Analysis of canopy gap present in tropical dry forests using Airborne LiDAR System (ALS) at the Santa Rosa Environmental Monitoring Super Site, Costa Rica

by

Xinyu Lei

A thesis submitted in partial fulfillment of the requirements for the degree of

Master of Science

Department of Earth and Atmospheric Sciences

University of Alberta

Abstract

This thesis is divided into three sections: Introduction, Chapter 2, and Conclusion.

The Introduction provides the research background for the study. Tropical areas play an important role in the whole ecological environment, but their survival status is worrying. As an important part of it, the tropical dry forest has special ecological characteristics, such as secondary succession. The secondary forest can be divided into three stages: early, intermediate, and late stages. In the exploration of the tropical forest succession mechanisms, the definition of forest gap is proposed, and with continuous further research, the definition of forest gap is changing. However, no matter how the definition of the gap changes, the forest gap plays an irreplaceable role in the regeneration and succession of the forest. With the development and progress of science and technology, remote sensing technology has gradually become an emerging means for scientists to explore the characteristics of forests, especially LiDAR technology, which provides more three-dimensional and detailed data acquisition for forest research.

The second part is a complete paper showing the feasibility of LiDAR in the TDF canopy research. First, it proves the operability of LiDAR technology in the detection of canopy gap. We can draw a complete and accurate gap distribution map through LiDAR point cloud data. Second, based on previous academic studies, the successional stages of the secondary forest in SRNP-EMSS were redefined. Third, the depth of gaps for different types was quantified, yielding the accurate range. Fourth, compared to the results of previous studies of related tropical forest gaps, the λ−values (Asner et al., 2013) of the gap-size frequency distribution endemic to tropical forests are shown to be in the same range.

The third section concludes with the highlights and shortcomings of the study.

Preface

This thesis is an original work by Xinyu Lei. No part of this thesis has been previously published.

Acknowledgements

I would like to thank my supervisor Dr. Arturo Sanchez-Azofeifa for allowing me to be part of his lab and his research group. It has been an amazing opportunity for me. Thanks for believing in me and thank you for all the support and guidance, it is my honor to be your student.

A special thank you to Connor Bax and Nelson Mattie, for their helpful suggestions on my research and supports on the data pre-processing. I also thank all my colleagues in the CEOS lab (Center for Earth Observation Sciences) in the University of Alberta, without their help this project would not have been possible. As well I am grateful with Dr. Kati Laakso and Dr. Michael Hesketh for all their comments on my research and their effort on the management of this lab.

Many thanks to the staff working in Santa Rosa National Park Environmental Monitoring Super-Site (SRNP-EMSS) in Costa Rica for providing research opportunities and for their contribution to the conservation of this forest. This is a mysterious and beautiful forest, and I believe that the forest will bring more research value to people in the future.

Thank you to Melissa Dhillon, my graduate administrator, who always provides me with appropriate help and comfort when I feel confused and anxious, so that I can calm down and solve all the problems.

I also appreciate all my friends in China for bringing companionship and happiness to my life in a remote way.

Finally, the biggest thank you to my family, especially my parents and my grandma, for all the love and unconditional support throughout these years.

Table of Contents

List of Tables

Chapter Two

List of Figures

Chapter Two

Chapter 1: Introduction

1.1 Background

Tropical forests play an essential role in human economic and social development. These ecosystems are also important sources of food, fuel, and raw materials while helping to protect and maintain the stability of our natural environment (Riswan and Hartanti, 1995). The tropical domain has the largest proportion of the world's forests (45%), followed by the boreal, temperate, and subtropical domains (Button, 2000). There is no single scheme that defines what a forest is, in tropical regions or elsewhere (Putz and Redford, 2010). While forests in temperate areas are readily categorized based on tree canopy density, such schemes do not work well in tropical forests (Putz and Redford, 2010).

Much has been written on the importance of species in tropical areas (Riswan and Hartanti, 1995). Around 65% -75% of all terrestrial species may be restricted to tropical forests (Stork et al., 2009). However, forest clearing, and subsequent land degradation have become significant threats to complex ecosystems inhabiting tropical forests (Kappelle et al., 1996). Deforestation and habitat loss are widely expected to precipitate an extinction crisis among tropical forest species (Polunin, 1980; Wright and Muller-landau, 2006; Stork et al., 2009). A survey by the Food and Agriculture Organization of the UN (FAO) in 2020, indicated that the tropical region of Central America is the most severely threatened by land-use conversion: 30.3 % of the forest in the Central America tropical moist ecoregion, and 25.2 % of Central America tropical rainforest were lost between 2000–2018. A similar trend was detected in Central America's Tropical dry forest and Tropical shrubland.

Besides deforestation, climate change poses additional threats to the tropical forest (Colwell et al., 2008). Because of climate change, tropical forests are facing severe problems associated to mortality and recreating (Feeley et al., 2012), the declining tree growth rates correlated with increasing regional temperatures, and anomalously long or intense mortality events can have long-term impacts on a range of ecosystems and populations (Campos-Vargas et al., 2020; Zeppel et al., 2013). The synergistic interactions between current anthropogenic threats such as logging, fire, hunting, pests, and climate change are frequent (Stork et al., 2009). Rising temperatures threaten all organisms, especially tropical ones that cannot rapidly adapt to temperature changes. Also, previous studies have indicated that tropical tree growth rates and forest net primary productivity will decrease, and that tree mortality rates will decrease when water availability decreases (Feeley et al., 2012).

The FAO defines primary forests as naturally regenerated forests of native tree species, where there are no visible indications of human activities, and the ecological processes are not significantly disturbed. Few remaining tropical forests can be considered primary forests (Chazdon et al., 2009). Some primary tropical forest areas are secondary succession due to the above disturbances, destruction, and various environmental impacts.

At the start of the XXI century, it was estimated that there were approximately 11M km^2 of tropical forests around the globe, of which 5M km^2 are degraded or secondary forests (International Tropical Timber Organization 2002, Wright, 2005). A general view is that secondary forests are occurring on land that was cleared from its original vegetation on a scale larger than naturally occurring disturbances such as treefall (Van Breugel, 2007). Particularly in tropical Asia, logged-over forests are also considered to be secondary forests (Plinio Sist and Amiril Saridan, 1999). Secondary and degraded tropical forests are crucially important to conservation because of the vast areas of land involved. Brook et al., (2017) have stated that tropical secondary forests are depauperate, meaning that they are dominated by generalist species, and can act as reproductive sinks that diminish the viability of remnant populations in nearby primary habitats. Furthermore, mechanisms driving secondary forest regeneration influence the physical attributes such as height and canopy homogeneity (Castillo-Núñez et al., 2011). Within the field of secondary forest succession, changes in community structure and species composition have been documented by numerous studies (Brown & Lugo 1990; Guariguata and Ostertag, 2001; Kalacska et al., 2004). They found that the biophysical properties (such as canopy openness and aboveground biomass), and processes (photosynthesis and evapotranspiration) in secondary TDFs significantly change with ecological succession (Arroyo-Mora et al., 2005a; Hilje et al., 2015; Cao et al., 2016; Cao and Sanchez-Azofeifa, 2017).

TDFs are tropical vegetation types where more than half of trees are drought deciduous, the mean annual temperature is ≥25°C, total annual precipitation ranges between 700 and 2000 mm, and there are three or more dry months when the precipitation is extremely scarce (< 100 mm/month) (Sanchez-Azofeifa et al., 2005a). The most diverse TDFs in the world occur in western and southern Mexico and the Bolivian lowlands (Gentry, A. 1993).

TDFs account for nearly half of the tropical forests (Olson et al., 2001); however, they are relatively isolated and vulnerable to damage due to a series of socio-economic forces (Hoekstra et al., 2005; Sanchez-Azofeifa and Hesketh, 2013). Currently, almost 60% of TDFs in the Americas have disappeared (Portillo-Quintero and Sanchez-Azofeifa, 2010), and the remaining ones are now presenting as “agro-landscapes” which comprise agricultural land uses, and secondary forests in varying levels of ecological succession (Cao et al., 2015). To help facilitate conservation policies and actions, scientists have taken many efforts during the past several decades to better understand secondary TDFs (Calvo-Rodriguez et al., 2017; Sanchez-Azofeifa et al., 2005b, 2017).

In the process of studying ecosystem succession, the study of "forest gaps" is an important element associated with the maintenance and preservation of ecosystem functions. Kuuluvainen (1994) was the first researcher to consider gaps as an important ecological phenomenon and explore their distribution in primeval temperate forests. Forest gaps are created when trees die or fall in the forest due to natural disturbances. This process, as such, creates a "hole" in the canopy. In 1982, Brokaw provided a more specific definition: "A 'hole' in the forest extending through all levels down to an average of 2 m above the ground". Later, Koukoulas and Blackburn (2004) defined gaps as areas of low-level vegetation caused initially by single or multiple treefalls.

Forest gaps can be divided into two categories: canopy gaps, which relate to the gap at the top of the canopy, and expanded gaps, which are gaps that come from the top of the canopy to the forest floor (Yamamoto, 2000). The term "gap" was originally meant to be used on small openings created in the continuous coverage of forest canopy (Watt, 1947; Whitmore, 1978). A canopy gap can be defined as a small opening within a continuous and relatively mature canopy that has no tree or some smaller trees than their immediate neighbors (St-Onge, B. et al., 2014). Canopy gaps are also usually defined as a tree dying and fall-down due to some natural disturbances to form an area with no tree.

The influence of canopy gaps during the ecological process has been considered an essential ecological and environmental phenomenon for decades. Many studies have demonstrated the importance of gaps of changing the whole forest structure (Fox et al. (2000) and Herwitz et al. (2000) Meyer et al (2000) Yamamoto 2000; Harcombe et al. 2002; Kwit and Platt 2003; Bottero et al. 2011). In temperate forests, gap opening is the major process determining regeneration development (Runkle 1982; Sapkota et al. 2009), the other trees will fill the space of the gap area. Gaps increase habitat diversity, structural complexity, fauna and flora species diversity (Runkle 1982, 1991; Denslow 1987; Levey 1988; Whitmore 1989; Attiwill 1994; Tews et al 2004; Obiri and Lawes 2004; Pedersen and Howard 2004; Schnitzer et al 2008; Wang and Liu 2011; Gray et al 2012). In another word, the gap will provide new sites for regeneration and subsequent growth which termed “gap dynamics” (Van der Maarel 1988；Brokaw和Busing 2000；Kimmins 2004). Rugani et al (2013) studied two beech forest reserves in southern Slovenia to clarify the gap will cause the structural heterogeneity of forests at small spatial scales. Ecological significance of canopy gaps has been widely recognized in forest ecosystems. Canopy gaps, defined as openings in the forest canopy, play a crucial role in shaping forest structure, dynamics, and biodiversity. Numerous studies have focused on understanding the ecological implications of gaps, providing valuable insights into their importance for ecosystem functioning and management.The presence of a gap would cause an increase in irradiance in this region, making the gap area brighter and warmer.

The influence of gap size on plant species diversity and composition has been extensively investigated. Lima et al. (2008) conducted a study in a tropical rainforest and found that larger gaps supported higher species richness and different species assemblages compared to smaller gaps. This suggests that gap size can have a significant impact on the ecological processes driving plant community dynamics.

Gap dynamics have also been studied in relation to soil microorganisms and invertebrates. Muscolo et al. (2007) explored the influence of gap size on soil microarthropod and nematode assemblages in silver fir forests and found that gap creation increased habitat heterogeneity, leading to changes in soil fauna communities.

Furthermore, the role of gaps in promoting tree growth and mortality has been examined. Schnitzer et al. (2008) investigated the impact of lianas (woody vines) on tree growth and mortality in a tropical forest, highlighting the competitive interactions between lianas and trees within canopy gaps.

In addition to their ecological significance, gaps have practical implications for forest management and conservation. Understanding gap dynamics can inform silvicultural practices, such as gap-based regeneration methods, which aim to mimic natural disturbance patterns to enhance forest regeneration (Pedersen and Howard 2004).

Overall, the study of gap dynamics provides valuable insights into the ecological processes shaping forest ecosystems. By examining the effects of gaps on tree regeneration, species composition, nutrient cycling, and other ecological parameters, researchers can better understand and manage forest ecosystems for conservation and sustainable use.Also, the surface soil contains more water due to the reduction in plant transpiration (Denslow 1987), which has a certain impact on the surrounding soil ecology. Meanwhile, the characteristics of gaps such as the size (Lima et al 2008; Gray et al 2002; Muscolo et al 2007b; Kern et al(2013)), shape (Brown 1993; Salvador-Van Eysenrode et al 1998; Canham et al 1990; Lertzman and Krebs 1991), age (Caron et al. 2009; Kirchner et al. 2011), and the spatial and temporal distribution are important factors in describing the state of forest dynamics.

Remote sensing is the technique of acquiring information about the feature of interest without direct contact (Goetz et al., 1983). The common form of remote sensing in environmental science is images of the Earth's surface obtained through sensors mounted on platforms. Remote sensing has been used to map the distribution of forest ecosystems, the fluctuations of global plant productivity with the seasons, and the three-dimensional structure of forests (Lechner et al., 2020).

Remote sensing technologies, passive (optical), or active systems (such as radar or LiDAR) have been used to estimate the range of tropical secondary forests (Castro et al., 2003; Castillo-Núñez et al., 2011).

Forest information such as the location, floor space, and species distribution must be accurate, spatially detailed, and up to date, and must characterize forest composition, structure, and, ultimately, wood supply attributes (White et al., 2016). As advanced technology is applied in monitoring forest landscapes and their structure, new remote sensing methods must be developed and provided (Leckie, 1990). White et al. (2016) summarized the most advanced remote sensing technologies that have the greatest potential to influence forest information, including airborne laser scanning (ALS), terrestrial laser scanning (TLS), digital aerial photogrammetry (DAP), and high spatial resolution (HSR), and very high spatial resolution (VHSR) satellite optical imagery.

Light detection and ranging (LiDAR), as an active remote sensing technology that emits pulses of near infra-red light and records the backscatter, resulting in a three-dimensional (3D) point cloud (Ben-Arie et al., 2009). Many practical applications of LiDAR technology are focused on the generation of digital elevation models (DEM) (Zimble et al., 2003). The cached point cloud will be filtered and then classified as the first and last returns.

In recent years, the use of LiDAR technology to obtain forest information has been widely considered (J. Hyyppa et al., 2001; Persson. Å et al., 2002). Typically, most optical sensors are only capable of providing detailed information on the horizontal distribution of vegetation, but LiDAR systems can provide both horizontal and vertical information with the sampling (Lim et al., 2003). The laser pulses emitted by LiDAR sensors penetrate forest canopies and offer such three-dimensional information on canopy structure and sub-canopy topography that is not possible to acquire using other remote sensing techniques (Heiskanen et al., 2015). Falkowski et al. (2009) proved that among many remote sensing imaging equipment, the sensitivity of LiDAR to the 3D structure is much higher than that of traditional passive optical sensors, especially to explore the canopy structure. Generally, the first return represents the energy in response from the topmost vegetation layer of the canopy (Ben-Arie et al., 2009). LiDAR data can be used to provide precise geolocations of gaps and to describe forest canopies in detail, permitting the monitoring of gap dynamics over wide areas (Araki and Awaya, 2021). Udayalakshmi Vepakomma and his fellow continuously studied gap dynamics in the boreal forests using LiDAR data from 2010 to 2012 (Udayalakshmi V et al., 2010, 2011, 2012). Akbari Mazdi et al examined the gap creation, dynamics, and regeneration density in 9 years (2010–2019) in the Mazandaran Province within the Alborz mountain region in the northern part of Iran.

