's *W*) and Spearman's rank test, respectively, to assess the concordance of COI and %LC values recorded by different observers, finding high degrees of concordance for both measures (Table 1). The same COI was recorded by all observers on 75% of occasions and on only 2% of occasions did all observers classify liana load differently. When classifications differed, this was most often by only one class (86%).

3.2 | Reproducibility (against a benchmarked method)

There was high concordance of COI scores between UAV and ground surveys for the full dataset (Kendall's $W = 0.947$, $p < 0.001$, $N = 3{,}555$; Tables 2 and 3), with liana load scored the same on 71.1% of occasions. Classifications differed by one class for 26.1%, and by two or more classes for 2.8% of the trees. The most frequent differences between UAV and ground surveys (43.2% of trees that differed) were when COI was scored 0 (liana-**free) by ground**-based surveys and 1 (low infestation) by UAV surveys (Tables 2 and 3). Similar trends were found for Danum and the different forest types in Sepilok separately (Supporting Information Appendix S3.1).

We used Model II regression to test the relationship between the UAV and the ground-derived %LC values. Model II regression performs better than standard Model I (OLS) regression when there are errors associated with both variables (Legendre & Legendre, 1998), with the estimated model having the same slope and r^2 values

TABLE 1 Degree of concordance between different observers in independently assessing liana infestation of tree crowns in UAV image data using crown occupancy index (COI) and percentage liana cover (%LC). Differences in COI and %LC were assessed with Kendall's *W* and Spearman's rank tests, respectively

	COI		%LC	
	W	*p*	*r*	*p*
All	0.950	<0.001		
Obs. 1 & 2	0.966	<0.001	0.961	<0.001
Obs. 1 & 3	0.966	<0.001	0.942	<0.001
Obs. 2 & 3	0.955	<0.001	0.927	<0.001

independent of which way round the axes are. To further evaluate the relationship between the UAV- and ground-based methods, we also calculated the RMSE with respect to the 1:1 line with lower RMSE values indicating greater concordance between the UAV and ground methods. We found a strong relationship between ground- and UAV-based assessments of %LC for the full dataset ($r^2 = 0.867$, $p < 0.001$, $N = 3{,}320$; Figure 3), for different forest types separately (Supporting Information Appendix S3.23) and when using a coarser spatial resolution (Supporting Information Appendix S3.3). Although UAV- and ground-based classifications were similar for more heavily infested trees, UAV-based %LC classification was higher for lightly infested trees, with the regression line significantly below the 1:1 line for %LC below 40% (Figure 3). This was mainly caused by the high number of tree crowns classed as liana-free by the ground survey but as low-level liana infestation by the UAV survey.

Since canopies of taller trees can be hard to see from the ground due to the stratified nature of tropical forests canopies, we also compared ground and UAV survey results for tree crowns located in different canopy strata. We found strong agreement between ground- and UAV-derived COI values (Kendall's $W > 0.9$) for all canopy stature classes except emergent trees (Kendall's $W = 0.750$; Table 2; Supporting Information Appendix S3.4a–d). The most common differences were again when COI was classed as 0 by the ground survey and 1 by the UAV survey, especially in the higher canopy strata (this was up to seven times more likely for emergent trees). Agreement between the two methods was greater for tree crowns in the lower canopy layers, and for more heavily infested individuals in upper canopy strata (Table 2; Supporting Information Appendix S3.4a–d). These patterns were also evident when comparing the %LC values; although ground- and UAV-derived %LC values were strongly related for all four canopy strata (Figure 4), the regression line deviated significantly from the 1:1 line for upper canopy and emergent trees. This was again caused by many trees classified as liana-free in the ground-based surveys and with low levels of liana infestation in the UAV-based surveys (Figure 4c,d).

At plot level, there was a strong, positive relationship between ground- and UAV-based classifications of (a) the proportion of liana-infested trees per plot, and plot level (b) mean COI and (c) %LC values ($r^2 = 0.719$, 0.899, and 0.920 respectively; Figure 5). This indicates

TABLE 2 Percentage of trees in each of the crown occupancy index (COI) classes for the ground (G) and UAV surveys, and the degree of concordance between the surveys (Kendall's *W*) for the full dataset (All trees) and the dataset partitioned by canopy strata. $p < 0.001$ for all comparisons

			COI 0 (%)		COI 1 (%)		COI 2 (%)		COI 3 (%)		COI 4 (%)	
	N	*W*	G	UAV	G	UAV	G	UAV	G	UAV	G	UAV
All trees	3,555	0.947	44.6	34.5	13.0	24.7	12.3	11.4	12.1	12.8	18.0	16.6
Lower	1,841	0.968	33.9	31.6	16.2	22.0	15.2	13.5	13.1	14.0	22.0	19.0
Mid	989	0.936	44.5	29.6	11.0	26.7	11.2	11.7	13.6	14.3	19.5	17.7
Upper	412	0.909	61.2	39.6	10.2	28.9	7.8	7.0	10.0	10.2	10.9	14.3
Emergent	313	0.750	86.9	60.7	4.2	29.1	4.2	3.8	3.2	4.5	1.6	1.9

TABLE 3 Error matrix showing the number of trees classified in each crown occupancy index (COI) class for the ground and UAV surveys for the full dataset. Counts in bold indicate when the two methods produced the same score

		Ground data COI				
		0	1	2	3	4
UAV data COI	0	**1,164**	54	7	2	0
	1	390	**358**	109	16	5
	2	25	43	**227**	93	18
	3	9	6	85	**259**	96
	4	1	1	8	59	**520**

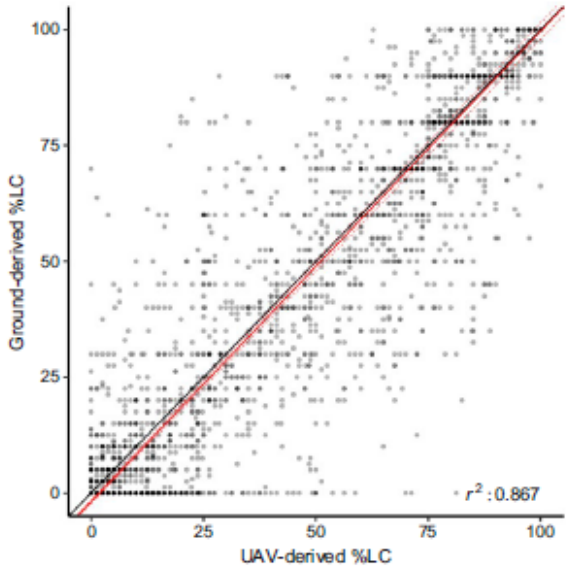


FIGURE 3 Relationship between the UAV-derived percentage liana cover (%LC) and the ground-derived percentage liana cover (%LC). The solid red line is the Model II regression line, and its associated r^2 is reported, dashed red lines are the 95% confidence intervals, and the black line is the 1:1 line (i.e., perfect match). *N* = 3,320; RMSE (with respect to the 1:1 line) = 12.73. Darker dots indicate more data points with similar ground and UAV values

that, although fewer tree crowns (of smaller trees) are discernible in the UAV image data (mean trees/ha: ground = 360; UAV = 270), the UAV method is nonetheless suitable for plot-level analysis. UAV-derived plot-level estimates of liana infestation were higher (i.e., under the 1:1 line in Figure 5) than ground-based estimates for almost all plots, with the difference more pronounced for plots with lower liana infestation.

3.3 | Efficiency

The UAV method was particularly time-efficient, with liana infestation assessment on average more than five times faster than the ground-based method, including both field and laboratory time (Table 4). Field campaigns are typically the most costly and time-limited phases of ecological research, and here the efficiency of the UAV survey over the ground survey is particularly enhanced. It reduces field time by 98.6% and the fixed costs of UAV hardware and software are recovered in the first 5.5 ha, with further UAV surveys costing 5.5% as much as the ground survey (Table 4). As fixed costs decrease with developments in UAV technology and popularity, the break-even point will occur even sooner than the 5.5 ha in this study.

4 | DISCUSSION

Here, we demonstrate, for the first time, that UAVs can be used as an accurate, accessible, agile, cost-effective, and time-efficient new tool for collecting data on liana infestation of tropical tree crowns, overcoming limitations of existing methods. Liana loads derived from UAV surveys and traditional ground surveys were strongly related at both individual tree- and plot level (Tables 2 and 3; Figures 3 and 4). Furthermore, we found little interobserver bias in visual classifications of liana loads derived from UAV image data, regardless of liana expertise or previous experience of liana surveys (Table 1), indicating high reproducibility of the UAV method. Additionally, the UAV method was much more time-efficient than the ground-based method, particularly in the field, and considerably more cost-efficient over multiple surveys (Table 4), with initial investment recouped within the first six plots. The UAV also remains cheaper than most suitable satellite or manned aerial survey image data.

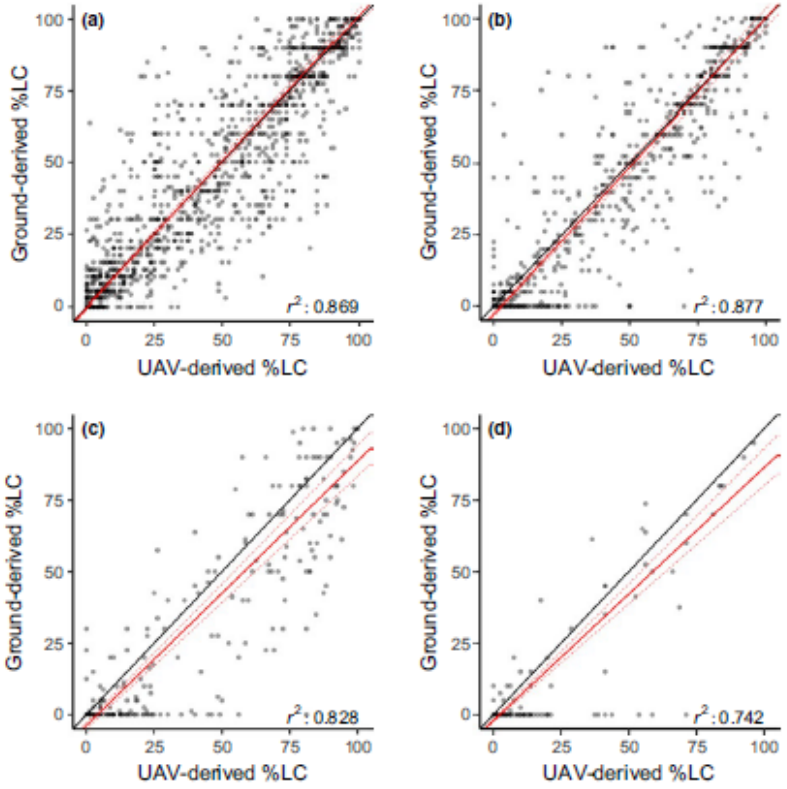


FIGURE 4 Relationships between the UAV-derived percentage liana cover (%LC) and the ground-derived percentage liana cover (%LC) for (a) lower canopy (N = 1,711; RMSE (with respect to the 1:1 line) = 12.79), (b) mid canopy (N = 931; RMSE (with respect to the 1:1 line) = 12.47), (c) upper canopy (N = 380; RMSE (with respect to the 1:1 line) = 14.96), (d) emergent trees (N = 298; RMSE (with respect to the 1:1 line) = 9.79). Solid red lines are the Model II regression lines with their associated r^2s reported, dashed red lines are the 95% confidence intervals, and black lines are the 1:1 lines (i.e., perfect match). Darker dots indicate more data points with similar ground and UAV values

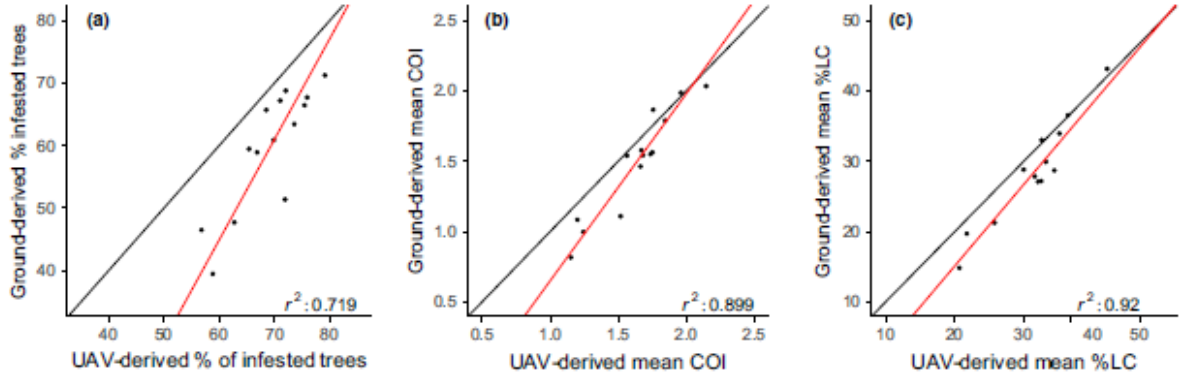


FIGURE 5 Relationships between ground and UAV-derived plot-level (a) proportion of infested trees (%; N = 14; RMSE (with respect to the 1:1 line) = 10.86), (b) mean liana crown occupancy index (COI; N = 14; RMSE (with respect to the 1:1 line) = 0.19), and (c) mean percentage liana cover (%LC; N = 13; RMSE (with respect to the 1:1 line) = 3.68) for the Danum Valley Conservation Area plots. The Model II regression lines are shown in red, with their associated r^2s reported, and the 1:1 lines in black. The 1:1 line fell within the 95% confidence bands, but as intervals were large they were excluded from the graph

Thus, UAVs make liana data collection more accessible to a wider variety of researchers and forest managers and may, therefore, enable canopy monitoring and mapping of lianas on unprecedented spatial and temporal scales.

At the plot level, UAV-based surveys consistently classed percent liana infestation higher than ground-based surveys (Figure 5). There are two explanations for this. Firstly, UAVs were better at recognizing low-level liana infestation (Tables 2 and 3; Figures 3 and 4). Secondly, plot-level estimates of liana infestation from ground surveys included understorey trees not visible on the UAV image data. As understorey trees are less frequently infested by lianas than larger trees (van der Heijden et al., 2008), their inclusion in

TABLE 4 Efficiency comparison of the time taken and costs required to collect crown occupancy index (COI) and percentage liana cover (%LC) using ground-based and UAV-based methods for a 1-ha plot, including the fixed costs (field and UAV equipment and processing software) required for the whole campaign (14.15 ha for ground; 150 ha for UAV). All timings are reported in "person-hours" (i.e., time taken to collect data considering number of people required) and exclude time to walk to the plots. All costs exclude international travel and costs/ha have been calculated based on number of days required at each plot with daily rates of £14.10 and £27.75 for accommodation/subsistence and field assistant costs, respectively. To replicate most grant budget costings, field assistant wages have been costed, whereas researcher input time has not