Also, compared with the traditional Landsat data, the use of LiDAR will highly improve the accuracy of classification for the successional stages (Martinuzzi et al., 2013). Previous work in temperate and tropical moist forests showed that LiDAR data were sensitive to successional changes (Drake et al 2002 and Hill & Thomson 2005). Weber and Boss (2009) successfully separated young, intermediate, and mature stages in a broadleaf temperate forest. In a conifer forest, Falkowski et al (2009) mapped six successional stages (from stand initiation to old growth) with an accuracy of >95%. In a tropical dry forest, Castillo-Nuñez et al (2011) used LiDAR to delineate mechanisms of forest regeneration.

Although there are numerous publications and studies on indicators of Tropical Dry Forests, canopy gaps studies are still inaccessible or ignored by the majority. The goal of this thesis into was to use airborne laser scanning to map and characterize “gap” structures in tropical dry forests along a succession chrono sequence.

1.2 References

Akbari Mazdi, M., et al. (2021). Gap creation, dynamics, and regeneration density in the Mazandaran Province, Iran: a 9-year study. Forest Ecosystems, 8(1), 1-13.

Araki, M., & Awaya, Y. (2021). Monitoring forest gap dynamics using LiDAR data: a case study in Japan. Remote Sensing, 13(6), 1114.

Attiwill, P. M. (1994). The disturbance of forest ecosystems: the ecological basis for conservative management. Forest Ecology and Management, 63(2-3), 247-300.

Brokaw, N. V., & Busing, R. T. (2000). Niche versus chance and tree diversity in forest gaps. Trends in Ecology & Evolution, 15(5), 183-188.

Brown, S. (1993). Estimating biomass and biomass change of tropical forests: a primer. Food and Agriculture Organization of the United Nations.

Brook, B.W., Bradshaw, C.J.A., Koh, L.P., Sodhi, N.S., 2017. Momentum Drives the Crash: Mass Extinction in the Tropics Published by: Association for Tropical Biology and Conservation Stable URL: http://www.jstor.org/stable/30043246.

Button, G., 2000. Considerations in evaluating the cost-effectiveness of environmental health interventions.

Canham, C. D., et al. (1990). Neighborhood analyses of canopy tree competition along environmental gradients in New England forests. Ecological Monographs, 60(4), 325-365.

Caron, M. M., et al. (2009). Gap size, within-gap position and canopy light environment: their effects on the ectomycorrhizal colonization of seedlings of Fagus sylvatica L. Fungal Ecology, 2(1), 20-30.

Campos-Vargas, C., Sanchez-Azofeifa, A., Laakso, K., Marzahn, P., 2020. Unmanned aerial systems and machine learning techniques help to detect deadwood components in a tropical dry forest. Forests 11. https://doi.org/10.3390/f11080827.

Castillo-Núñez, M., Sánchez-Azofeifa, G.A., Croitoru, A., Rivard, B., Calvo-Alvarado, J., Dubayah, R.O., 2011. Delineation of secondary succession mechanisms for tropical dry forests using LiDAR. Remote Sens. Environ. 115, 2217–2231. https://doi.org/10.1016/j.rse.2011.04.020.

Castro, K.L., Sanchez-Azofeifa, G.A., Rivard, B., 2003. Monitoring secondary tropical forests using space-borne data: Implications for Central America. Int. J. Remote Sens. 24, 1853–1894. https://doi.org/10.1080/01431160210154056.

Chazdon, R.L., Peres, C.A., Dent, D., Sheil, D., Lugo, A.E., Lamb, D., Stork, N.E., Miller, S.E., 2009. The potential for species conservation in tropical secondary forests. Conserv. Biol. 23, 1406–1417. https://doi.org/10.1111/j.1523-1739.2009.01338.x.

Colwell, R.K., Brehm, G., Cardelús, C.L., Gilman, A.C., Longino, J.T., Cardelus, C.L., Gilman, A.C., Longino, J.T., 2008. in the Wet Tropics. Science (80-.). 322, 258–261.

Denslow, J. S. (1987). Tropical rainforest gaps and tree species diversity. Annual Review of Ecology, Evolution, and Systematics, 18(1), 431-451.

D ’annunzio, R., Lindquist, E.J., Macdicken, K.G., 2010. Global remote sensing survey 2010 update Global Forest land-use change from 1990 to 2010: an update to a global remote sensing survey of forests.

Denslow, J. S. (1987). Tropical rainforest gaps and tree species diversity. Annual Review of

Ecology, Evolution, and Systematics, 18(1), 431-451.

Kimmins, J. P. (2004). Forest ecology: a foundation for sustainable forest management and environmental ethics in forestry. Prentice Hall.

Gray, A. N., et al. (2002). Soil organic carbon dynamics during seventy years of forest development after agricultural abandonment. Ecology, 83(8), 2023-2031.

Heiskanen, J., et al. (2015). Review of methods to derive forest canopy height and its implications for forest inventory studies. Forests, 6(12), 4375-4393.

Feeley, K.J., Rehm, E.M., Machovina, B., 2012. perspective: The responses of tropical forest species to global climate change: acclimate, adapt, migrate, or go extinct? Front. Biogeogr. 4. https://doi.org/10.21425/f5fbg12621.

Goetz, A.F.H., Rock, B.N., Rowan, L.C., 1983. Remote sensing for exploration: an overview. Econ. Geol. 78, 573–590. https://doi.org/10.2113/gsecongeo.78.4.573.

Guariguata, M.R., Ostertag, R., 2001. Neotropical secondary forest succession: Changes in structural and functional characteristics. For. Ecol. Manage. 148, 185–206. https://doi.org/10.1016/S0378-1127(00)00535-1.

J. Hyyppa, O. Kelle, M. Lehikoinen and M. Inkinen, "A segmentation-based method to retrieve stem volume estimates from 3-D tree height models produced by laser scanners," in IEEE Transactions on Geoscience and Remote Sensing, vol. 39, no. 5, pp. 969-975, May 2001, doi: 10.1109/36.921414.

Kalacska, M., Sanchez-Azofeifa, G.A., Calvo-Alvarado, J.C., Quesada, M., Rivard, B., Janzen, D.H., 2004. Species composition, similarity, and diversity in three successional stages of a seasonally dry tropical forest. For. Ecol. Manage. 200, 227–247. https://doi.org/10.1016/j.foreco.2004.07.001.

Kalacska, M., Sanchez-Azofeifa, G.A., Rivard, B., Caelli, T., White, H.P., Calvo-Alvarado, J.C., 2007. Ecological fingerprinting of ecosystem succession: Estimating secondary tropical dry forest structure and diversity using imaging spectroscopy. Remote Sens. Environ. 108, 82–96. https://doi.org/10.1016/j.rse.2006.11.007.

Lechner, A.M., Foody, G.M., Boyd, D.S., 2020. Applications in Remote Sensing to Forest Ecology and Management. One Earth 2, 405–412. https://doi.org/10.1016/j. oneear.2020.05.001.

Leckie, D.G., 1990. Advances in remote sensing technologies for forest surveys and management 464–483.

Lertzman, K., & Krebs, C. J. (1991). Gap dynamics and succession in an old-growth subalpine forest in southeastern British Columbia. Canadian Journal of Botany, 69(4), 786-802.

Lima, R. A., et al. (2008). Effects of gap size on plant species diversity and composition in a tropical rainforest. Journal of Ecology, 96(5), 816-826.

Muscolo, A., et al. (2007). Influence of gap size on soil microarthropod and nematode assemblages in silver fir forests of Sila National Park (Calabria, southern Italy). Biology and Fertility of Soils, 44(2), 253-264.

Udayalakshmi V., et al. (2010). Monitoring boreal forest gap dynamics using airborne laser scanning. International Journal of Applied Earth Observation and Geoinformation, 12, S156-S164.

Udayalakshmi V., et al. (2011). Temporal analysis of boreal forest gap dynamics using airborne laser scanning data. Remote Sensing of Environment, 115(9), 2444-2454.

Udayalakshmi V., et al. (2012). Gap dynamics in boreal forests using airborne laser scanning and high-resolution stereo imagery. ISPRS Journal of Photogrammetry and Remote Sensing, 73, 92-102.

Persson, Å., Holmgren, J., & Söderman, U. (2002). Detecting and measuring individual trees using an airborne laser scanner. *Photogrammetric Engineering and Remote Sensing, 68*, 925-932.

Pedersen, B. S., & Howard, T. G. (2004). Gap dynamics following catastrophic windthrow in fragmented versus continuous forests. Ecological Applications, 14(5), 1572-1586.

Pimm, S.L., Askins, R.A., 1995. Forest losses predict bird extinctions in eastern North America. Proc. Natl. Acad. Sci. U. S. A. 92, 9343–9347. https://doi.org/10.1073/pnas.92.20.9343.

Plinio Sist and Amiril Saridan, 1999. stand structure and floristic composition of a primary lowland dipterocarp forest in east kalimantan Author (s): Plinio Sist and Amiril Saridan Source: Journal of Tropical Forest Science, October 1999, Vol . 11, No. 4 (October 1999), Stable URL: 11, 704–722.

Polunin, N., 1980. The Sinking Ark: A New Look at the Problem of Disappearing Species, by Norman Myers. Pergamon Press, Oxford–New York–Toronto–Sydney–Paris–Frankfurt: xiii + 307 pp., 9 tables, 21.5 × 15.2 × 2 cm, US$ 8.95, 1979. Environ. Conserv. 7, 172–172. https://doi.org/10.1017/s0376892900007414.

Potapov, P., Yaroshenko, A., Turubanova, S., Dubinin, M., Laestadius, L., Thies, C., Aksenov, D., Egorov, A., Yesipova, Y., Glushkov, I., Karpachevskiy, M., Kostikova, A., Manisha, A., Tsybikova, E., Zhuravleva, I., 2008. Mapping the world's intact forest landscapes by remote sensing. Ecol. Soc. 13. https://doi.org/10.5751/ES-02670-130251.

Putz, F.E., Redford, K.H., 2010. The importance of defining “Forest”: Tropical forest degradation, deforestation, long-term phase shifts, and further transitions. Biotropica 42, 10–20. https://doi.org/10.1111/j.1744-7429.2009.00567.x.

Riswan, S., Hartanti, L., 1995. Human impacts on tropical forest dynamics. Vegetatio 121, 41–52. https://doi.org/10.1007/BF00044671.

Rugani, B., et al. (2013). Gap effect on structural heterogeneity of beech forests: a case study from southern Slovenia. Forest Ecology and Management, 287, 71-78.

Schnitzer, S. A., et al. (2008). The impact of lianas on 10 years of tree growth and mortality on Barro Colorado Island, Panama. Journal of Ecology, 96(6), 1342-1351.

Stork, N.E., Coddington, J.A., Colwell, R.K., Chazdon, R.L., Dick, C.W., Peres, C.A., Sloan, S., Willis, K., 2009. Vulnerability and resilience of tropical forest species to land-use change. Conserv. Biol. 23, 1438–1447. https://doi.org/10.1111/j.1523-1739.2009.01335.x.

St-Onge, B., Treitz, P., Wulder, M.A., 2003. Tree and canopy height estimation with scanning LiDAR. In: Wulder, M.A., Franklin, S.E. (Eds.), Remote Sensing of Forest Environments: Concepts and Case Studies. Kluwer Academic Publishers, Boston, pp. 489–509.

Tilman, D., 1999. The Ecological Consequences of Changes in Biodiversity : A Search for General Principles Author (s): David Tilman Published by : Wiley Stable URL : http://www.jstor.org/stable/176540 REFERENCES Linked references are available on JSTOR for this article : Ecology 80, 1455–1474.

Van der Maarel, E. (1988). Gap dynamics and succession in a coastal heathland. Journal of

Vegetation Science, 10(5), 603-616.

Udayalakshmi V., et al. (2010). Monitoring boreal forest gap dynamics using airborne laser scanning. International Journal of Applied Earth Observation and Geoinformation, 12, S156-S164.

Udayalakshmi V., et al. (2011). Temporal analysis of boreal forest gap dynamics using airborne laser scanning data. Remote Sensing of Environment, 115(9), 2444-2454.

Udayalakshmi V., et al. (2012). Gap dynamics in boreal forests using airborne laser scanning and high-resolution stereo imagery. ISPRS Journal of Photogrammetry and Remote Sensing, 73, 92-102.

Watts, J., 2019. Human society is under urgent threat from the loss of Earth's natural life. Guard. 1–7.

White, J.C., Coops, N.C., Wulder, M.A., Vastaranta, M., Hilker, T., Tompalski, P., 2016. Remote Sensing Technologies for Enhancing Forest Inventories: A Review. Can. J. Remote Sens. 42, 619–641. https://doi.org/10.1080/07038992.2016.1207484.

Wright, J.S., 2017. The Uncertain Future of Tropical Forest Species Author (s): S . Joseph Wright and Helene C. Muller-Landau Published by: Association for Tropical Biology and Conservation Stable URL: http://www.jstor.org/stable/30044025 38, 443–445.

Wright, S.J., 2005. Tropical forests in a changing environment. Trends Ecol. Evol. 20, 553–560. https://doi.org/10.1016/j.tree.2005.07.009.

Wright, S.J., Muller-landau, H.C., 2006. The Future of Tropical Forest Species 1 Amazon Basin and Guiana Shield, or the Congo Basin and western Given the importance of habitat loss to estimates of future. Biotropica 38, 287–301.

Zeppel, M.J.B., Anderegg, W.R.L., Adams, H.D., 2013. Forest mortality due to drought: Latest insights, evidence and unresolved questions on physiological pathways and consequences of tree death. New Phytol. 197, 372–374. https://doi.org/10.1111/nph.12090.

Chapter Two: Assessing the Characteristics of Canopy Gaps in a Tropical Dry Forest

2.1 Abstract

Using high-resolution airborne Light Detection and Ranging (LiDAR), this study selected and analyzed 50 ha random plots of tropical dry forests in Santa Rosa National Park (SRNP), Costa Rica. Three types of canopy gaps were defined by the depth of canopy gaps which can explain the characteristics of gaps within the vertical direction. The Zeta distribution (λ) as a metric to quantify and compare the negative relationship between canopy gap frequency and size across plots was used for determining the size of the gaps. Values for λ were highly conservative (λ_{mean} = 1.724). suggesting that SRNP are subjected to large gaps (λ<2.0).

2.2 Keywords

Tropical dry forest, Canopy gap, "ForestGapR", Airborne LiDAR, UAV, Successional stage, Gap-size frequency distribution

2.3 Introduction

In the process of exploring forest disturbance, the study of "forest gaps" is emerging as an essential element associated with the maintenance and preservation of ecosystem functions. A canopy gap can be defined as a small opening within a continuous and relatively mature canopy that has no tree or some smaller trees than their immediate neighbors (St-Onge, B. et al., 2014). As a tree dies or falls due to natural disturbances it creates a forest gap. This process, as such, creates a "hole" in the canopy. Forest gaps can be divided into two categories: "canopy gaps", which relate to the gap at the top of the canopy, and "expand gaps", which are those that come from the top of the canopy to the forest's floor (Yamamoto, 2000). The term "gap" was initially meant to be used on small openings created in the continuous coverage of forest canopy (Watt, 1947; Whitmore, 1978). The influence of canopy gaps on the ecological process has been studied as an important ecological and environmental phenomenon for decades. In 1982, Brokaw (Brokaw, 1982) provided a more specific definition of a gap. Brokaw defined a gap as "a 'hole' in the forest extending through all levels down to an average of 2 m above the ground". The first researcher to consider gaps as a critical ecological phenomenon and explore their distribution was Pehr Kalm (Kuuluvainen, 1994). Later, Koukoulas and Blackburn (2004) defined gaps as “areas of low-level vegetation caused initially by single or multiple treefalls.” For the detection of canopy gaps, vertical and horizontal limits define what are gaps in the forest matrix (Kabasele, 1994). The vertical limit refers in general to the maximum vegetation height, and the horizontal limit is the minimum gap size (Hunter et al., 2015a).

Gaps help to preserve bio- and pedo-diversity, influence nutrient cycles, and maintain the complex structure of the late-successional forests (Muscolo et al., 2014). In addition to their importance for ecological processes, canopy gaps affect the energy and mass exchange between forests and the atmosphere (Seidel et al., 2012). Canopy gaps play an essential role in forest regeneration, turnover, and successional dynamics of the forest ecosystem (St-Onge, B. et al., 2014). Today, most "gap" oriented research in tropical forests is based on short-term dynamics (i.e., years to decades) using large-scale permanent plot studies (Condit R. 1995; Yamamoto, 1992), or on long-term dynamics (i.e., centuries to millennia) through palaeo-ecological studies (Bush and Colinvaux, 1994). Short- and long-term dynamics are generally associated with changes in forest composition and structure, which requires measurement of changes in such characteristics through time. Gap dynamics are important drivers associated with forest succession and regeneration (Quesada et al., 2009). The importance of gaps in forest ecology has been widely studied in tropical and temperate ecosystems (Asner et al., 2013; Biology, 2016; Chambers et al., 2009; Garbarino et al., 2012; Negrón-Juárez et al., 2011), while these are significant knowledge gaps in tropical dry forests.

Even though there is a significant body of literature showing the importance of gaps in tropical forest ecology (Schnitzer et al., 2000; Nagel et al., 2010); Whitmore, 2011; Negrón-Juárez et al., 2011; Asner et al., 2013; Hunter et al., 2015; Biology, 2016; Silva et al., 2019), most studies today have aimed at the quantification of forest gaps generated by selective logging in primary forests with little work or no work dealing with the quantification of gap density in secondary forests. Compared to field observations, which require extensive experience and time in a large study area, remote sensing offers an efficient and accurate alternative for automated gap identification (Yang et al., 2015). Despite the advantage that remote sensing provides for large gap identification, small gaps cannot be recorded using conventional aerial photography or satellite images. As such, new and cost-effective methodologies for forest gap assessment and monitoring are needed (Getzin et al., 2014). In this context, Light Detection and Ranging (LiDAR) has recently become one of the essential sources for analyzing canopy gap dynamics (Yang et al., 2015). The basic physical principle of LiDAR-radiation provides a close link between the concepts of a gap as an ecological feature, and that of a remotely sensed object (Koukoulas and Blackburn, 2004). LiDAR systems offer the opportunity to overcome many problems related to passive optical remote sensing of canopy gaps by providing high spatial resolution measurements of canopy heights without the effects of solar angle and the variation in spectral reflectance (Koukoulas and Blackburn, 2004). Moreover, small-footprint LiDAR allows also for a more precise estimation of canopy gaps related to tree loss at the canopy level (Dalagnol et al., 2019; Hunter et al., 2015).

Moreover, the development of Unmanned Aerial Vehicles (UAVs) as an alternative remote sensing platform offers advantages, including high resolution and low cost. UAVs carrying LiDAR payloads can be the future choice as a 3D data-capture platform for gap assessment and monitoring (Wallace et al., 2012). UAV LiDAR provides proxies of canopy gap fraction in the near-vertical direction (Heiskanen et al., 2015), allowing several gap metrics to be measured with higher accuracy because of the highly improved point cloud density from UAV LiDAR compared with traditional LiDAR systems (Wallace et al., 2012).Hence, the main objective of this chapter is to explore the use of high-resolution airborne-base LiDAR to quantify, characterize, and map canopy gaps of different successional stages in a secondary tropical dry forest. This paper addresses three main issues: (1) the characterization of different types of canopy gaps; (2) the evaluation of the number of gaps in the different successional stages for randomly selected plots; and (3) the estimation of gap size-frequency distributions for secondary tropical dry forests.

2.4 Materials and methods

2.4.1 Study area

The study was conducted at the Santa Rosa National Park Environmental Monitoring Super-Site (SRNP-EMSS: 10°48′53″N and 85°36′54″W), Guanacaste, Costa Rica (Figure 2.1). The SRNP-EMSS presents two well-defined seasons: from April to December, the rainy season, with heavy rainfall; and from the end of December to April the following year, the dry season, also known as summer. The topography of this area is relatively flat, with an average slope of 7%. The elevation ranges from 325 meters above sea level in the northwest to sea level in the southeast. The SRNP-EMSS is a secondary successional TDF, where more than half of the trees are drought-deciduous and semi-deciduous trees with heights between 5 to 15m (Hilje et al., 2015).

Since the creation of the SRNP-EMSS in 1971, the park evolved into a mosaic of diverse, segregated plant communities primarily consisting of pastures and secondary tropical dry forests in different stages of succession (Castillo-Núñez et al., 2011; Kalacska et al., 2004) being most of the plant species drought-deciduous (Calvo-Rodriguez et al., 2021). Currently, the forests in the park are classified into five age groups (0-10 years, 10-20 years, 20-30 years, 30-50 years, and 50+ years) (Sun et al., 2019; Zhao et al. 2021). For this study (Figure 2.2), we have classified these age classes into three successional stages: Early (0-20 years old), Intermediate (20-50 years old), and Late (50+ years old). The early successional forests at SRNP-EMSS are a mixture of woody vegetation, shrubs, and pastures with 100% deciduous species. The intermediate successional stage has fast-growing trees and lianas, of which up to 80% are deciduous. The late successional stage contains three layers of vegetation, with 50–90% of the canopy occupied by evergreen crowns (Castillo-Núñez et al., 2011; Kalacska et al., 2004). Although the study area contains all three types of successional stages, small patches of old-growth tropical dry forest in climax cannot be completely ruled out (Zhao et al., 2021).

2.4.2 Data

2.4.2.1 LiDAR data collection

The LiDAR data used in this study was collected using an Airborne LiDAR System (ALS) on May 21st, 2021. A helicopter (R44-II) was used in this flying mission. The flight was performed in a measurement campaign under a combined photogrammetric and LiDAR configuration. The parameters of the flights are detailed in Table 2.3.

The data collection used a LiteMapper IGI 680i System (sn.10-0104) that integrates into the same platform a LiDAR system (RIEGL LMS-Q680), a Photogrammetric camera (DigiCAM H5D-50), a Video Camera, and GPS INS. The equipment has an electronic device for the compensation of the drag of the image, and a microprocessor for the automatic control of the exposure. The characteristics of sensors are presented in Table 2.4.

2.4.2.2 Raw data processing

Along with the processing of the information related to the position and orientation of the sensor, leading to the calculation of the trajectory, the data was post-processed to obtain the required 3D point cloud, together with the additional information necessary for its subsequent treatment (filtering, classification, visualization, etc.). From the data processing, binary files are obtained in Laser Airborne Scanner format (*.las) and contain information regarding planimetric and altimetric coordinates of the LiDAR point cloud, as well as additional complementary information. From the control points, an altimetric difference model is established to adjust the LiDAR point cloud to the level dimensions using the Strip-Aligment software. The point cloud used a geodetic control to ensure that the LiDAR data was adjusted and grouped. Figure 2.5 shows the canopy height model (CHM) mosaic after normalization.

2.4.2.3 Datasets selection

For processing and analysis, a total of 60 1-ha study plots were randomly selected, 20 for each succession stage. After overlapping and combining the point cloud data, canopy height model, and succession stage map: 13 early-stage plots, 19 intermediate-stage plots, and 18 late-stage plots, for a total of 50 plots were finally used for the following analysis (Figure 2.1). At the same time, 50 path profiles of the cross-section for the forest were randomly selected using Global Mapper (Figure 2.1). This step provides intuitive images to look for different canopy gaps, including gaps buried in the space lower than the canopy (sub-canopy gaps).

2.4.3 Methods

In total, 50 hectares of ALS data crossing the study area were analyzed to define the different types of gaps. From this, all the point clouds were used to create the height distribution and the cross-section profiles. Then, the whole study area was used to analyze the gap-size frequency distribution by three different thresholds.

This study contains three specific goals: (1) Define the characteristics of different types of canopy gaps; (2) Evaluate the number of gaps in the different successional stages of the randomly selected plots; (3) Estimate the gap size frequency distribution for the whole study area. Two parts of data processing approvement were done independently to solve these questions. In the first part, I defined the depth of different types of gaps using the cross-section path profile. In the second part, I chose the height threshold according to the statistics of the canopy height of every plot. Then "ForestGapR", an open-source r package (Silva et al., 2019a), was used to detect canopy gaps. In the third part, the Gap-size frequency distribution was estimated.

2.4.3.1 Cross-section profile

Since a gap is not just a horizontal area but a vertical space (Brokaw, 1982), here we follow St-Onge et al., (2014) definitions of vertical gaps (Figure 2.6). St-Onge et al., (2014) summarized all gaps along different types: “A”, “B”, “C1” and “C2”. This definition was complemented with the annotation of the canopy layer, sub-canopy layer, and understory layer for each plot. The result (gap level and annotation) was assigned to two layers to show the mean height range for the canopy and sub-canopy in different successional stages. The final cross-section can give a vertical structure of the forest; but also hidden gap areas, such as the sub-canopy gaps that cannot be observed from the top of the canopy (Connell et al., 1997). To account for these hidden gaps, 50 random cross-section profiles (100m by 5 m) were created across the three different successional stages (Figure 2.1).

2.4.3.2 "ForestGapR"

"ForestGapR," an open-source R package for forest gap analysis from CHMs derived from ALS and other remote sensing sources was used in this study (Silva et al., 2019a). “ForestGapR” was selected since it can automatically detect canopy gaps, define gap size-frequency distributions (Farrior et al., 2016; White et al., 2008), delineate gap dynamics, and convert forest canopy gaps into a raster or spatial vector formats (Silva et al., 2019a). There are three primary functions used to analyze the canopy gaps: "getForestGaps" (Asner et al., 2013; Stark et al., 2012); "GapStats" (Heiskanen et al., 2015; Hunter et al., 2015a); "GapSizeFDist" (Asner et al., 2013; Farrior et al., 2016; White et al., 2008).

2.4.3.3 Gap detection

The function "getForestGaps" was used to extract a raster layer after detecting the canopy gaps. Inputting the canopy height model as the raster layer can also be generated from other remote sensing sources besides the LiDAR point cloud I used in this research (Silva et al., 2019b). Then a binary raster layer object of gap areas is output.

To obtain the gap height threshold for each succession stage, the point cloud data and the gap height threshold to be used using the height value of the highest density were visualized. Meanwhile, in addition to obtaining the visual image of the gap area, the function "GapStats" was used to sort out the detailed parameters of the gap area. Parameters include the number of gaps, gap area, gap canopy height range, and the standard deviation of the gap height. It is not easy to obtain the appropriate gap height threshold for different succession stages, as the height range variation of trees is large even at the same stage. Therefore, I divided the statistic height of the trees in each succession stage according to the threshold of two meters apart. To better assess the number of gaps in each succession stage, the threshold with the largest number of gaps was determined as the height threshold for each succession stage. Following the statistics of the gap quantity in Figure 2.7, 6m, 12m, and 16m, were used as the height threshold in three successional stages separately. The same minimum size threshold (5m^2) and the same maximum size threshold (which was used in the original code) in the function "getForestGaps" were used.

2.4.3.4 Gap-size Frequency Analysis

Because LiDAR-based analyses yield gap data at all heights above ground, this paper used 50 plots (Figure 2.1) to seek ways of reducing the data volume to a few meaningful thresholds at which to report gap size-frequency results. Through the analyses to be presented in the results section, three gap thresholds were found, ≤6m, ≤12 m, and ≤16 m. These thresholds are sufficient to represent the overall pattern of static gaps. Gaps associated with the ≤6 m threshold can be thought of as the gap shown in the lower trees in the early stage; the ≤12m threshold can be suitable for gap detection of trees in the intermediate stage; those with the ≤16 m threshold can be considered as the gap created in the top trees in the late stage. The 6m, 12m, and 16m thresholds were applied to the whole study area throughout the LiDAR cloud point, facilitating comparisons of gap-size frequency at different stage scales. Also, according to Hunter et al. (2015), a height threshold of 10 m and a minimum area of 5 m^2 were used to provide the results.

2.5 Results

2.5.1 Canopy height distribution

To better follow the classical interpretation of gaps, the return points below two meters were ignored. Throughout the data, in selected plots crossing the three successional stages, the canopy height of the early, intermediate, and late stages is very distinct (Figure 2.8). The median heights of the return points are around 6m, 9.5m, and 14m for the early, intermediate, and late stages respectively. The variation of the heights is so considerable even in the same stage. Then we use Figure 2.8 to show the canopy height distribution of three different successional stages by box plots and use Figure 2.9 to show by density line plots.

More specifically, in the early stage, the canopy height ranged from the minimum of 5.6m to the highest of 15m, and the average of most trees at this age is 10.25m. The range of canopy height is 12m to 20m in the intermediate stage, with 16.6m on average. In the late stage, the range of canopy height is from 15m to 40m, and the average is 24m. Table 2.10 show a similar height scale and trends for each successional stage with the results compared with Kalacska et al. (2007) (7.5±2.2m in early, 10.3±3.4m in intermediate, 15.0±2.2m in late). Moreover, the random cross-sections for each stage present similar results.

2.5.2 Gap type definition

According to the cross-section analysis, three kinds of gaps (B, A, and C2) were found in the 50 sampling sites. Based on the definition of different types of gaps from (St-Onge et al., 2014) and visual observation of the cross-section results, typically, the "B" gap is well resolved as it presents a closed irregular area in the canopy or sub-canopy layer, maybe cross these two layers. For the other two kinds of gaps, "A" and "C2", the difference between them is that: "A" gaps show up only in the top canopy layer, and the depth of these gaps would not be larger than the thickness of the canopy, but "C2" gap will be more profound and more extensive than "A" and will go down and run through the crown and sub-canopy layer.

A collection of the parameters for each kind of gap in different successional stages is shown in Table 2.11. In the early stage, only "A" gaps can be found. The main reason is that the trees in the early stages are not fully developed. They are generally at a low height level and do not have a well-developed canopy. This means smaller and denser gaps (such as type "A") will appear more in this stage. In the intermediate and late-stage forests, all three types of gaps ("A", "B", and "C2") appeared. From the comparison, more "A" gaps appear in the intermediate stage than in the late, but fewer "B" and "C2" (especially type "C2") show up in this.

From the randomly selected cross-section profiles, the canopy of the early-stage forest showed a more stable shape, which has little height change, and proves, on the other hand, only "A" type gaps appeared in this stage, and the gap depth is less variable. The intermediate stage will be more complex, with apparent changes in canopy height, so the other two types of gaps will appear. High trees with a large canopy can be easily found in later stages, often with larger, deeper, and more "C2" gaps next to them. The "B" gap also appears more at this stage because the later-stage trees are high, and the area under the canopy is enough to allow more trees to grow.

According to the depth statistics of the three types of gaps in each successional stage, in the early stage, the range of "A" gap is around 3.5m(±2.5m); in the intermediate stage, the range of "A" gap is around 5.0m(±3.5m), the range of "B" gap is around 4.0m(±3.0m), the range of "C2" gap is around 9.0m(±3.5m); in the late stage, the range of "A" gap is around 6.0(±4.0) m, the range of "B" gap is around 6.0(±4.0) m, the range of "C2" gap is around 17.0(±10.5) m (Table 2.11). These results show that the gap depth increases with early to late changes, and although there is a numeric overlap, this is because a highly variable canopy height still appears during the same stage.