	Ground			UAV		
	Time/ha (h)	Fixed costs (£)	Cost/ha (£)	Time/ha (h)	Fixed costs (£)	Cost/ha (£)
Field[a]						
Accommodation/subsistence	–	–	84.60	–	–	4.70[b]
Field assistants	–	–	166.50	–	–	9.25[b]
UAV flight (inc. take-off/landing)	–	–	–	0.5	1,336	–
COI and %LC assessments	40	450	–	–	–	–
Laboratory						
Data type up	5	–	–	–	–	–
Processing image data	–	–	–	9	427.10	–
Mapping trees on orthomosaics	–	–	–	1	–	–
COI and %LC assessment	–	–	–	2	–	–
Total	45	450	251.10	12.5	1,763.10	13.95

[a]Training time is not included as it is not measured per ha. We found 5 hr ground and 2 hr UAV training was sufficient. Ground-measurement training must take place in the field; UAV training can take place beforehand, although some flight training in a tropical forest is recommended. [b]We found it possible to survey three 1-ha plots, at two altitudes in a single day. To generate costs/ha, we have divided the daily accommodation/subsistence and field assistant costs by three.

ground surveys reduces plot-level values of percent liana infestation. Despite these differences between the ground- and UAV-based surveys, there was a strong positive relationship between their results for plot-level liana infestation. This suggests either method can be used to compare plot-level liana infestation rates across sites (cf. van der Heijden et al., 2010), provided that the same method is used.

The fine spatial resolution of UAV image data, combined with the top-of-the-canopy view, provides an enhanced perspective to study liana infestation. This makes UAVs particularly useful for silvicultural systems, where liana cutting is routinely performed for improving timber and fruit production (Kainer et al., 2014; Sist, Fimbel, Sheil, Nasi, & Chevallier, 2003; Verwer, Peña-Claros, Van Der Staak, Ohlson-Kiehn, & Sterck, 2008), and for forest management or restoration purposes, where liana cutting has been shown to regenerate biomass (Marshall et al., 2017). With UAVs, users can quickly, efficiently, and accurately pinpoint which trees or areas suffer from heavy liana infestation, and those at risk of heavy liana infestation in the future. This is feasible over much larger areas than normally possible with ground-based methods, enabling better targeting of management practices such as liana cutting, and saving time, effort, and money.

UAVs improve liana infestation assessment for canopy and emergent trees, compared to ground surveys (Table 2; Figure 4c,d; Supporting Information Appendix S3.4c,d). These tall trees store and sequester the most carbon and are the main commercial species. Liana-induced changes in them may, therefore, be an important mechanism affecting forest-level and tree-level carbon storage and sequestration, for which UAVs represent a particularly useful management tool. Successful liana management may also help to increase timber and fruit productivity, and carbon storage and sequestration of degraded forests (van der Heijden et al., 2015). In particular, UAVs increased our ability to detect low-level liana infestation in these trees, which is particularly difficult from the ground as they are often partly obscured by shorter canopy trees (Table 3; Figure 4c,d). Although lianas exert limited effects at low levels (<50% crown coverage; for example Ingwell et al., 2010), identifying them quickly is important as infestation progression is likely as lianas utilize each other to climb into the tree crown (Putz, 1984), stressing the importance of repeated surveys of liana infestation.

Unmanned aerial vehicles answer this need, offering user-controlled deployment times, potential for high temporal frequency and an increased likelihood of recognizing low-level liana infestation (Table 2; Figure 4c,d). This allows for a flexible approach to liana management, tailoring it for trees or areas of forests at risk of heavy liana infestation. The new technique also facilitates monitoring and assessment of the success of management practices after they are put in place (Zahawi et al., 2015), including changing where management efforts are concentrated,

as spatial patterns of liana infestation change over time. It will also help track temporal changes, not only in liana infestation but also in wider canopy phenomena, such as tree crown shape and area, and timber, fruit, and forest-level biomass productivity and phenology, over shorter time-scales than is possible with ground-based surveys. The ability to track temporal changes enables investigation of the effects of short-term phenomena, such as drought events, on liana infestation and other processes in the canopy. The image data also represent an archive of detailed information about the forest canopy that allows (a) reproducibility, as people can check previous results; (b) additional metrics to be derived, for example, 3D models or digital elevation models (Supporting Information Appendix S2.5); (c) users to go back in time and measure variables that were not measured at the time but are later deemed important. For example, orangutan nests are clearly visible in our imagery (Supporting Information Appendix S3.5).

Advances in UAV technology and competitive price pressures are likely to improve the current UAV method and expand its applicability for forest management. We cannot specify at what resolution lianas (or other canopy phenomena) become indistinguishable (lianas remained clearly identifiable in our coarser spatial resolution images; Supporting Information Appendix S3.3), but the advent of newer UAVs with larger high-resolution image sensors, bright lenses, and zoom lens technology will enable even higher flights while retaining the ability to identify lianas, which may increase areal coverage (it is unlikely that this will be possible using satellite data in the next few decades). Further research could usefully investigate this for lianas, as well as for other canopy phenomena. The wide array of UAV platforms and sensors already available (Pajares, 2015) allows tailoring of system choice towards individual research and/or monitoring requirements. Additionally, rapid advances in the miniaturization of hyperspectral and LiDAR sensors increasingly enable them to be mounted on UAVs (Sankey, Donager, McVay, & Sankey, 2017) alongside RGB cameras and predicted future price drops will increase their accessibility. While RGB images allow visual species identification (Baena, Boyd, & Moat, 2018; Getzin, Wiegand, & Schöning, 2012), multispectral or hyperspectral sensors may allow this to be automated (Baena, Moat, Whaley, & Boyd, 2017; Sankey et al., 2018), further increasing the speed and ease of liana identification. Future work could test whether a suitably equipped UAV could automate mapping of liana infestation and changes in infestation similar to the approach adopted by Marvin et al. (2016) using airborne-collected data, but at much finer spatial and temporal resolutions, and at a small fraction of the cost. Also, as liana and tree species differ spectrally (e.g., Sánchez-Azofeifa et al., 2009), hyperspectral UAVs may help discern liana and tree species, supporting monitoring of tropical forest biodiversity, which is particularly important for the management of degraded forests (e.g., Marshall et al., 2017). With the emergence of a new platform and sensor capabilities, the opportunities for using UAVs in both liana, and canopy research more generally, will increase. Thus, the UAV method presented here offers a wealth of opportunities for forest canopy research and monitoring, including liana monitoring, over space and time to assist with tailored management of tropical forests, and forms a firm foundation for exploiting future advances.

5 | CONCLUSIONS

The recent proliferation of lianas, coupled with their large impacts on the carbon balance and cycle of tropical forests, has made it important to study liana infestation of tree canopies more comprehensively and frequently than feasible with current methods. Here, we show, for the first time, how capturing RGB images of tree canopies via an inexpensive, lightweight UAV can be used accurately and efficiently to assess liana infestation and help make such data collection more accessible. Liana infestation data derived from UAV image data are at least as accurate as traditional ground data, and superior in assessing liana infestation of tree crowns in upper canopy layers, enabling future advances in liana and tropical forest ecology research. The support for frequent surveys, data archiving, wealth of additional data captured, and larger geographical extent covered will enable more detailed monitoring of liana infestation and forest canopies over space and time with the potential to revolutionize both liana and canopy research. These advantages will be enhanced by rapidly developing protocols for UAV use in science (Duffy et al., 2018) and the potential for additional sensors offered by UAV platforms. UAVs also provide potential for tailored and targeted liana management protocols to effectively manage liana infestation to aid restoration of degraded forests, silvicultural systems, and projects designed to increase carbon storage and sequestration in tropical forests.

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AUTHORS' CONTRIBUTIONS

C.E.W., G.M.F.v.d.H., R.F., and D.S.B. designed the research; C.E.W. performed UAV data capture and processing, analysed data, and wrote the paper; G.M.F.v.d.H. was responsible for ground data collections; all authors developed the analytical approach, contributed to manuscript revisions, and approved publication. This work is a component of C.E.W.'s PhD which is supervised by D.S.B. and R.F.

DATA ACCESSIBILITY

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.21t1805 (Waite, van der Heijden, Field, & Boyd, 2019).

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SUPPORTING INFORMATION

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

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Appendix 2: Supporting Information

S2.1 Logistical information on using UAVs in tropical forests

These notes and thoughts arise from our experiences using a UAV in tropical forests, and a suggestion that it may be a useful aid to other ecologists/ researchers, or forest managers considering using UAVs in their own research or work.

S2.1.1 UAV practicalities

Training

We recommend some training before attempting to fly in any challenging environment, and tropical forest can certainly be considered that. We found that only a very brief period of training (~30-40 minutes) was sufficient to become comfortable piloting the UAV directly and using the 'DJI Go' app, and another brief period (~30-40 minutes) to become confident with automated UAV surveying through the 'Map Pilot' app. It is essential to be comfortable controlling the UAV in case the automated software fails, and you need to manually pilot the UAV back. We also recommend manually checking the tree height before starting any automated survey (as detailed in S3-1.2). This requires the skill to manually pilot the UAV up through a canopy gap, and estimate tree height by noting the altitude at which the UAV is level with the tops of the tallest trees. Then to fly across the surface of the canopy, to estimate any changes in terrain (and therefore, relative tree height) and pilot the UAV back down safely.

This training can be done before arriving at the field site, in a comfortable location. We do recommend another training session in the forest, to become comfortable manually piloting the UAV up and down through dense understorey and canopy gaps. What can be especially useful is to train using small canopy gaps, to increase

confidence and dexterity and so that it becomes easier to pilot through any larger canopy gaps encountered whilst undertaking surveys, and so you will not be unable to fly if only small canopy gaps are available.

What we took to the field

For this campaign, we took one iPad mini, two 32 GB SD cards and two complete UAV systems (Phantom 3 Advanced) into the field, each comprising UAV, controller, battery, battery charger and 16 GB SD card. This would ensure that if one UAV encountered any problems (crashing is not unknown, nor are flyaways) we would have a back-up to enable us to continue surveying. In our case, we did not encounter any problems and, therefore, only used one of the UAV systems. For anyone taking a UAV into remote territory as an essential tool for their work, however, we would recommend taking a back-up.

In addition to the two complete UAV systems, we took 6 sets of replacement propellers, spare iPad charging and connection leads, and 4 extra batteries and chargers (bringing the total up to six). Due to the distance from the camp site to the field plots, we were unable to re-charge the batteries during the day, and thus, surveying was limited by battery numbers to ~6 flights per day (although more are possible if a smaller survey is undertaken and a battery not fully discharged).

All equipment necessary for a day of flying: one complete UAV system with 5 additional batteries (6 in total), packed into a single backpack (weight: ~4.1 kg) that was easily carried by one person. It is possible to fly most small UAVs single-handedly, but we would recommend two people undertake the UAV flights if in an environment such as a tropical forest: one person to pilot the UAV and the second to assist in launching and landing the UAV (holding it just above the ground or dense ground vegetation to launch and catching it on its descent). This avoids any

part of the UAV contacting and potentially being damaged by rough terrain or vegetation (in particular the propellers and camera).

How much can you fly a day?

The six batteries we had for our system provided a total flight time of approximately 2 hours, sufficient to survey approximately 50-60 ha of contiguous area at 100 metres with conservative battery use (i.e. completing each survey without fully discharging the battery), and approximately 80-90 ha with full battery use. Due to the fact that we undertook ground-based liana surveys concurrently, we did not collect the UAV data as rapidly as would be possible. As can be noted from our flights of the 50 ha plot, we managed up to five flights of ~10 ha per day. This was possible due to the close proximity of each of our survey areas. However, walking between individual plots could easily take more than an hour, which is why we propose a conservative estimate that three plots may be flown (at two altitudes each) in a single day.

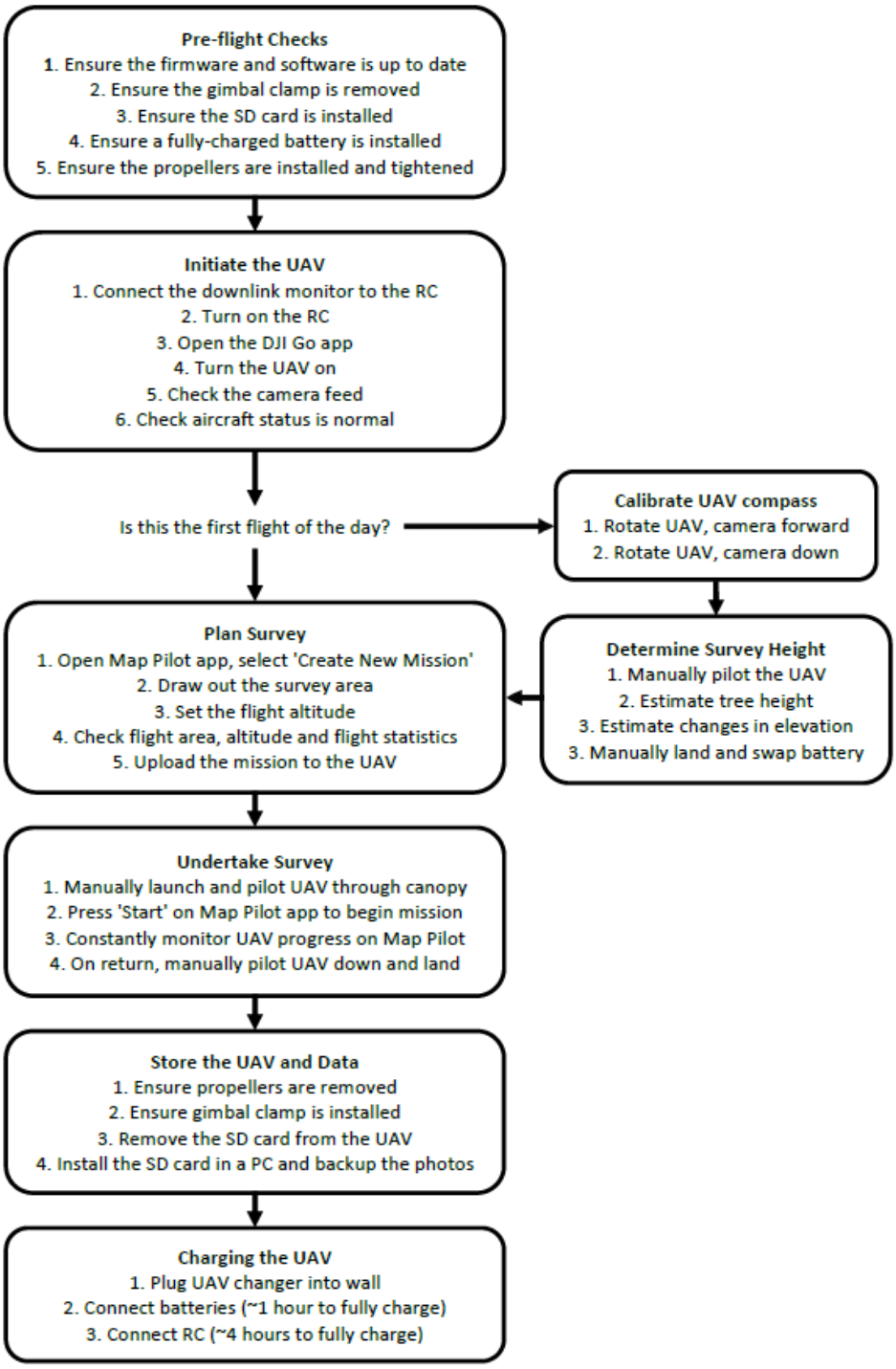
Battery re-charging and data backup

Battery recharging is a key element in UAV use. We used DJI equipment and charging a single, high-capacity battery takes approx. 1 hour. To give ourselves a chance to fly 6 times in the morning and 6 in the afternoon, we took one charger for each battery. In the event, the distance of the research plots from the research base meant that re-charging during the day was not possible and, thus, fewer chargers could have sufficed as we recharged during the evening. We would recommend taking adequate charging facilities, but a charger for each battery is probably not necessary unless the plots are close enough to re-charge at midday. Also, for anyone that can have vehicle access during their field work, it is also possible to purchase 12 V recharging systems which would allow re-charging on-the-go whilst in the field.