2.5.3 Gap-size frequency distribution

As the canopy height (6m, 12m, and 16m) best represents the three successional stages, they were used to detect the canopy gaps throughout the study area to solve goals (2) and (3) (Figure 2.13). 16,948 gaps with vegetation ≤6m in canopy height across the study area were mapped; the λ-value for those gaps is 1.762. When using the height threshold ≤12m, there were 9,490 gaps mapped, and the λ-value is 1.624. Only 1,103 gaps were detected when the height threshold ≤16m and the λ-value is 1.785 (Figure 2.14).

2.6 Discussion

Tropical dry forests are one of the global biodiversity hotspots, with unique vertical and horizontal structures and playing an important role in maintaining biodiversity and ecosystem services. The vertical structure includes different levels of trees, shrubs, and herbs, while the horizontal structure includes rivers, rocks, forest crowns, and open space. These structures provide different habitats and environmental conditions that support the survival and reproduction of different species and communities. At present, an increasing number of studies show that both vertical and horizontal gaps have very important effects on the species diversity and ecosystem function of terrestrial ecosystems (Jones et al., 2018; Lao et al., 2021). In tropical dry forests, vertical and horizontal gaps have important effects on community composition and species distribution, and large gaps can support higher species diversity but may also confer higher ecological risk.

2.6.1 Vertical gaps

Vertical gap is the space between the canopy and is an important part of the vertical structures of tropical arid forests. The size of the vertical gap is determined by factors such as tree height and crown length, which affects the distribution, competition, and growth of plants, and then affects the food source, habitat and movement of animals.

The results show that vertical gaps are evenly distributed in tropical arid forests, from Columbina talpacoti to Nasua narica can find their habitat in vertical gaps. The presence of different-sized vertical gaps contributes to the overall diversity of the ecosystem. Larger vertical gaps, typically exceeding 30 meters in diameter, are associated with greater species richness, higher species diversity, and enhanced ecosystem functioning. These larger gaps create more varied microhabitats, allowing for the coexistence of a wider array of plant and animal species.

However, it is important to recognize that large vertical gaps also introduce potential ecological risks. One notable risk is the heightened susceptibility to the spread of wildfires. The open and exposed structure of these gaps facilitates the ingress of fire, posing a significant threat to the surrounding vegetation and overall ecosystem stability. Therefore, while acknowledging the ecological benefits offered by large vertical gaps, their presence must be considered within the context of comprehensive fire management strategies and prevention measures. By integrating effective fire control practices, we can mitigate the potential hazards associated with these gaps while still harnessing their ecological advantages.

In summary, the distribution and characteristics of vertical gaps in tropical arid forests play a critical role in shaping the biodiversity, species interactions, and overall functioning of the ecosystem. Understanding the intricate dynamics of these gaps provides valuable insights for ecosystem management, emphasizing the importance of balancing conservation efforts with appropriate fire management strategies to ensure the long-term sustainability and resilience of these unique forest environments.

2.6.2 Horizontal gaps

Horizontal gap is the concept of understory clearing in tropical arid forests. The size of the horizontal gap depends on the number and morphology of stones, rocks, ruins, and bare ground. Some studies have shown that the formation of horizontal gaps can be triggered either by natural processes such as wind blowing, water flow and fire, or by human activities such as logging, agriculture and road construction (Tokola et al., 2011).

We provide valuable insights into the distribution and ecological implications of horizontal gaps in tropical arid forests. Small horizontal gaps are often observed, but their suitability for supporting various species may be limited due to specific habitat requirements. In contrast, larger horizontal gaps, exceeding 20 meters in diameter, have been found to play a crucial role in promoting species diversity and community stability.

However, we need to note that excessive fragmentation and disturbance of the forest structure can disrupt important ecological processes, result in habitat loss, and even alter resource availability.

In conclusion, research in this part has shed light on their distribution, formation processes, and ecological implications. By implementing appropriate strategies to maintain a suitable balance of horizontal gaps, we can promote the resilience and sustainability of tropical arid forest ecosystems.

2.6.3 Significance of canopy gaps for tropical ecology

There is no doubt that canopy gaps, which are openings in the forest canopy caused by tree falls, mortality, play a crucial role in shaping tropical ecosystems. These gaps have significant ecological significance and influence various aspects of tropical ecology, including species composition, diversity, regeneration dynamics, and nutrient cycling.

One key aspect of canopy gaps is their influence on light availability within the forest understory. When a gap forms, it allows direct sunlight to reach the forest floor, creating a unique microenvironment with increased light intensity. This change in light conditions has profound effects on plant growth and regeneration strategies. Shade-intolerant species seize this opportunity to establish and grow rapidly, while shade-tolerant species may persist in the shaded areas surrounding the gap.

The formation of canopy gaps also promotes habitat heterogeneity within the forest. Gaps create distinct microhabitats with different temperature, moisture, and nutrient levels compared to the surrounding closed canopy. These variations provide opportunities for specialized plant species and facilitate the coexistence of a diverse array of organisms, including understory plants, insects, birds, and small mammals. Canopy gaps act as important ecological "hotspots" within the forest, harboring unique assemblages of species and supporting higher levels of biodiversity.

Furthermore, canopy gaps play a crucial role in the dynamics of forest ecosystems. They serve as critical points for ecological processes such as nutrient cycling, carbon sequestration, and water infiltration. The increased light availability in gaps stimulates photosynthesis and boosts primary productivity, contributing to overall ecosystem productivity.

2.6.4 Trans-successional stages

Information about the function of ecosystem services as a secondary TDFs succession stage is scarce and limited. Secondary TDFs succession was defined as regeneration after cattle growth or complete forest clearance by agricultural activities (Li et al., 2017). From a purely ecological perspective, forest vertical and horizontal structure, Leaf Area Index (LAI), Active Photosynthetic Radiation (PAR), seasonality, and species composition drive differences between the stages of different secondary TDFs. These differences allow us to divide TDFs along an ecological gradient to detect early, intermediate, or old-growth succession (Arroyo-Mora et al., 2005; Kalacska et al., 2004; Li et al., 2017).

In 2017, Li et al. (2017) used a Multi-Task Learning based Machine Learning Classifier (MLC-MTL) to divide the intermediate TDFs into three classes: early-intermediate (10–20 years old), intermediate–intermediate (20–40 years old), and intermediate-late (> 40 years old). Even if detecting tropical secondary forests has always followed deterministic methods that define sharp boundaries between succession stages, these methods cannot adequately represent the continuous process of TDF evolution from early succession to middle to late succession stages. Such sharp boundaries are absent in virtual nature environments (Li et al., 2017). Therefore, when defining the secondary succession stage, there is always a certain degree of variation and differences (Cao et al., 2015; Zhao et al., 2021). During the dynamic succession process, there would be a transition period that is easily overlooked, shifting between different periods: from early to intermediate (early-inter), and from intermediate to late (inter-late) (Li et al., 2017).

The newest paper by Duan et al. (2023) proved the existence of trans-successional stages (transition): at the SRNP-EMSS. Duan et al (2023) concluded that a transition II (from intermediate to late successions) dominates the entire study area. This conclusion is consistent with the increase of species richness and canopy openness in the intermediate stage and the late stage and confirms the results on the size and number of canopy gaps.

At the SRNP-EMSS TDF ecosystem, the size-frequency distribution of canopy gaps is mainly unchanged despite the forest across three successional stages, and the canopy heights are primarily variable. The λ-value is around 1.7(±0.08), meaning the noticeable gaps are described as large. Despite these differences in λ, the vertical distribution of λ-values in the forest canopies was similarly shaped across forest successional stages (Figure 2.13). This range is similar to Asner et al. (2013) in the Peruvian Amazon, although slightly less than their mean calculated λ value of 1.83.

Also, to better compare, a gap detection with a height threshold of 10m applied to the data was consistent with the dynamic gap definition for tropical forests from Hunter et al. (2015b) and Silva et al. (2019a). They use the 10m height threshold to detect the gap dynamics separately in tropical moist forests and the TDF. Silva et al. (2019a) showed that the λ-value varied from a low of 1.515 for La Selva (Costa Rica) to a high of 1.654 for Adolfo Duken (Brazil). Results (Figure 2.14) show that, at the SRNP-EMSS, the λ-value is 1.609, which is smaller than all results using other thresholds (6m, 12m, 16m), but still in the range of the above values. 10m is the average canopy height in the intermediate stage. The λ-value is smaller because, during the ecological transition from early stage to late stage, the intermediate TDF at the SRNP-EMSS has the highest species diversity and more considerable variability in canopy openness (Kalácska et al., 2004; Li et al., 2017).

Even with different gap frequency distribution sizes at different geographical locations, and different height thresholds, this striking similarity of the gap size frequency distribution suggests convergence in the structural response to canopy disruption, independent of regional and landscape-scale changes in soil fertility, hydrological conditions, and many other factors (Asner et al., 2013).

Several factors can increase the error during the whole study process. Some are associated with the instrument used, and the instrument itself has some unavoidable error values; some are very variable and cannot be controlled such as the weather condition. Finally, like most LiDAR-based studies, this study imaged static gaps in the canopy. A static gap is an opening in a forest canopy at a given time (Asner et al., 2013). We cannot document the exact time when the gaps at the SRNP-EMSS were formed, although it will not change too much over a long time, and thus static the time and the disturbance intensity (i.e., square meters of canopy loss (Asner et al., 2013)).

2.7 Conclusion

This study aimed to use of LiDAR for canopy gap delineation for a structurally complex forest, and it proves that the use of airborne LiDAR data is efficient in exploring gap distribution.

This study contains three highlights. First, this study fills the research gap in canopy gap studies in the Tropical Dry Forests, most of the experience of canopy gaps are taking in tropical rain/moist forests. Second, this study defines the detail of different types of canopy gaps and gives the scale of the depth for three types of canopy gaps (A, B, and C2) showed up in SR-EMSS. Third, this study gives the λ-value for the gap size-frequency distribution which can express the trend of gap size across the whole forest.

2.8 Reference

Arroyo-Mora, J.P., Sánchez-Azofeifa, G.A., Kalacska, M.E.R., Rivard, B., Calvo-Alvarado, J.C., Janzen, D.H., 2005. Secondary forest detection in a neotropical dry forest landscape using Landsat 7 ETM+ and IKONOS imagery. Biotropica 37, 497–507. https://doi.org/10.1111/j.1744-7429.2005.00068.x

Asner, G.P., Kellner, J.R., Kennedy-Bowdoin, T., Knapp, D.E., Anderson, C., Martin, R.E., 2013. Forest Canopy Gap Distributions in the Southern Peruvian Amazon. PLoS One 8. https://doi.org/10.1371/journal.pone.0060875

Biology, T., 2016. Gap Partitioning among Tropical Rainforest Trees Author (s): Julie Sloan Denslow Source : Biotropica, Vol . 12, No. 2, Supplement : Tropical Succession (Jun ., 1980), pp . 47-55 Published by : Association for Tropical Biology and Conservation Stab 12, 47–55.

Brokaw, N.V.L., 1982. The Definition of Treefall Gap and Its Effect on Measures of Forest Dynamics. Biotropica 14, 158. https://doi.org/10.2307/2387750

Brown, J. C. (1993). A review of techniques for deriving fractional vegetation cover from NDVI. Remote Sensing Reviews, 7(3-4), 283-291.

Brokaw, N. V., & Busing, R. T. (2000). Niche versus chance and tree diversity in forest gaps. Trends in Ecology & Evolution, 15(5), 183-188.

Canham, C. D., et al. (1990). Neighborhood models of plant population dynamics: 2. Ecological consequences of variation in seed production and distribution. Canadian Journal of Forest Research, 20(7), 1216-1223.

Gray, A. N., et al. (2002). Effects of fire intensity on stand structure, composition, and nutrient cycling in a heterogeneous landscape. Canadian Journal of Forest Research, 32(11), 1905-1914.

Calvo-Rodriguez, S., Sánchez-Azofeifa, G.A., Durán, S.M., Espírito-Santo, M.M. Do, Nunes, Y.R.F., 2021. Dynamics of carbon accumulation in tropical dry forests under climate change extremes. Forests 12, 1–15. https://doi.org/10.3390/f12010106

Cao, S., Yu, Q., Sanchez-Azofeifa, A., Feng, J., Rivard, B., Gu, Z., 2015. Mapping tropical dry forest succession using multiple criteria spectral mixture analysis. ISPRS J. Photogramm. Remote Sens. 109, 17–29. https://doi.org/10.1016/j.isprsjprs.2015.08.009

Castillo-Núñez, M., Sánchez-Azofeifa, G.A., Croitoru, A., Rivard, B., Calvo-Alvarado, J., Dubayah, R.O., 2011. Delineation of secondary succession mechanisms for tropical dry forests using LiDAR. Remote Sens. Environ. 115, 2217–2231. https://doi.org/10.1016/j.rse.2011.04.020

Connell, J.H., Lowman, M.D., Noble, I.R., 1997. Subcanopy gaps in temperate and tropical forests. Austral Ecol. 22, 163–168. https://doi.org/10.1111/j.1442-9993.1997.tb00655.x

Duan, M., Bax, C., Laakso, K., Sanchez-azofeifa, A., Mashhadi, N., Mattie, N., 2023. Characterizing Transitions between Successional Stages in a Tropical Dry Forest Using LiDAR Techniques.

Farrior, C.E., Bohlman, S.A., Hubbell, S., Pacala, S.W., 2016. The dominance of the suppressed: Power-law size structure in tropical forests. Science (80-.). 351, 155–157. https://doi.org/10.1126/science.aad0592

Fox, T. R., et al. (2000). Tree species diversity in southern forests: An evaluation of the potential for high-value hardwood silviculture. In Proceedings of the Southern Forest Economics Workshop.

Garbarino, M., Mondino, E.B., Lingua, E., Nagel, T.A., Dukić, V., Govedar, Z., Motta, R., 2012. Gap disturbances and regeneration patterns in a Bosnian old-growth forest: A multispectral remote sensing and ground-based approach. Ann. For. Sci. 69, 617–625. https://doi.org/10.1007/s13595-011-0177-9

Getzin, S., Nuske, R.S., Wiegand, K., 2014. Using unmanned aerial vehicles (UAV) to quantify spatial gap patterns in forests. Remote Sens. 6, 6988–7004. https://doi.org/10.3390/rs6086988

Heiskanen, J., Korhonen, L., Hietanen, J., Pellikka, P.K.E., 2015. Use of airborne LiDAR for estimating canopy gap fraction and leaf area index of tropical montane forests. Int. J. Remote Sens. 36, 2569–2583. https://doi.org/10.1080/01431161.2015.1041177

Harcombe, P. A., et al. (2002). The influence of canopy open area on ground floor seed bank dynamics in a moist tropical forest. Plant Ecology, 160(1), 11-29.

Hilje, B., Calvo-Alvarado, J., Jiménez-Rodríguez, C., Sánchez-Azofeifa, A., 2015a. Tree species composition, breeding systems, and pollination and dispersal syndromes in three forest successional stages in a tropical dry forest in Mesoamerica. Trop. Conserv. Sci. 8, 76–94. https://doi.org/10.1177/194008291500800109

Hoekstra, J. M., et al. (2005). The Global Distribution of Biodiversity: An Indicator of Earth's Health. Frontiers in Ecology and the Environment, 3(9), 328-334.

Hunter, M.O., Keller, M., Morton, D., Cook, B., Lefsky, M., Ducey, M., Saleska, S., De Oliveira, R.C., Schietti, J., Zang, R., 2015a. Structural dynamics of tropical moist forest gaps. PLoS One 10, 1–19. https://doi.org/10.1371/journal.pone.0132144

Herwitz, S. R., et al. (2000). Object-oriented mapping and analysis of forest landscape structure and change in New England, USA. Remote Sensing of Environment, 74(1), 84-99.