After a day of flying, we backed up the SD card(s) used that day, and cleared it for use on subsequent days of surveying. As the UAV saves images to an on-board SD card during the survey, we recommend taking multiple SD cards, in case of corruption or failure, as well as to swap if one becomes full during a day of flying. We would also recommend that it is worth purchasing the fastest SD card possible, as it ensures the card write speed is not limiting the camera capacity to take images and, subsequently, the UAV airspeed.

S2.1.2 The UAV survey protocol

We present a flow chart to show the protocol we followed when undertaking the UAV surveys. The 'RC' is the UAV remote controller. The 'DJI Go' app was the base app for flying any DJI UAV and was free to obtain, produced by DJI. The 'Map Pilot' app is an automated surveying app, produced by the company Maps Made Easy for a small fee ~£7.



S2.1.3 Image overlap settings for imaging the forest canopy.

The high overlap used is largely a result of the height of the forest, in combination with the fact that the overlap refers to ground level (this is how the settings of the software we used work when operating the UAV). The amount of overlap between images decreases at tree top or canopy level compared to ground level due to the tops of the trees being closer to the sensor. This reduced distance between the canopy to the sensor compared to the distance between the ground and the sensor, means that a smaller area of forest canopy is captured in each image than would be captured if imaging the forest floor, and this reduction in area captured results in a reduction in overlap between images. This has been noted in other studies, e.g. Nevalainen et al. (2017) who report ~10% reduction in overlap between ground level and tree top level. For our data, the overlap at ground level (i.e. 100 m away from the sensor) is 90%, but the actual overlap in our images at a canopy level of 50-60 m (i.e. only 40-50 m away from the sensor) is closer to 75-80%.

To demonstrate:

At 100 m distance from the sensor (ground level), an image captures a rectangular area with a long side of 10 x metres, where x is the distance between image centroids. To get 90% overlap, the UAV takes an image every x metres, and the overlap is: (9 x/10 x) * 100 = 90%

At 50m distance (canopy level), the area captured has a side half as long at 5x metres. Images are still taken every x metres, so the greatest overlap possible is: (4 x/5 x) * 100 = 80%

At 40m distance (emergent level), area side is 4x, so greatest overlap is: (3 x/4 x) * 100 = 75%

Maintaining a high overlap between our images in this way is also beneficial as high overlap enables processing of other products in a Structure from Motion (SfM) workflow (i.e. point clouds and canopy height models). Indeed, Dandois et al. (2015) found that the most accurate UAV measures of canopy height compared to field measures is at high image overlap >80%. Additionally, point-matching stability between images decreases rapidly after the view-angle of particular features within the image exceeds 20^{o}, with view-angles increasing with decreasing overlap. This will vary depending on the camera and UAV settings but for Dandois et al. (2015) was (at an altitude of ~80 m) with less than ~72% overlap. Finally, in a different context than that presented in this paper, we have found that raising the overlap between images at the canopy level increases the accuracy of the resultant orthomosaic. We are confident that for forests, where the overlap at the canopy level will be lower than that set at the ground, setting high overlaps at the ground level in order to maintain overlap at the canopy level is beneficial, and we recommend it for other forest studies.

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S2.1.4 Details for each survey flight undertaken.

In the table below we present information on each of the UAV surveys that we undertook.

Plot	Date	Time	Duration (m/s)	Batteries	Images	Area (ha)	Storage (GB)	Height above canopy (m)
DAN-01	11.5.16	12:54	21m 14s	1	329	6.94	1.59	30
	10.5.16	09:50	11m 12s	1	145	5.70	0.72	60
DAN-02	2.6.16	10:57	09m 04s	1	104	3.66	0.52	30
	2.6.16	10:42	07m 49s	1	88	3.09	0.43	60
DAN-03	7.6.16	11:28	10m 10s	1	134	2.84	0.65	30
	7.6.16	11:55	12m 52s	1	69	6.76	0.33	60
IND-03	17.6.16	12:18	09m 13s	1	118	3.50	0.57	30
	17.6.16	13:40	09m 30s	1	119	5.43	0.59	60
IND-04	18.6.16	11:19	16m 00s	1	270	5.50	1.32	30
	18.6.16	13:02	05m 29s	1	100	5.29	0.5	60
Alluvial	18.5.16	12:33	28m 18s	2	494	10.55	2.35	30
	18.5.16	10:24	15m 18s	1	424	15.18	2.03	60
Sandstone	20.5.16	11:17	22m 03s	1	380	7.86	1.82	30
	19.5.16	15:06	12m 29s	1	168	6.54	0.82	60
Kerangas	27.5.16	15:59	19m 34s	1	342	6.95	1.65	30
	27.5.16	12:15	16m 42s	1	231	7.02	1.10	60
50 ha (covers the additional 9 plots: DAN50-01 to DAN50-05, DAN50-06 to DAN50-09, and IND-05)								
Flight 1	14.6.16	09:59	23m 48s	1	419	9.69	1.95	30
Flight 2	14.6.16	11:08	23m 15s	1	410	10.41	1.95	30
Flight 3	14.6.16	12:10	17m 09s	1	244	7.26	1.16	30
Flight 4	14.6.16	12:49	24m 24s	1	435	10.08	2.05	30
Flight 5	14.6.16	13:54	22m 43s	1	375	10.83	2.28	30
Flight 6	15.6.16	10:17	24m 36s	1	443	10.17	2.07	30
Flight 7	15.6.16	10:54	24m 32s	1	443	10.23	2.09	30
Flight 8	15.6.16	12:21	18m 00s	1	302	8.54	1.43	30
Flight 9	15.6.16	13:27	25m 14s	2	426	12.26	2.00	30
Flight 10	16.6.16	09:44	22m 18s	1	390	11.30	1.83	30

S2.2 Agisoft PhotoScan processing report

This section presents the Agisoft PhotoScan Processing Report. The report contains the details of all processing undertaken and can be automatically generated after processing is complete.

S2.2.1 Agisoft PhotoScan Processing Report: title page.

This page shows the orthomosaic of the plot, as well as the date the processing report was generated. In this case, the report is for one of our plots (IND-04) in the Danum Valley Conservation Area.

Agisoft PhotoScan

Processing Report - IND-04
04 October 2018



S2.2.2 Agisoft PhotoScan Processing Report: survey data information.

This page shows information on the UAV survey including number of images, coverage, altitude, and overlap statistics. Note: the "Ground resolution" given is the effective resolution averaged over all aligned images if considering an object at ground-level. As we were imaging the forest canopy, our actual resolution is much higher, due to the reduced distance between the canopy and the UAV sensor.

Survey Data

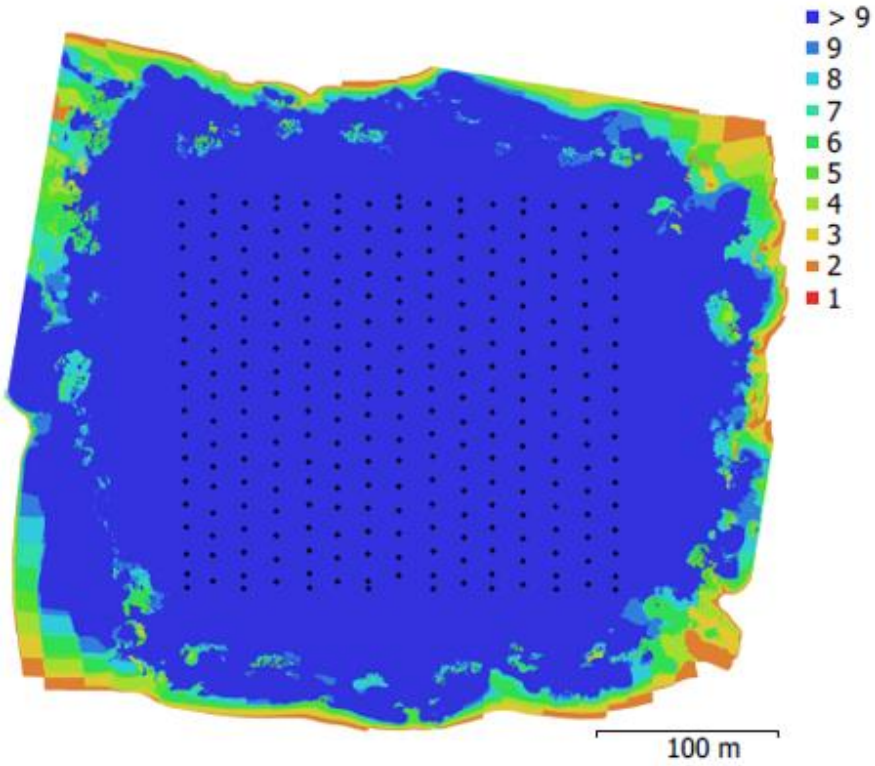


Fig. 1. Camera locations and image overlap.

Number of images:	269	Camera stations:	269
Flying altitude:	105 m	Tie points:	12,320
Ground resolution:	4.3 cm/pix	Projections:	65,466
Coverage area:	0.141 km²	Reprojection error:	0.532 pix

Camera Model	Resolution	Focal Length	Pixel Size	Precalibrated
FC300S (3.61mm)	4000 x 3000	3.61 mm	1.56 x 1.56 µm	No

Table 1. Cameras.

S2.2.3 Agisoft PhotoScan Processing Report: camera calibration.

The internal camera parameters are given. The image residuals show the average vector of the reprojection error for the pixels in the corresponding cells.

Camera Calibration

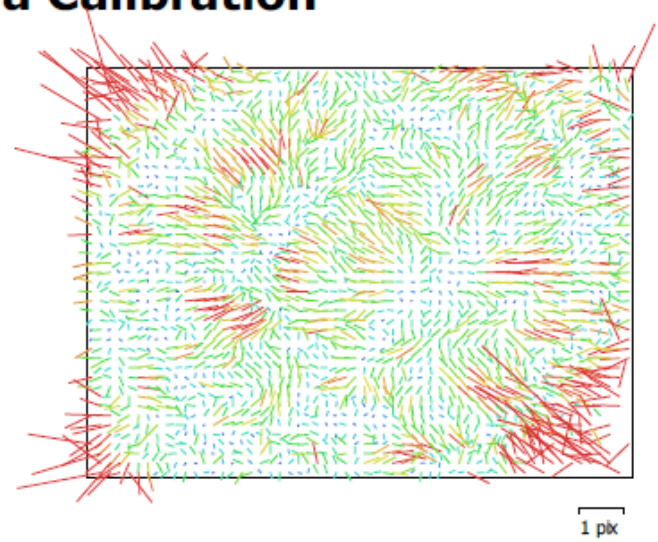


Fig. 2. Image residuals for FC300S (3.61mm).

FC300S (3.61mm)

269 images

Type	Resolution	Focal Length	Pixel Size
Frame	**4000 x 3000**	**3.61 mm**	**1.56 x 1.56 µm**

	Value	Error	F	Cx	Cy	B1	B2	K1	K2	K3	P1	P2
F	**2289.36**	0.83	1.00	-0.35	0.95	-0.12	0.03	-0.03	0.13	0.28	-0.07	-0.01
Cx	**-36.1546**	0.018		1.00	-0.36	-0.01	0.25	0.00	-0.04	-0.10	0.81	-0.08
Cy	**-23.1624**	0.042			1.00	-0.13	0.01	-0.03	0.12	0.27	-0.10	0.20
B1	**-3.66483**	0.18				1.00	-0.01	-0.00	0.02	-0.02	0.02	-0.04
B2	**-1.88927**	0.16					1.00	-0.02	0.01	-0.00	0.08	-0.03
K1	**-0.0120537**	6.5e-05						1.00	-0.75	0.69	-0.06	0.34
K2	**0.00757533**	8.5e-05							1.00	-0.90	0.01	-0.06
K3	**0.00677919**	5.2e-05								1.00	-0.04	0.07
P1	**-0.000309178**	2.6e-06									1.00	-0.14
P2	**-0.000819181**	2.2e-06										1.00

Table 2. Calibration coefficients and correlation matrix.

S2.2.4 Agisoft PhotoScan Processing Report: camera locations.

This page details information on camera positioning and error estimates. The X, Y and Z errors are the root mean square error for all cameras, with X and Y being longitudinal and latitudinal errors, and Z altitudinal error.

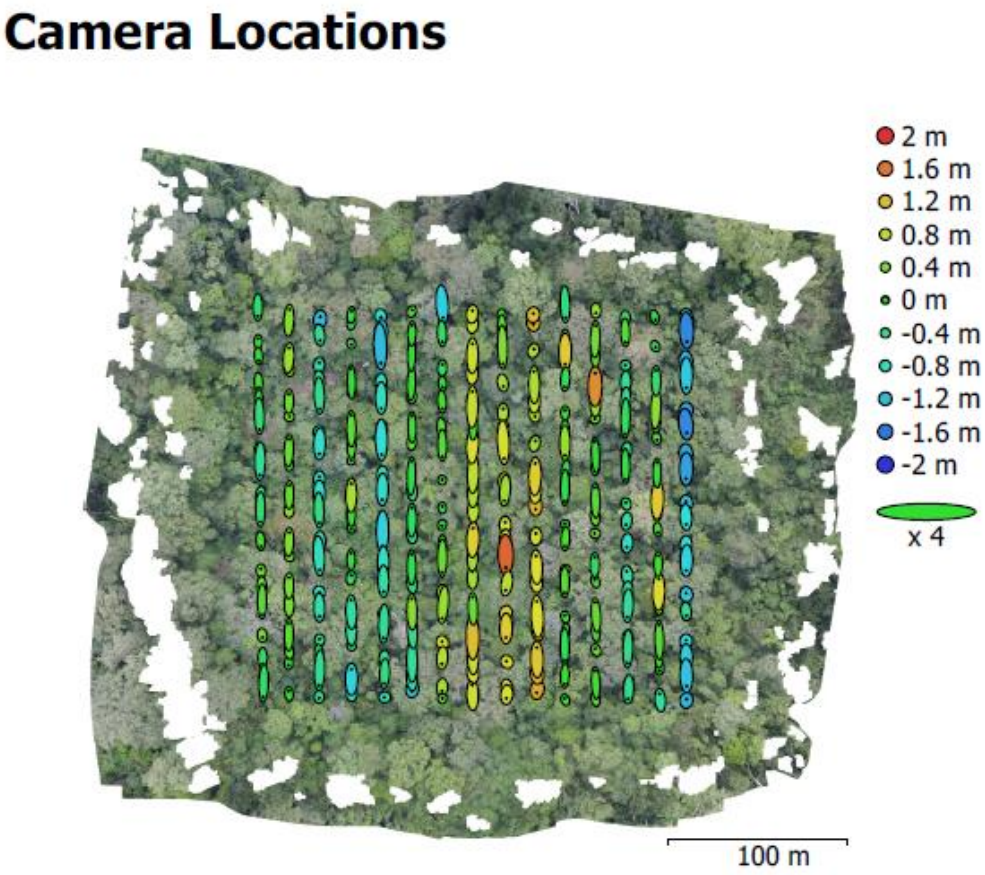


Fig. 3. Camera locations and error estimates.
Z error is represented by ellipse color. X,Y errors are represented by ellipse shape.
Estimated camera locations are marked with a black dot.