Kalacska, M., Sanchez-Azofeifa, G.A., Calvo-Alvarado, J.C., Quesada, M., Rivard, B., Janzen, D.H., 2004. Species composition, similarity, and diversity in three successional stages of a seasonally dry tropical forest. For. Ecol. Manage. 200, 227–247. https://doi.org/10.1016/j.foreco.2004.07.001

Kaya, E., Agca, M., Adiguzel, F., Cetin, M., 2019. Spatial data analysis with R programming for the environment. Hum. Ecol. Risk Assess. 25, 1521–1530. https://doi.org/10.1080/10807039.2018.1470896

Kimmins, J. P. (2004). Forest ecology: a foundation for sustainable management. Prentice Hall.

Kern, C. C., et al. (2013). Long-term herbaceous vegetation dynamics in response to annual and biennial prescribed fire and mechanical mastication in a California oak woodland. Forest Ecology and Management, 289, 38-47.

Koukoulas, S., Blackburn, G.A., 2004. Quantifying the spatial properties of forest canopy gaps using LiDAR imagery and GIS. Int. J. Remote Sens. 25, 3049–3072. https://doi.org/10.1080/01431160310001657786

Kwit, C., & Platt, W. J. (2003). Gap ecology in a flood-scoured forest: tree life-history trade-offs and habitat associations. Ecology, 84(7), 1762-1772.

Li, W., Cao, S., Campos-Vargas, C., Sanchez-Azofeifa, A., 2017. Identifying tropical dry forests extent and succession via the use of machine learning techniques. Int. J. Appl. Earth Obs. Geoinf. 63, 196–205. https://doi.org/10.1016/j.jag.2017.08.003

Lertzman, K., & Krebs, C. J. (1991). Gap dynamics and old-growth forest.

Lima, R. A., et al. (2008). Gap disturbance regime in a montane forest in Brazil: effects on seedling dynamics of two shade-tolerant species. Revista Brasileira de Botânica, 31(4), 605-613.

Meyer, G. A., et al. (2000). Spatial patterns of treeline advance and their relation to climatic and disturbance factors in the American West. In Tree line dynamics (pp. 193-212). Springer Netherlands.

Olson, D. M., et al. (2001). Terrestrial Ecoregions of the World: A New Map of Life on Earth. BioScience, 51(11), 933-938.

Nagel, T.A., Svoboda, M., Rugani, T., Diaci, J., 2010. Gap regeneration and replacement patterns in an old-growth Fagus-Abies forest of Bosnia-Herzegovina. Plant Ecol. 208, 307–318. https://doi.org/10.1007/s11258-009-9707-z

Negrón-Juárez, R.I., Chambers, J.Q., Marra, D.M., Ribeiro, G.H.P.M., Rifai, S.W., Higuchi, N., Roberts, D., 2011. Detection of subpixel treefall gaps with Landsat imagery in Central Amazon forests. Remote Sens. Environ. 115, 3322–3328. https://doi.org/10.1016/j.rse.2011.07.015

Sanchez-Azofeifa, G. A., & Hesketh, J. D. (2013). Deforestation in Costa Rica: A Quantitative Analysis Using Remote Sensing Imagery. Biotropica, 35(1), 74-78.

Sapkota, I. P., et al. (2009). Gap dynamics under the influence of cyclonic disturbances in subtropical wet hill forests of Sikkim Himalaya, India. Forest Ecology and Management, 258(10), 2272-2278.

Schnitzer, S.A., Dalling, J.W., Carson, W.P., 2000. The impact of lianas on tree regeneration in tropical forest canopy gaps: Evidence for an alternative pathway of gap-phase regeneration. J. Ecol. 88, 655–666. https://doi.org/10.1046/j.1365-2745.2000.00489.x

Silva, C.A., Valbuena, R., Pinagé, E.R., Mohan, M., de Almeida, D.R.A., North Broadbent, E., Jaafar, W.S.W.M., de Almeida Papa, D., Cardil, A., Klauberg, C., 2019a. ForestGapR: An r Package for forest gap analysis from canopy height models. Methods Ecol. Evol. 10, 1347–1356. https://doi.org/10.1111/2041-210X.13211

St-Onge, B., Vepakomma, U., Sénécal, J.-F., Kneeshaw, D., Doyon, F., 2014. Canopy Gap Detection and Analysis with Airborne Laser Scanning 419–437. https://doi.org/10.1007/978-94-017-8663-8_21

Stark, S.C., Leitold, V., Wu, J.L., Hunter, M.O., de Castilho, C. V., Costa, F.R.C., Mcmahon, S.M., Parker, G.G., Shimabukuro, M.T., Lefsky, M.A., Keller, M., Alves, L.F., Schietti, J., Shimabukuro, Y.E., Brandão, D.O., Woodcock, T.K., Higuchi, N., de Camargo, P.B., de Oliveira, R.C., Saleska, S.R., 2012. Amazon forest carbon dynamics predicted by profiles of canopy leaf area and light environment. Ecol. Lett. 15, 1406–1414. https://doi.org/10.1111/j.1461-0248.2012.01864.x

Sun, C., Cao, S., Sanchez-Azofeifa, G.A., 2019. Mapping tropical dry forest age using airborne waveform LiDAR and hyperspectral metrics. Int. J. Appl. Earth Obs. Geoinf. 83, 101908. https://doi.org/10.1016/j.jag.2019.101908

Runkle, J. R. (1982). Patterns of disturbance in some old-growth mesic forests of eastern North

America. Ecology, 63(5), 1533-1546.

Rugani, B., et al. (2013). Gap characteristics and regeneration status of two beech forest reserves in southern Slovenia. Acta Silvae et Ligni, 100, 41-52.

Van der Maarel, E. (1988). Ecological classification and ranking of dune slacks in the Netherlands. Vegetatio, 76(1-2), 43-53.

Wallace, L., Lucieer, A., Watson, C., Turner, D., 2012. Development of a UAV-LiDAR system with application to forest inventory. Remote Sens. 4, 1519–1543. https://doi.org/10.3390/rs4061519

Wang, G. G., & Liu, H. (2011). Gap dynamics and species replacement in a temperate deciduous forest. Forest Ecology and Management, 261(3), 447-453.

White, E.P., Enquist, B.J., Green, J.L., 2008. On estimating the exponent of power-law frequency distributions. Ecology. https://doi.org/10.1890/07-1288.1

Whitmore, T.C., 2011. Canopy Gaps and the Two Major Groups of Forest Trees Author (s): T . C. Whitmore Published by : Ecological Society of America Stable URL : http://www.jstor.org/stable/1940195. CANOPY GAPS AND THE TWO MAJOR GROUPS OF FOREST TREES. America (NY). 70, 536–538.

Yamamoto, S.I., 1992. The gap theory in forest dynamics. Bot. Mag. Tokyo 105, 375–383. https://doi.org/10.1007/BF02489426

Yang, J., Jones, T., Caspersen, J., He, Y., 2015. Object-based canopy gap segmentation and classification: Quantifying the pros and cons of integrating optical and LiDAR data. Remote Sens. 7, 15917–15932. https://doi.org/10.3390/rs71215811

Yavitt, J.B., Battles, J.J., Lang, G.E., Knight, D.H., 1995. The canopy gap regime in a secondary neotropical forest in Panama. J. Trop. Ecol. 11, 391–402. https://doi.org/10.1017/S0266467400008853

Zhao, G., Sanchez-Azofeifa, A., Laakso, K., Sun, C., Fei, L., 2021. Hyperspectral and full waveform LiDAR improve mapping of tropical dry forest's successional stages. Remote Sens. 13. https://doi.org/10.3390/rs13193830

2.9 Figures and Tables

Figure 2.1. (a) The study area at the Santa Rosa National Park Environmental Monitoring Super Site (SRNP-EMSS), Guanacaste, Costa Rica; (b) The flight trajectory of this study using R44-II Helicopter; (c) 50 study plots randomly selected across three secessional stages and the canopy height distribution of the SRNP-EMSS, and (d) 50 cross-sections in total selected from each plot.

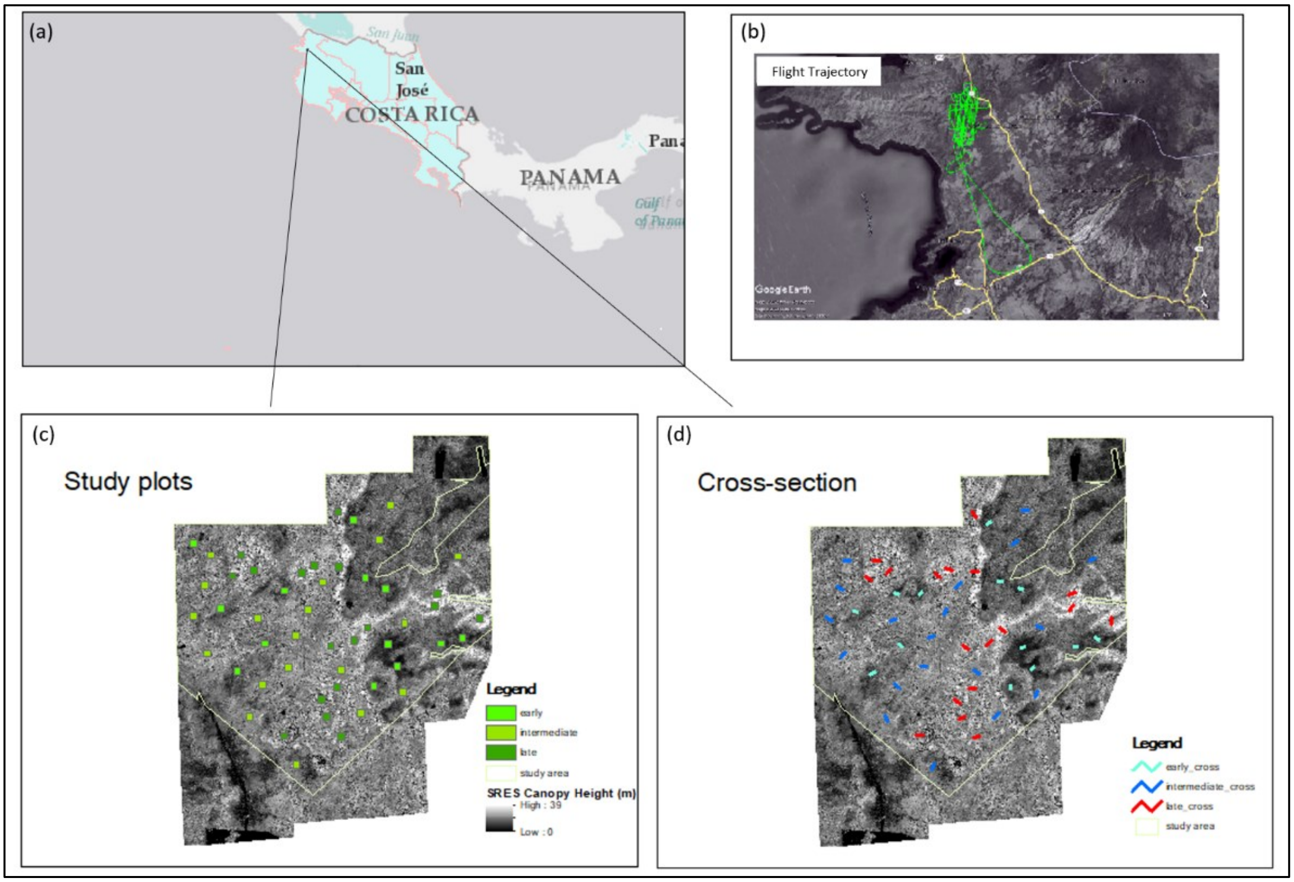


Figure 2.2. The original successional stage distribution map from (Zhao et al., 2021) generated with LVIS and HyMap data. Re-distributed by three successional stages: early (0-20years); intermediate (20-50); late (50+ years).

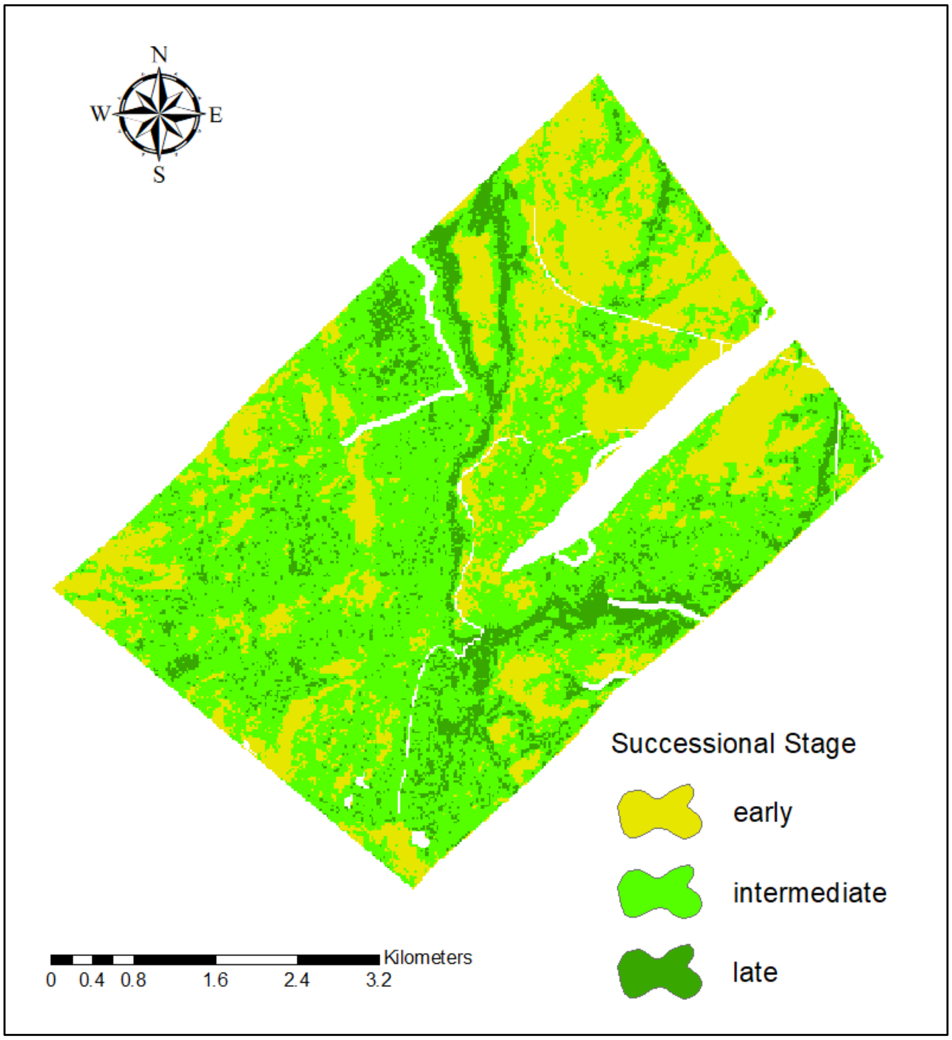


Table 2.3. Technical specifications of the flight parameters and sensors of the study. Data were acquired in the SRNP-EMSS on 21 May 2021. Abbreviations: GSD = ground sampling distance, FOV = field of view.

	Parameters	**Data**
R44-II Helicopter	Average flight height (H)	500m
	Flight speed	85 knots
	Number of passes	15
	Flying distance	288 km
DigiCAM Camera	GSD	6.0 cm
	Width of stripes	488m
	FOV	60°
	Longitudinal overlaps	60%
	Transverse overlaps	50%
LiDAR Riegl LMS-Q680i	Average density	11 points/m^2 average

Table 2.4. Technical specification of the feature information of the sensors.