X error (m)	Y error (m)	Z error (m)	XY error (m)	Total error (m)
0.103622	2.31601	0.676561	2.31833	2.41503

Table 3. Average camera location error.
X - Longitude, Y - Latitude, Z - Altitude.

S2.2.5 Agisoft PhotoScan Processing Report: digital elevation model (DEM).

A DEM sketch of the plot is given, including information on resolution and point density. Resolution is the effective resolution of the DEM, dependent on the Quality parameter set by the user when building the point cloud. Point Density is the average number of dense cloud points per square meter.

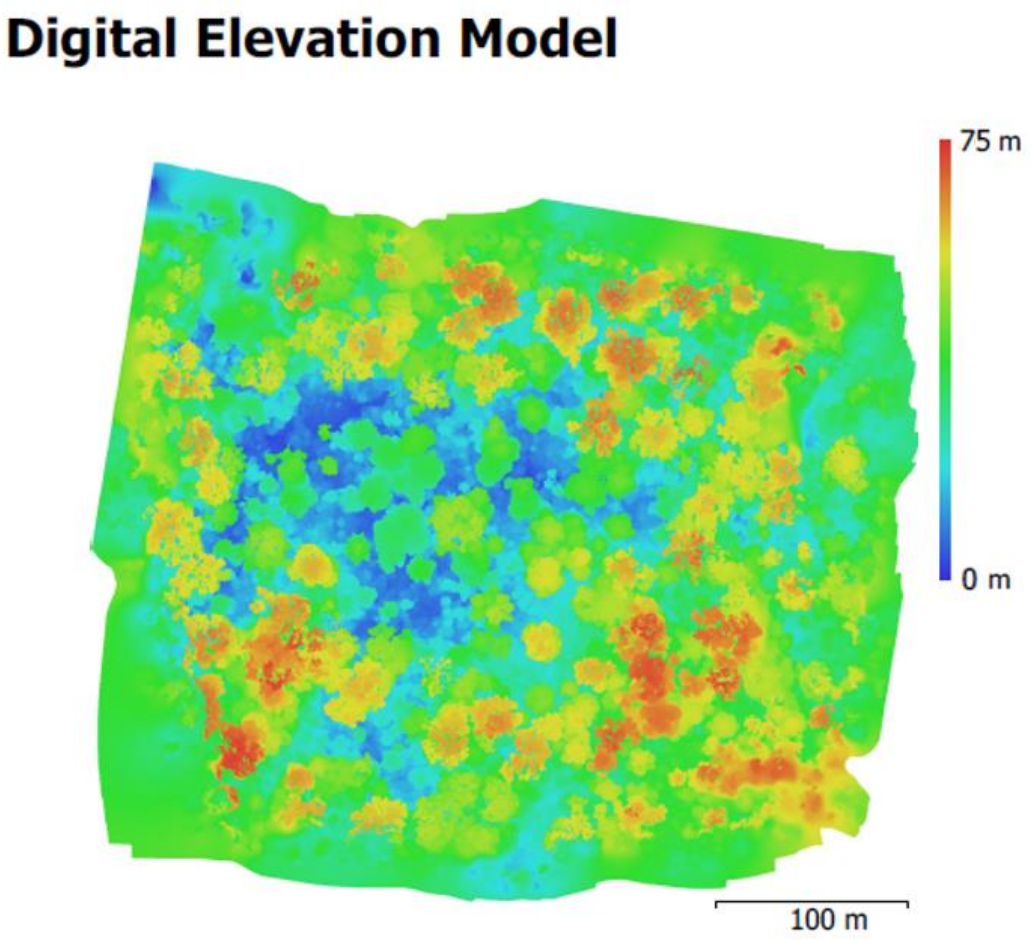


Fig. 4. Reconstructed digital elevation model.

Resolution:	4.3 cm/pix
Point density:	541 points/m²

S2.2.6 Agisoft PhotoScan Processing Report: processing parameters.

The processing parameters used at each stage of the project are given, along with information on processing time.

Processing Parameters

General	
Cameras	269
Aligned cameras	269
Coordinate system	WGS 84 (EPSG::4326)
Rotation angles	Yaw, Pitch, Roll
Point Cloud	
Points	12,320 of 278,704
RMS reprojection error	0.257474 (0.532475 pix)
Max reprojection error	0.499985 (4.99911 pix)
Mean key point size	2.02716 pix
Point colors	3 bands, uint8
Key points	No
Average tie point multiplicity	3.16628
Alignment parameters	
Accuracy	Highest
Generic preselection	Yes
Reference preselection	Yes
Key point limit	50,000
Tie point limit	4,000
Adaptive camera model fitting	Yes
Matching time	8 minutes 21 seconds
Alignment time	1 minutes 16 seconds
Optimization parameters	
Parameters	f, b1, b2, cx, cy, k1-k3, p1, p2
Adaptive camera model fitting	No
Optimization time	4 seconds
Depth Maps	
Count	267
Reconstruction parameters	
Quality	Ultra High
Filtering mode	Moderate
Processing time	1 hours 8 minutes
Dense Point Cloud	
Points	204,999,739
Point colors	3 bands, uint8
Reconstruction parameters	
Quality	Ultra High
Depth filtering	Moderate
Depth maps generation time	1 hours 8 minutes
Dense cloud generation time	6 hours 7 minutes
DEM	
Size	11,098 x 10,298
Coordinate system	WGS 84 (EPSG::4326)
Reconstruction parameters	
Source data	Dense cloud
Interpolation	Enabled
Processing time	1 minutes 27 seconds
Orthomosaic	
Size	10,022 x 8,942
Coordinate system	WGS 84 (EPSG::4326)
Colors	3 bands, uint8
Reconstruction parameters	
Blending mode	Mosaic
Surface	DEM
Enable hole filling	Yes
Processing time	18 minutes 58 seconds
Software	
Version	1.4.2 build 6205
Platform	Windows 64