SENSOR	**FEATURES**
CAMARA DIGICAM HSD-50	• 50 megapixels • FOV: 60º • 3-band RGB spectral resolution • Geometric resolution: 6 microns • Capture frequency: 1/125 seconds
LIDAR RIEGL LMS Q680	• FOV: 60º • Pulse rate: 200Hz • Maximum scanning frequency: 400Hz • Working height: 200 – 2000 meters

Figure 2.5. Canopy height model of the whole Santa Rosa National Park Environmental Monitoring Super Site (SRNP-EMSS).

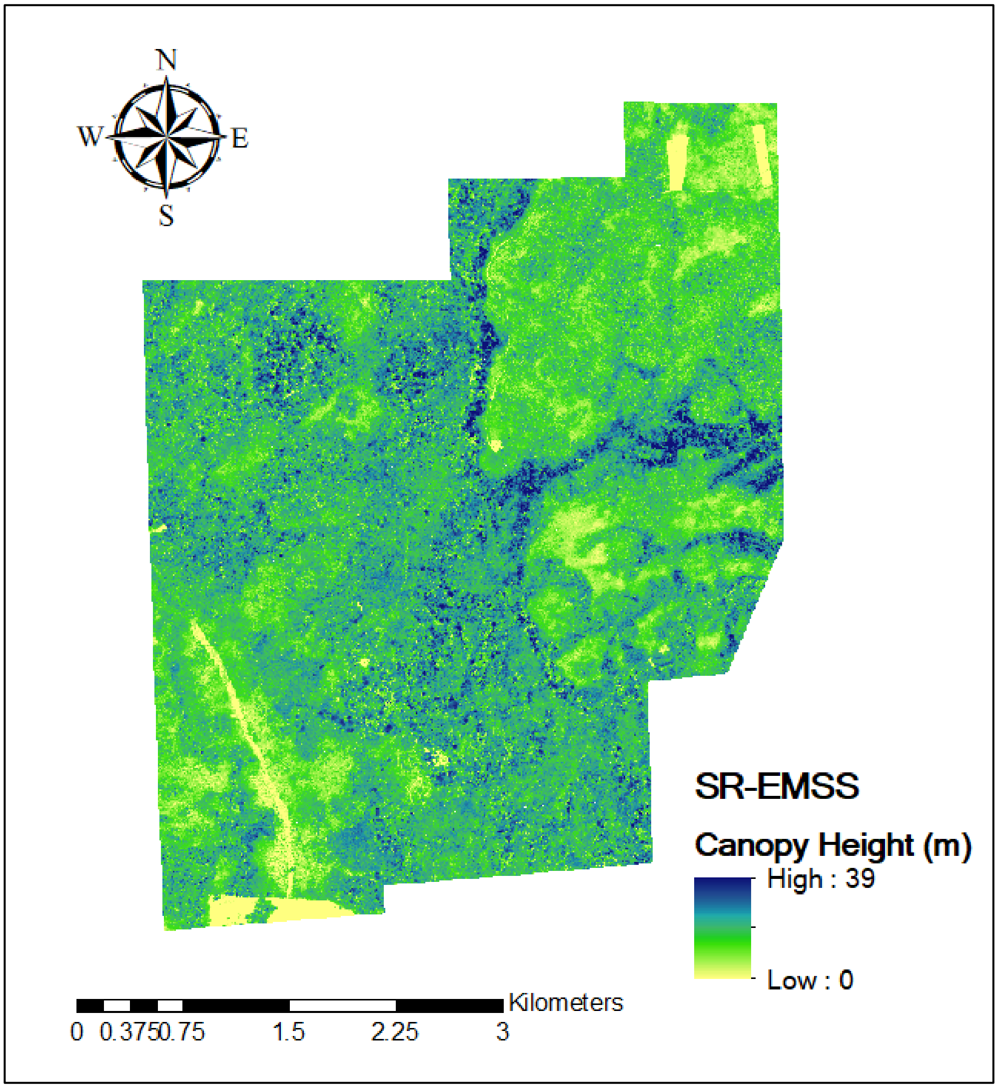


Figure 2.6. The definitions of vertical gaps from St-Onge et al., (2014), summarized all gaps along different types: “A”, “B”, “C1” and “C2”

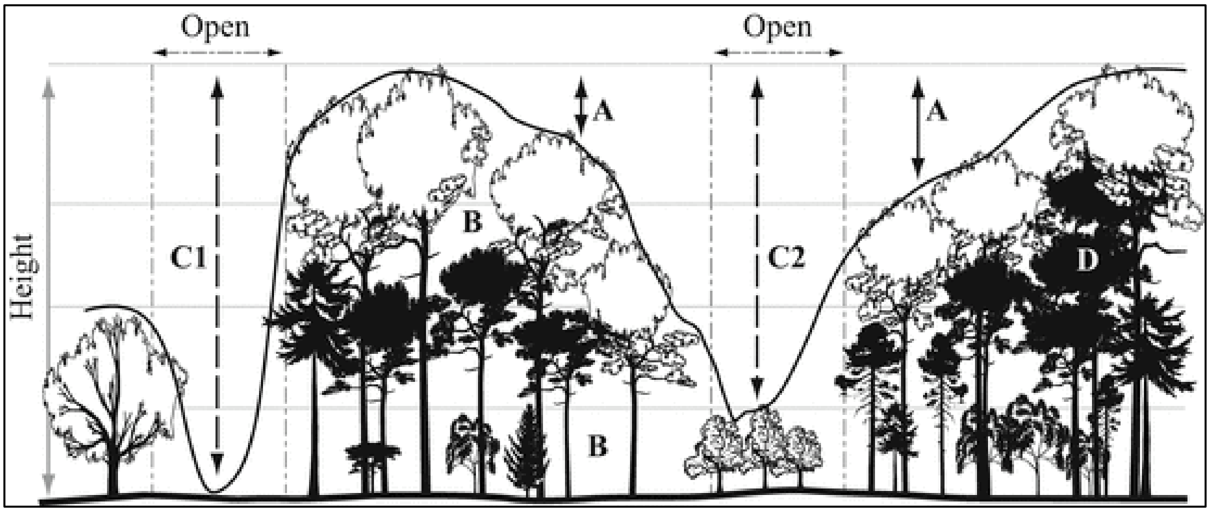


Figure 2.7. The canopy height distribution of three different successional stages by gap quantity line plots.

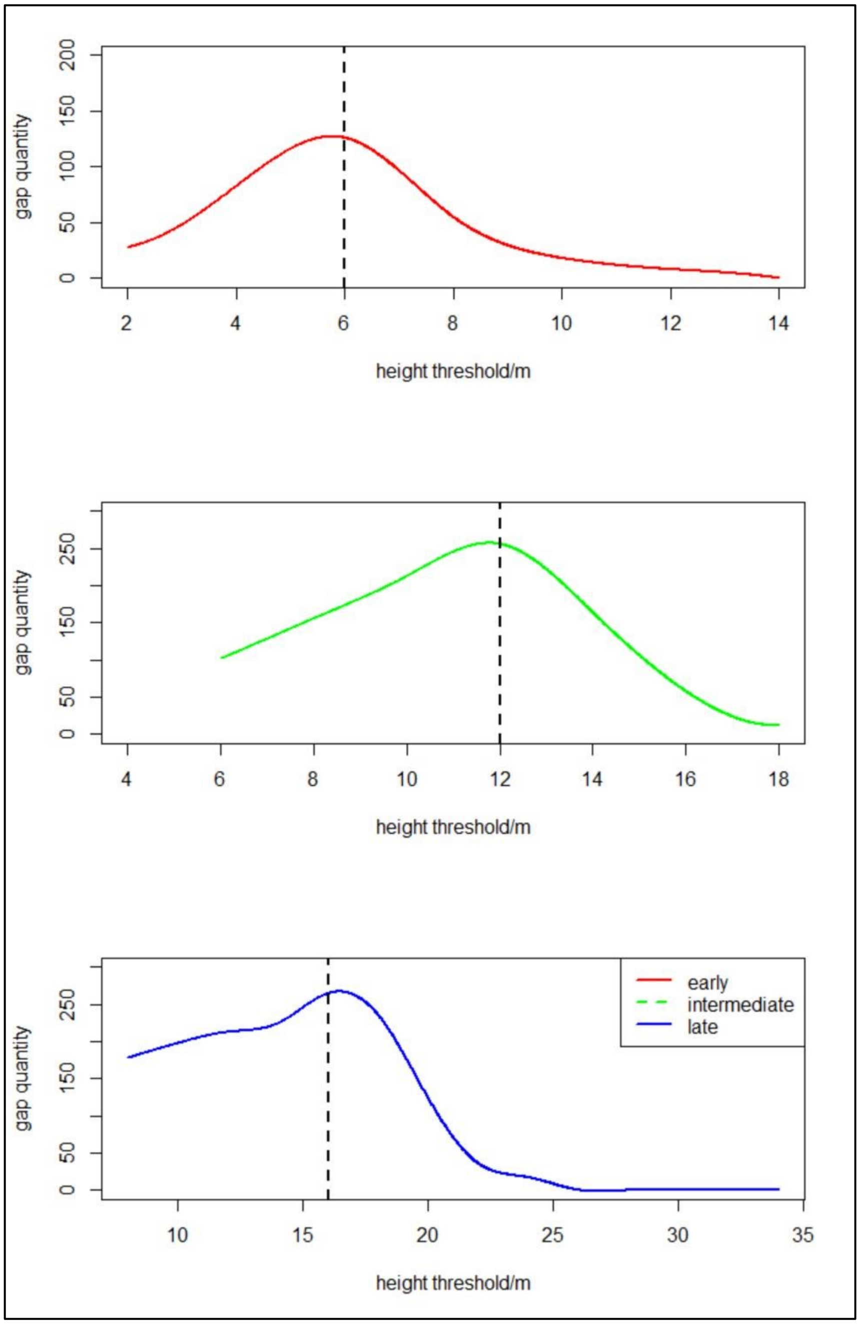


Figure 2.8. The canopy height distribution of three different successional stages by box plots

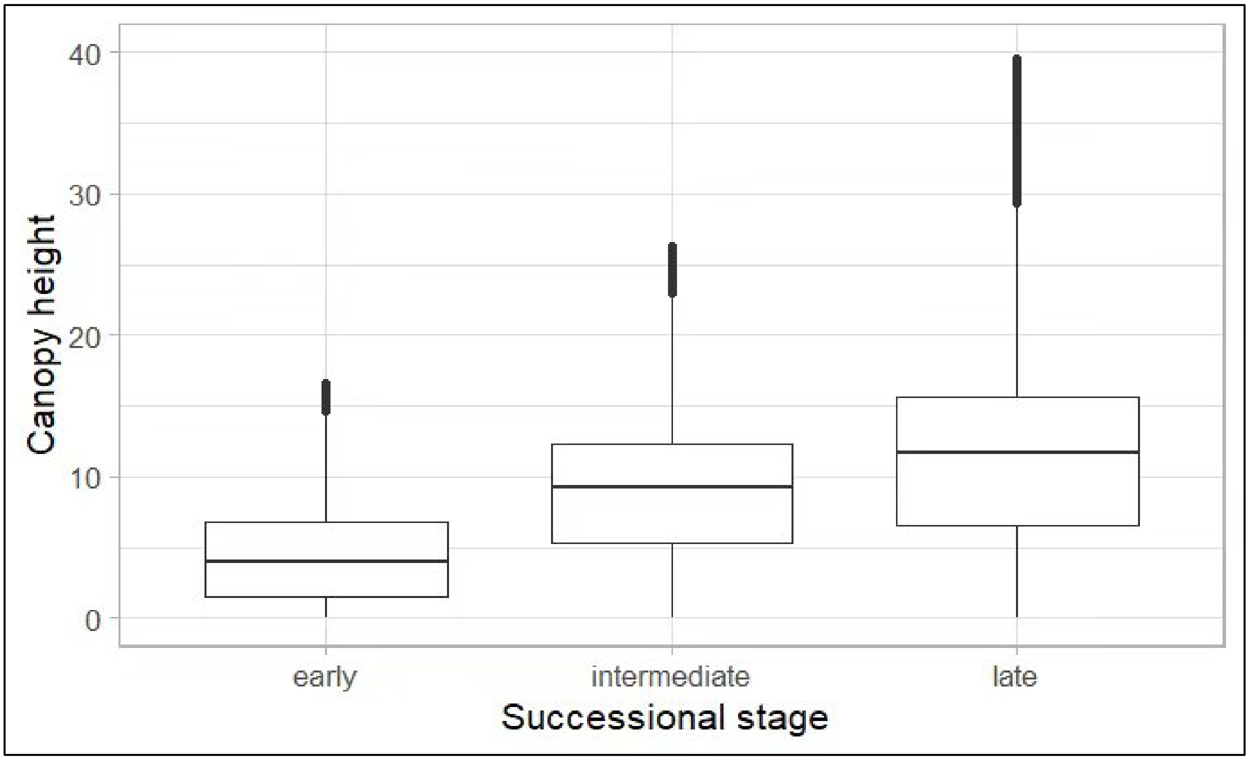


Figure 2.9. The canopy height distribution of three different successional stages by density line plots.

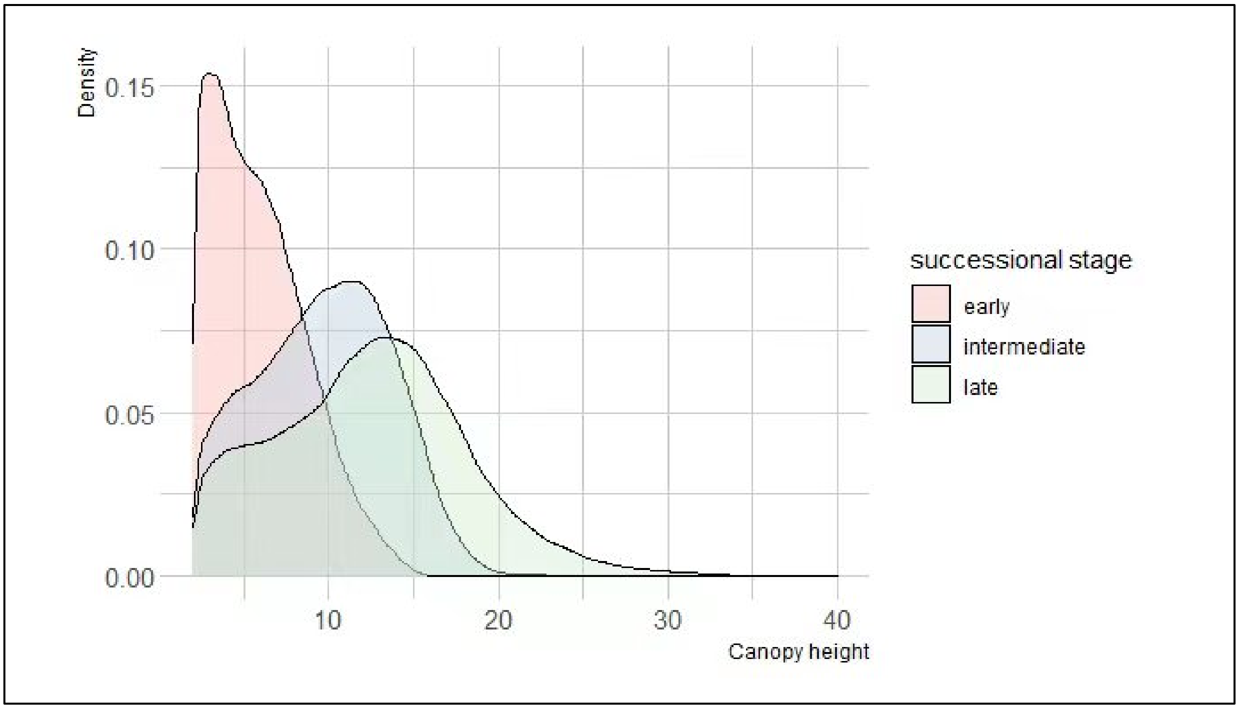


Table 2.10. The tree height statistics for the three different successional stages, including the average height, maximum height, and the minimum height, also including the previous statistics from the reference (Kalacska et al., 2007).