S2.3 Supplementary results for Chapter 3

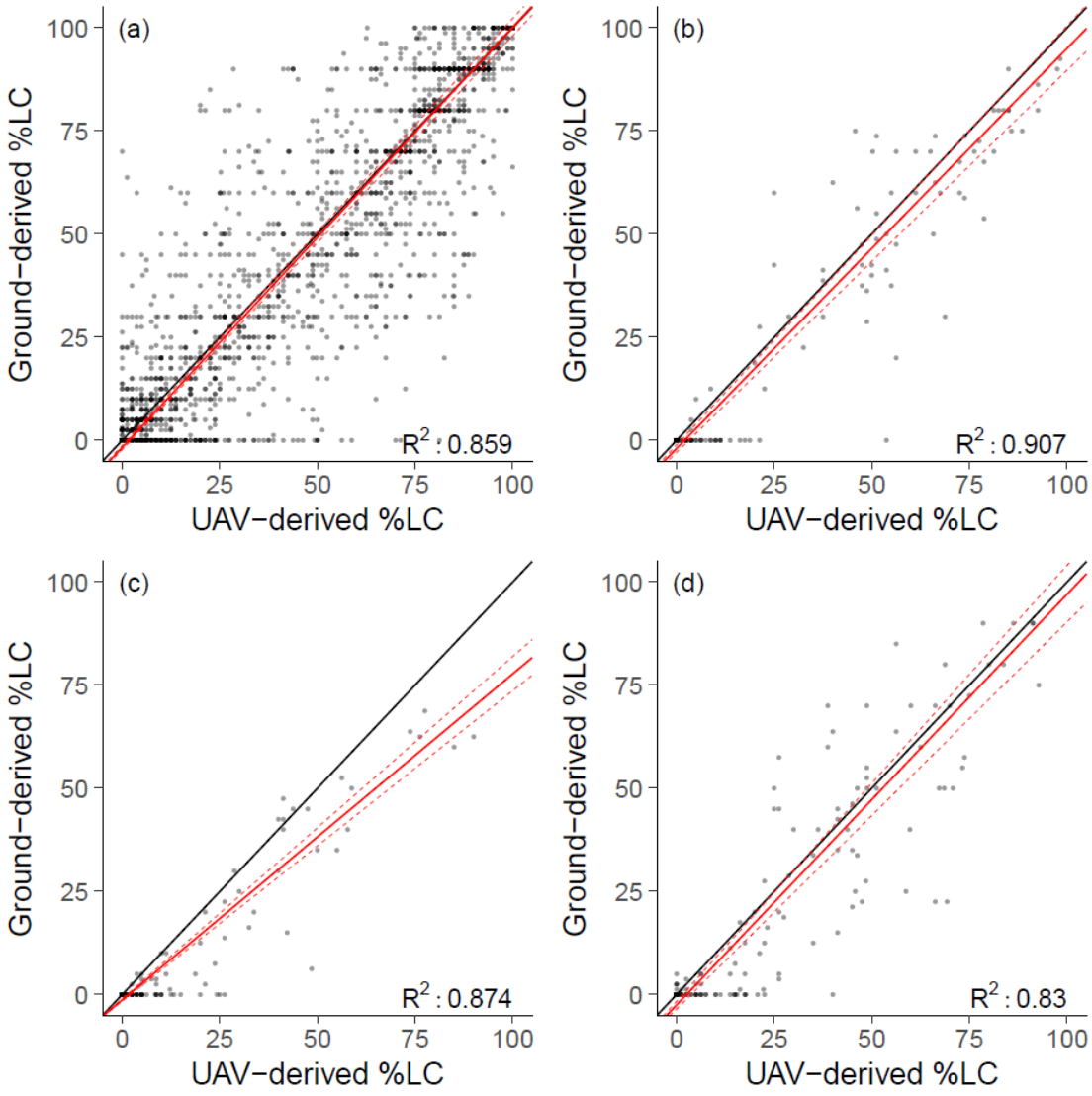
S2.3.1 Reproducibility of crown occupancy index (COI) scores between the UAV method and the ground method for different forest types.

Percentage of trees in each of the crown occupancy index (COI) classes for the ground (G) and UAV surveys (UAV), the degree of concordance between ground- and UAV-based surveys (Kendall's W) for the different forest types. $p < 0.001$ for all comparisons.

			COI 0 (%)		COI 1 (%)		COI 2 (%)		COI 3 (%)		COI 4 (%)	
	N	**W**	**G**	**UAV**	**G**	**UAV**	**G**	**UAV**	**G**	**UAV**	**G**	**UAV**
Danum	2,896	0.950	39.0	30.2	13.9	25.6	14.5	12.8	13.9	15.1	18.0	16.3
Alluvial	192	0.922	67.2	45.8	3.1	24.0	9.9	10.4	13.0	12.0	6.8	7.8
Kerangas	238	0.838	82.4	62.6	9.7	26.9	5.0	6.7	2.9	2.1	0.0	1.7
Sandstone	229	0.913	63.8	51.5	14.8	24.0	7.9	12.7	9.6	8.7	3.9	3.1

S2.3.2 Reproducibility of percentage liana cover (%LC) values between the UAV method and the ground method for different forest types.

Relationships between the UAV-derived percentage liana cover (%LC) and the ground-derived percentage liana cover (%LC) for trees located in (a) Danum (N = 2,661; RMSE = 13.50), (b) Sepilok Alluvial (N = 192; RMSE = 9.38), (c) Sepilok Kerangas (N = 238; RMSE = 6.84), (d) Sepilok Sandstone (N = 229; RMSE = 10.49). Solid red lines indicate the regression lines, dashed red lines the 95% confidence intervals, and black lines the 1:1 lines (i.e. perfect correlation). Darker dots indicate more data points with similar ground and UAV values.



S2.3.3 Reproducibility of percentage liana cover (%LC) values between the UAV method and the ground method for different spatial resolutions.

Degree of concordance between the ground and UAV surveys with different spatial resolutions in assessing liana infestation of tree crowns using crown occupancy index (COI) and percentage liana cover (%LC). Differences in COI and %LC were assessed with Kendall's *W* and Spearman's rank tests, respectively.

	COI		%LC	
	W	**p**	**r**	**p**
Ground & UAV (10 mm)	0.867	<0.001	0.781	<0.001
Ground & UAV (20 mm)	0.847	<0.001	0.731	<0.001
UAV (10 mm) & UAV (20 mm)	0.932	<0.001	0.892	<0.001

S2.3.4 Reproducibility of crown occupancy index (COI) scores between the UAV method and the ground method for different canopy strata.

Error matrices showing the number of trees classified in each crown occupancy index (COI) class for the ground and UAV surveys for the (a) lower canopy, (b) mid canopy, (c) upper canopy and (d) emergent trees. Counts in bold font indicate when the two methods produced the same score.

(a) Lower canopy trees

		Ground Data COI				
		0	**1**	**2**	**3**	**4**
UAV data COI	**0**	**542**	37	2	0	0
	1	81	**232**	78	11	2
	2	2	26	**149**	64	8
	3	0	3	47	**146**	62
	4	0	0	4	21	**324**

(b) Mid canopy trees

		Ground Data COI				
		0	**1**	**2**	**3**	**4**
UAV data COI	**0**	**274**	14	3	2	0
	1	151	**83**	22	5	3
	2	10	12	**61**	23	10
	3	5	0	24	**84**	28
	4	0	0	1	22	**152**

(c) Upper canopy trees

		Ground Data COI				
		0	**1**	**2**	**3**	**4**
UAV data COI	**0**	**160**	1	2	0	0
	1	82	**33**	4	0	0
	2	8	4	**13**	4	0
	3	1	3	10	**22**	6
	4	1	1	3	15	**39**

(d) Emergent trees

		Ground Data COI				
		0	**1**	**2**	**3**	**4**
UAV data COI	**0**	**187**	2	0	0	0
	1	76	**10**	5	0	0
	2	5	1	**4**	2	0
	3	3	0	4	**7**	0
	4	0	0	0	1	**5**

S2.3.5 An example of additional information that can be collected from the UAV imagery: orang-utan nests.

An example image taken using the DJI Phantom 3 Advanced. A section of the image has been selected to show a tree crown with an orang-utan nest in it, indicated by a white circle.