	Average	**Maximum**	**Minimum**	**Reference (Kalacska et al., 2007)**
Early	10.3m	15.0m	5.6m	7.5 ± 2.2m
Intermediate	16.6m	20.0m	12.0m	10.3 ± 3.4m
Late	24.1m	38.5m	15.0m	15.0 ± 2.2m

Table 2.11. The height of canopy, subcanopy, and the understory layers of three different successional stages. And the previous study (Connell et al., 1997) of the height distribution.

	This study			**Reference (Connell et al., 1997)**
	Early	Intermediate	Late	
Canopy	> 5.5m	> 12.0m	> 20m	> 20m
Subcanopy	none	5.1 – 11.9m	10 – 19.9m	10 – 19.9m
Understory	2 – 5.4m	2 – 5m	2 – 9.9m	2 – 9.9m

Table 2.12. The statistics of the quantity of three kinds of canopy gaps (A, B, C2) in three different successional stages; The statistics of the range of depth for three kinds of canopy gaps in different successional stages.

	“A”	**“B”**	**“C2”**	**Total**
Early stage	102	0	0	102
Intermediate stage	80	54	43	177
Late stage	69	74	75	218
	Range “A”	**Range “B”**	**Range “C2”**	
Early stage	3.5(±2.5) m	none	none	
Intermediate stage	5.0(±3.5) m	4.0(±3.0) m	9.0(±3.5) m	
Late stage	6.0(±4.0) m	6.0(±4.0) m	17.0(±10.5) m	

Figure 2.13. a\b\c:The canopy gap distribution under the three different height thresholds (6m, 12m, 16m); d\e\f: the spatial polygon of the gap area shows in the 100m*100m plot in three different successional stages (early, intermediate, late).

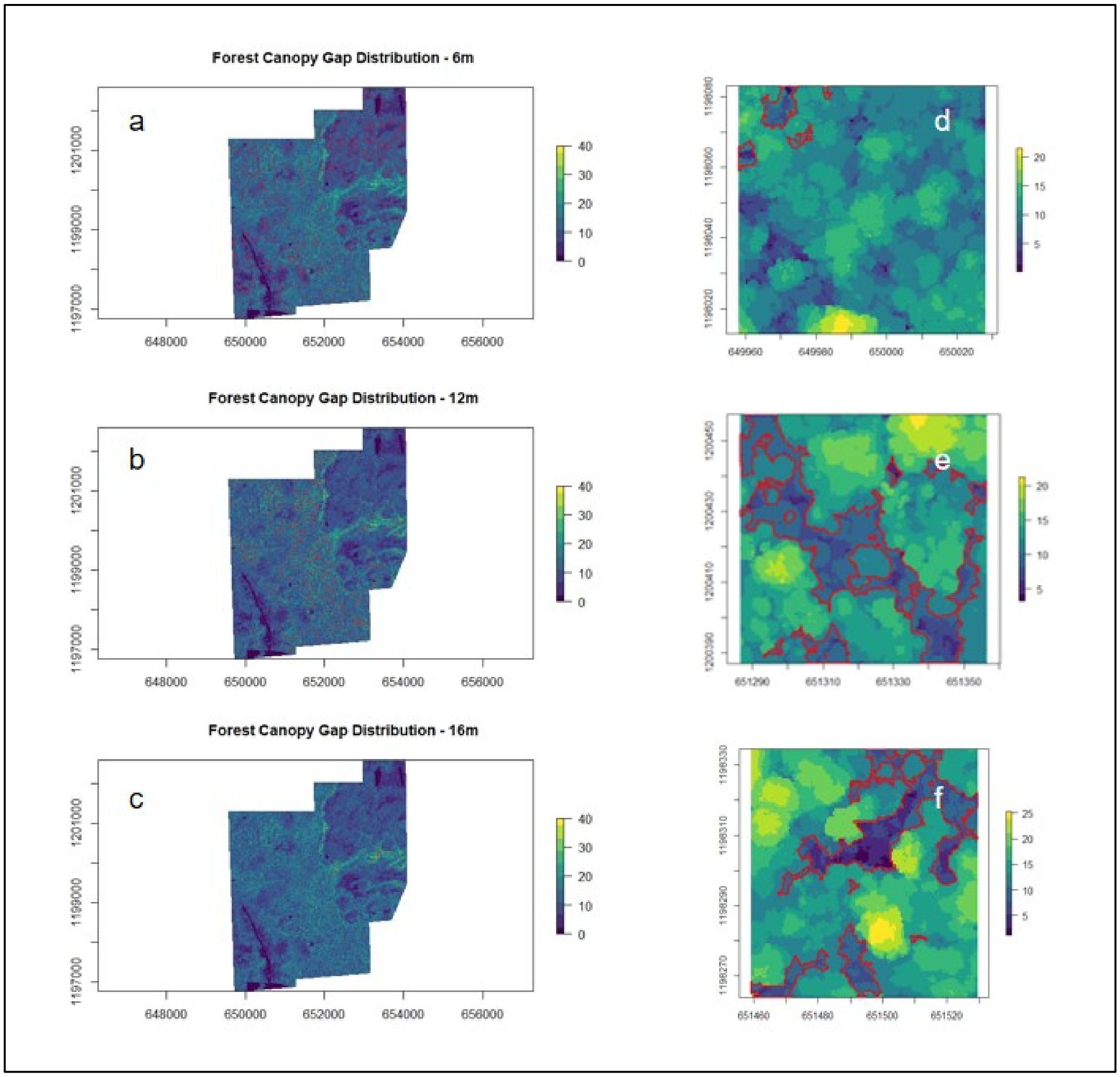
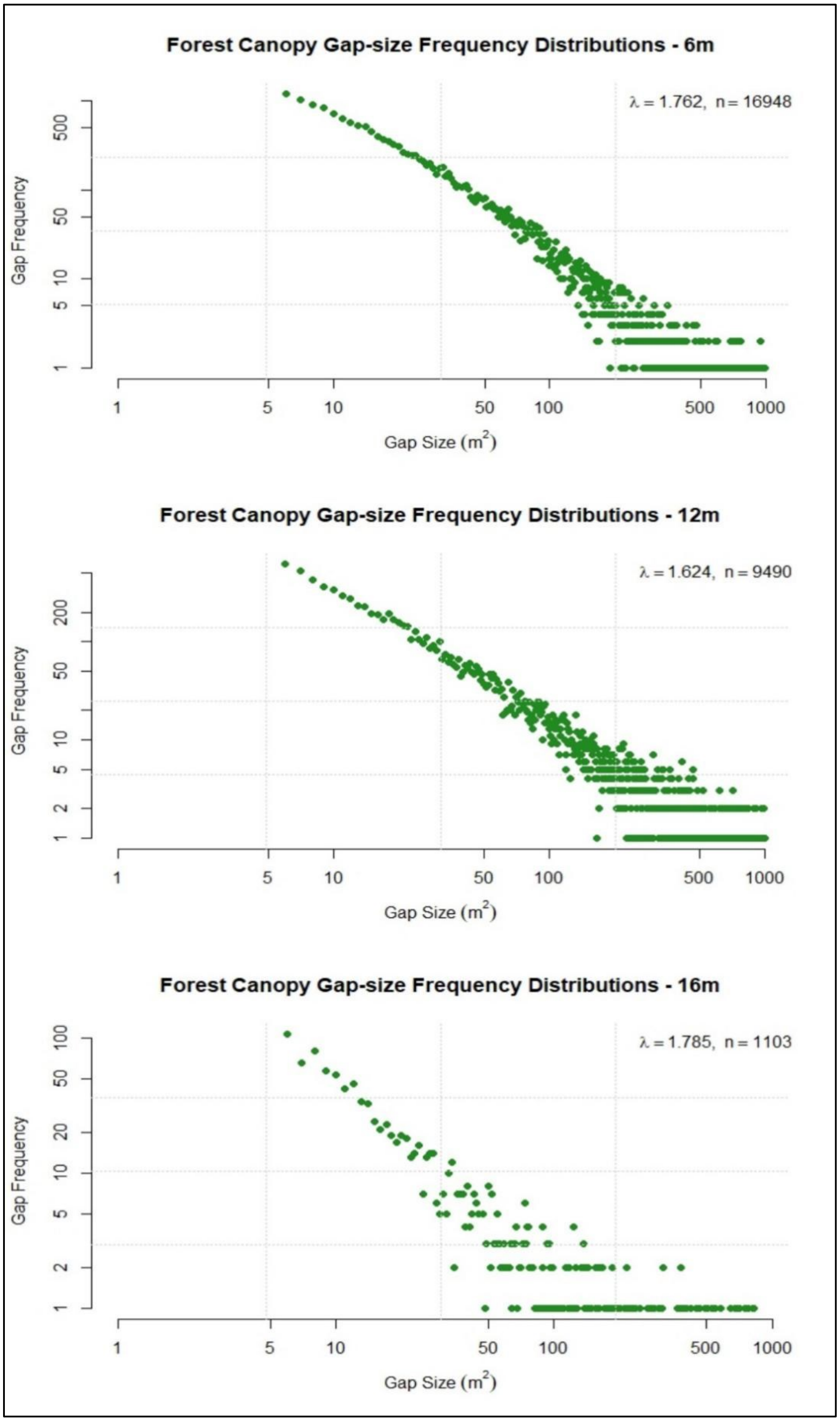


Figure 2.14. The gap-size frequency distribution under the three different height thresholds (6m, 12m, 16m).



Forest Canopy Gap-size Frequency Distributions - 6m

Forest Canopy Gap-size Frequency Distributions - 12m

Forest Canopy Gap-size Frequency Distributions - 16m

Chapter Three: Conclusions

This thesis aimed to assess the use of LiDAR data adopted for canopy gap delineation in a structurally complex forest at the Santa Rosa National Park (SRNP) Environmental Monitoring Super Site, Costa Rica. The study contained in Chapter Two explored the use of airborne-based LiDAR to quantify, characterize, and map canopy gaps of different successional stages in a secondary tropical dry forest during the leaf-on season. In this study, the gap distribution of the wholeNP under three different height thresholds as shown in the images (Figure 2.12), represents the change in the gap distribution at different height thresholds. Three kinds of gaps (A, B, and C2) based on the definition by St-Onge et al., (2014) were found in 50 sampling sites and were given a specific explanation. Meanwhile, through comparison, it was found that the observed gap-size frequency distribution of the study area is very similar to other observations from tropical dry forests.

3.1 Significant contribution

The important contribution of this study is to demonstrate the efficiency and accuracy of using airborne LiDAR data in exploring canopy gaps and related information in complex structured forests. Previous research has mainly focused on analyzing canopy gaps in tropical rainforests, and quantitative studies on canopy gaps in tropical dry forests, a specific ecosystem, have not been reported. Therefore, this study conducted a quantitative analysis of canopy gaps in tropical dry forests using the case study of Santa Rosa National Park, filling the research gap regarding canopy gap characteristics in tropical dry forest research.

Canopy gaps are crucial elements in forest ecosystems and essential for understanding forest structure and function. They reflect spatial heterogeneity and competition pressure within forests and significantly influence carbon cycling, maintenance of species diversity, and forest ecosystem restoration. However, quantifying canopy gaps in complex structured forests like tropical dry forests poses challenges due to limitations of traditional observation methods caused by vegetation density and shading effects.

In this study, airborne LiDAR data was utilized to acquire high-resolution three-dimensional information of canopy structures and effectively delineate canopy gaps. Through detailed analysis of 50 sample points, we successfully identified different types of canopy gaps and quantified their distribution characteristics. This provides a solid foundation for further studying the relationships between canopy gaps and ecological processes.

Furthermore, the results of this study have significant implications for management and conservation. Understanding the distribution and changes of canopy gaps can provide a scientific basis for sustainable forest management. For example, when implementing forest restoration measures, the size and distribution of canopy gaps can serve as indicators for evaluating restoration success. Moreover, a comprehensive understanding of canopy gap characteristics is crucial for developing effective conservation strategies to preserve the integrity and diversity of tropical dry forest ecosystems.

In conclusion, this study made important breakthroughs in quantifying canopy gaps using airborne LiDAR data. By filling the research gap in the field of tropical dry forests, it revealed the distribution characteristics and variation patterns of canopy gaps in tropical dry forests. These findings are of significant importance for gaining a deeper understanding of forest ecosystem functions, promoting sustainable management, and conserving tropical dry forests.

3.2 Challenges

This study presented two challenges: the first one was to define the minimum size of a gap opening. In the final study, and based on the literature review, 5 m^2 was selected as the minimum value of gap detection to ensure the gap was visible enough. The second challenge was the selection of the height threshold to detect gaps. Even in the same successional stage forest, there is not a uniform distribution of height, which makes it difficult to determine the height threshold to confirm where the gap is. Finally, three thresholds for gap detection (6m, 12m, 16m) were obtained by counting the canopy height of all 50 plots.

In addition to the aforementioned challenges, this study also faced some difficulties and limitations. Firstly, acquiring and processing airborne LiDAR data require expensive equipment and specialized knowledge, which may limit the application of this method in certain regions or research projects. Secondly, this study focused solely on the spatial distribution characteristics of canopy gaps without delving into their ecological functions. Further research can integrate various methods such as remote sensing data, ground monitoring, and ecological surveys to explore the linkages between canopy gaps and ecological processes in more depth. Additionally, although this study conducted quantitative analysis of canopy gaps in tropical dry forests, variations may exist in different types of forests and ecosystems. Therefore, when applying and generalizing the findings of this study, the applicability and generalizability in different geographical regions and habitat conditions need to be considered.

Overall, despite making significant breakthroughs and providing valuable insights, there are still challenges and limitations in utilizing airborne LiDAR data for quantitative studies of canopy gaps. Future research can build upon these challenges to enhance the accuracy, comprehensiveness, and applicability of canopy gap research.

3.3 Future Research

Like most LiDAR -based studies, this study quantified static gaps in the canopy. However, the formation and disappearance of the gaps are always accompanied by long-term dynamic processes. Using ALS data and spatially explicit information about the disturbance, the gap dynamics of intact and selectively destroyed forests over five years (Silva et al., 2019). Thus, if we want to get a complete, planned conservation decision for the TDFs, decades of monitoring would be the next important task for the gap research.

Despite the significant progress made in quantifying canopy gaps in this study, there are still many directions worth further exploration. Firstly, for the dynamic changes and succession processes of canopy gaps, longer-term monitoring and research are needed. Long-term monitoring can reveal the mechanisms of canopy gap formation and disappearance and their impacts on forest ecosystems. Therefore, future research can combine LiDAR data with spatially explicit disturbance information to conduct long-term studies on gap dynamics in intact and selectively disturbed forests.

Additionally, this study primarily focused on the static characteristics of canopy gaps, i.e., the distribution of gaps at a given time point. However, in reality, the formation and succession of gaps are dynamic processes influenced by various factors such as climate change and human disturbances. Future research can integrate time-series LiDAR data with other environmental parameters to gain a more comprehensive understanding of the dynamic mechanisms driving canopy gap changes.

Furthermore, although this study has quantitatively studied canopy gaps in tropical dry forests, different types of forests and ecosystems may exhibit variations. Future research can consider conducting similar studies in different geographical regions and habitat conditions to further validate the findings of this study and extend them to a broader range of areas.

3.4 Reference

Asner, G.P., Kellner, J.R., Kennedy-Bowdoin, T., Knapp, D.E., Anderson, C., Martin, R.E., 2013. Forest Canopy Gap Distributions in the Southern Peruvian Amazon. PLoS One 8. https://doi.org/10.1371/journal.pone.0060875

St-Onge, B., Vepakomma, U., Sénécal, J.-F., Kneeshaw, D., Doyon, F., 2014. Canopy Gap Detection and Analysis with Airborne Laser Scanning 419–437. https://doi.org/10.1007/978-94-017-8663-8_21

Akbari Mazdi, R., Mataji, A., Fallah, A., 2021. Canopy Gap Dynamics, Disturbances, and Natural Regeneration Patterns in a Beech-Dominated Hyrcanian Old-Growth Forest. Balt. For. 27. https://doi.org/10.46490/bf535

Araki, K., Awaya, Y., 2021. Analysis and prediction of gap dynamics in a secondary deciduous broadleaf forest of central japan using airborne multi-lidar observations. Remote Sens. 13, 1–20. https://doi.org/10.3390/rs13010100

Asner, G.P., Kellner, J.R., Kennedy-Bowdoin, T., Knapp, D.E., Anderson, C., Martin, R.E., 2013. Forest Canopy Gap Distributions in the Southern Peruvian Amazon. PLoS One 8. https://doi.org/10.1371/journal.pone.0060875

Ben-Arie, J.R., Hay, G.J., Powers, R.P., Castilla, G., St-Onge, B., 2009. Development of a pit filling algorithm for LiDAR canopy height models. Comput. Geosci. 35, 1940–1949. https://doi.org/10.1016/j.cageo.2009.02.003

Biology, T., 2016. Gap Partitioning among Tropical Rainforest Trees Author (s): Julie Sloan Denslow Source : Biotropica , Vol . 12 , No . 2 , Supplement : Tropical Succession (Jun ., 1980), pp . 47-55 Published by : Association for Tropical Biology and Conservation Stab

12, 47–55.

Brokaw, N.V.L., 1982. The Definition of Treefall Gap and Its Effect on Measures of Forest Dynamics. Biotropica 14, 158. https://doi.org/10.2307/2387750

Chambers, J.Q., Robertson, A.L., Carneiro, V.M.C., Lima, A.J.N., Smith, M.L., Plourde, L.C., Higuchi, N., 2009. Hyperspectral remote detection of niche partitioning among canopy trees driven by blowdown gap disturbances in the Central Amazon. Oecologia 160, 107–117. https://doi.org/10.1007/s00442-008-1274-9

Garbarino, M., Mondino, E.B., Lingua, E., Nagel, T.A., Dukić, V., Govedar, Z., Motta, R., 2012. Gap disturbances and regeneration patterns in a Bosnian old-growth forest: A multispectral remote sensing and ground-based approach. Ann. For. Sci. 69, 617–625. https://doi.org/10.1007/s13595-011-0177-9

Heiskanen, J., Korhonen, L., Hietanen, J., Pellikka, P.K.E., 2015. Use of airborne LiDAR for estimating canopy gap fraction and leaf area index of tropical montane forests. Int. J. Remote Sens. 36, 2569–2583. https://doi.org/10.1080/01431161.2015.1041177

Kuuluvainen, T., 1994. Gap disturbance, ground microtopography, and the regeneration dynamics of boreal coniferous forests in Finland: a review. Ann. Zool. Fennici 31, 35–51.

Lim, K., Treitz, P., Wulder, M., St-Ongé, B., Flood, M., 2003. LiDAR remote sensing of forest structure. Prog. Phys. Geogr. 27, 88–106. https://doi.org/10.1191/0309133303pp360ra

Martinuzzi, S., Gould, W.A., Vierling, L.A., Hudak, A.T., Nelson, R.F., Evans, J.S., 2013. Quantifying Tropical Dry Forest Type and Succession: Substantial Improvement with LiDAR. Biotropica 45, 135–146. https://doi.org/10.1111/j.1744-7429.2012.00904.x

Negrón-Juárez, R.I., Chambers, J.Q., Marra, D.M., Ribeiro, G.H.P.M., Rifai, S.W., Higuchi, N., Roberts, D., 2011. Detection of subpixel treefall gaps with Landsat imagery in Central Amazon forests. Remote Sens. Environ. 115, 3322–3328. https://doi.org/10.1016/j.rse.2011.07.015

Silva, C.A., Valbuena, R., Pinagé, E.R., Mohan, M., de Almeida, D.R.A., North Broadbent, E., Jaafar, W.S.W.M., de Almeida Papa, D., Cardil, A., Klauberg, C., 2019. ForestGapR: An r Package for forest gap analysis from canopy height models. Methods Ecol. Evol. 10, 1347–1356. https://doi.org/10.1111/2041-210X.13211

Zhao, G., Sanchez-Azofeifa, A., Laakso, K., Sun, C., Fei, L., 2021. Hyperspectral and full-waveform lidar improve mapping of tropical dry forest’s successional stages. Remote Sens. 13. https://doi.org/10.3390/rs13193830

Zimble, D.A., Evans, D.L., Carlson, G.C., Parker, R.C., Grado, S.C., Gerard, P.D., 2003. Characterizing vertical forest structure using small-footprint airborne LiDAR. Remote Sens. Environ. 87, 171–182. https://doi.org/10.1016/S0034-4257(03)00139-1

Bibliography

Arroyo-Mora, J.P., Sánchez-Azofeifa, G.A., Kalacska, M.E.R., Rivard, B., Calvo-Alvarado, J.C., Janzen, D.H., 2005. Secondary forest detection in a neotropical dry forest landscape using Landsat 7 ETM+ and IKONOS imagery. Biotropica 37, 497–507. https://doi.org/10.1111/j.1744-7429.2005.00068.x

Asner, G.P., Kellner, J.R., Kennedy-Bowdoin, T., Knapp, D.E., Anderson, C., Martin, R.E., 2013. Forest Canopy Gap Distributions in the Southern Peruvian Amazon. PLoS One 8. https://doi.org/10.1371/journal.pone.0060875

Biology, T., 2016. Gap Partitioning among Tropical Rainforest Trees Author (s): Julie Sloan Denslow Source : Biotropica, Vol . 12, No. 2, Supplement: Tropical Succession (Jun ., 1980), pp . 47-55 Published by : Association for Tropical Biology and Conservation Stab 12, 47–55.

Brook, B.W., Bradshaw, C.J.A., Koh, L.P., Sodhi, N.S., 2017. Momentum Drives the Crash: Mass Extinction in the Tropics Published by: Association for Tropical Biology and Conservation Stable URL : http://www.jstor.org/stable/30043246.

Brokaw, N.V.L., 1982. The Definition of Treefall Gap and Its Effect on Measures of Forest Dynamics. Biotropica 14, 158. https://doi.org/10.2307/2387750

Button, G., 2000. Considerations in evaluating the cost-effectiveness of environmental health interventions.

Calvo-Rodriguez, S., Sánchez-Azofeifa, G.A., Durán, S.M., Espírito-Santo, M.M. Do, Nunes, Y.R.F., 2021. Dynamics of carbon accumulation in tropical dry forests under climate change extremes. Forests 12, 1–15. https://doi.org/10.3390/f12010106

Cao, S., Yu, Q., Sanchez-Azofeifa, A., Feng, J., Rivard, B., Gu, Z., 2015. Mapping tropical dry forest succession using multiple criteria spectral mixture analysis. ISPRS J. Photogramm. Remote Sens. 109, 17–29. https://doi.org/10.1016/j.isprsjprs.2015.08.009

Campos-Vargas, C., Sanchez-Azofeifa, A., Laakso, K., Marzahn, P., 2020. Unmanned aerial systems and machine learning techniques help to detect deadwood components in a tropical dry forest. Forests 11. https://doi.org/10.3390/f11080827.

Castillo-Núñez, M., Sánchez-Azofeifa, G.A., Croitoru, A., Rivard, B., Calvo-Alvarado, J., Dubayah, R.O., 2011. Delineation of secondary succession mechanisms for tropical dry forests using LiDAR. Remote Sens. Environ. 115, 2217–2231. https://doi.org/10.1016/j.rse.2011.04.020.

Castro, K.L., Sanchez-Azofeifa, G.A., Rivard, B., 2003. Monitoring secondary tropical forests using space-borne data: Implications for Central America. Int. J. Remote Sens. 24, 1853–1894. https://doi.org/10.1080/01431160210154056.

Castillo-Núñez, M., Sánchez-Azofeifa, G.A., Croitoru, A., Rivard, B., Calvo-Alvarado, J., Dubayah, R.O., 2011. Delineation of secondary succession mechanisms for tropical dry forests using LiDAR. Remote Sens. Environ. 115, 2217–2231. https://doi.org/10.1016/j.rse.2011.04.020

Chazdon, R.L., Peres, C.A., Dent, D., Sheil, D., Lugo, A.E., Lamb, D., Stork, N.E., Miller, S.E., 2009. The potential for species conservation in tropical secondary forests. Conserv. Biol. 23, 1406–1417. https://doi.org/10.1111/j.1523-1739.2009.01338.x.

Colwell, R.K., Brehm, G., Cardelús, C.L., Gilman, A.C., Longino, J.T., Cardelus, C.L., Gilman, A.C., Longino, J.T., 2008. in the Wet Tropics. Science (80-.). 322, 258–261.

Connell, J.H., Lowman, M.D., Noble, I.R., 1997. Subcanopy gaps in temperate and tropical forests. Austral Ecol. 22, 163–168. https://doi.org/10.1111/j.1442-9993.1997.tb00655.x

D ’annunzio, R., Lindquist, E.J., Macdicken, K.G., 2010. Global remote sensing survey 2010 update Global forest land---use change from 1990 to 2010: an update to a global remote sensing survey of forests.

Duan, M., Bax, C., Laakso, K., Sanchez-azofeifa, A., Mashhadi, N., Mattie, N., 2023. Characterizing Transitions between Successional Stages in a Tropical Dry Forest Using LiDAR Techniques.

Farrior, C.E., Bohlman, S.A., Hubbell, S., Pacala, S.W., 2016. The dominance of the suppressed: Power-law size structure in tropical forests. Science (80-.). 351, 155–157. https://doi.org/10.1126/science.aad0592

Feeley, K.J., Rehm, E.M., Machovina, B., 2012. perspective: The responses of tropical forest species to global climate change: acclimate, adapt, migrate, or go extinct? Front. Biogeogr. 4. https://doi.org/10.21425/f5fbg12621.

Fox, T. R., et al. (2000). Tree species diversity in southern forests: An evaluation of the potential for high-value hardwood silviculture. In Proceedings of the Southern Forest Economics Workshop.

Garbarino, M., Mondino, E.B., Lingua, E., Nagel, T.A., Dukić, V., Govedar, Z., Motta, R., 2012. Gap disturbances and regeneration patterns in a Bosnian old-growth forest: A multispectral remote sensing and ground-based approach. Ann. For. Sci. 69, 617–625. https://doi.org/10.1007/s13595-011-0177-9

Getzin, S., Nuske, R.S., Wiegand, K., 2014. Using unmanned aerial vehicles (UAV) to quantify spatial gap patterns in forests. Remote Sens. 6, 6988–7004. https://doi.org/10.3390/rs6086988

Goetz, A.F.H., Rock, B.N., Rowan, L.C., 1983. Remote sensing for exploration: an overview. Econ. Geol. 78, 573–590. https://doi.org/10.2113/gsecongeo.78.4.573.

Guariguata, M.R., Ostertag, R., 2001. Neotropical secondary forest succession: Changes in structural and functional characteristics. For. Ecol. Manage. 148, 185–206. https://doi.org/10.1016/S0378-1127(00)00535-1.

Heiskanen, J., Korhonen, L., Hietanen, J., Pellikka, P.K.E., 2015. Use of airborne lidar for estimating canopy gap fraction and leaf area index of tropical montane forests. Int. J. Remote Sens. 36, 2569–2583. https://doi.org/10.1080/01431161.2015.1041177

Hilje, B., Calvo-Alvarado, J., Jiménez-Rodríguez, C., Sánchez-Azofeifa, A., 2015a. Tree species composition, breeding systems, and pollination and dispersal syndromes in three forest successional stages in a tropical dry forest in Mesoamerica. Trop. Conserv. Sci. 8, 76–94. https://doi.org/10.1177/194008291500800109

Hoekstra, J. M., et al. (2005). The Global Distribution of Biodiversity: An Indicator of Earth's Health. Frontiers in Ecology and the Environment, 3(9), 328-334.

Hunter, M.O., Keller, M., Morton, D., Cook, B., Lefsky, M., Ducey, M., Saleska, S., De Oliveira, R.C., Schietti, J., Zang, R., 2015a. Structural dynamics of tropical moist forest gaps. PLoS One 10, 1–19. https://doi.org/10.1371/journal.pone.0132144

Hunter, M.O., Keller, M., Morton, D., Cook, B., Lefsky, M., Ducey, M., Saleska, S., De Oliveira, R.C., Schietti, J., Zang, R., 2015b. Structural dynamics of tropical moist forest gaps. PLoS One 10, 1–20. https://doi.org/10.1371/journal.pone.0132144

Herwitz, S. R., et al. (2000). Object-oriented mapping and analysis of forest landscape structure and change in New England, USA. Remote Sensing of Environment, 74(1), 84-99.

J. Hyyppa, O. Kelle, M. Lehikoinen and M. Inkinen, "A segmentation-based method to retrieve stem volume estimates from 3-D tree height models produced by laser scanners," in IEEE Transactions on Geoscience and Remote Sensing, vol. 39, no. 5, pp. 969-975, May 2001, doi: 10.1109/36.921414.

Kalacska, M., Sanchez-Azofeifa, G.A., Calvo-Alvarado, J.C., Quesada, M., Rivard, B., Janzen, D.H., 2004. Species composition, similarity, and diversity in three successional stages of a seasonally dry tropical forest. For. Ecol. Manage. 200, 227–247. https://doi.org/10.1016/j.foreco.2004.07.001

Kaya, E., Agca, M., Adiguzel, F., Cetin, M., 2019. Spatial data analysis with R programming for the environment. Hum. Ecol. Risk Assess. 25, 1521–1530. https://doi.org/10.1080/10807039.2018.1470896

Koukoulas, S., Blackburn, G.A., 2004. Quantifying the spatial properties of forest canopy gaps using LiDAR imagery and GIS. Int. J. Remote Sens. 25, 3049–3072. https://doi.org/10.1080/01431160310001657786

Lai HR, Hall JS, Turner BL, van Breugel M. Liana effects on biomass dynamics strengthen during secondary forest succession. Ecology. 2017 Apr;98(4):1062-1070. doi: 10.1002/ecy.1734. Epub 2017 Mar 20. PMID: 28072458.

Lechner, A.M., Foody, G.M., Boyd, D.S., 2020. Applications in Remote Sensing to Forest Ecology and Management. One Earth 2, 405–412. https://doi.org/10.1016/j.oneear.2020.05.001.

Leckie, D.G., 1990. Advances in remote sensing technologies for forest surveys and management 464–483.

Li, W., Cao, S., Campos-Vargas, C., Sanchez-Azofeifa, A., 2017. Identifying tropical dry forests extent and succession via the use of machine learning techniques. Int. J. Appl. Earth Obs. Geoinf. 63, 196–205. https://doi.org/10.1016/j.jag.2017.08.003

Nagel, T.A., Svoboda, M., Rugani, T., Diaci, J., 2010. Gap regeneration and replacement patterns in an old growth Fagus-Abies Forest of Bosnia-Herzegovina. Plant Ecol. 208, 307–318. https://doi.org/10.1007/s11258-009-9707-z

Negrón-Juárez, R.I., Chambers, J.Q., Marra, D.M., Ribeiro, G.H.P.M., Rifai, S.W., Higuchi, N., Roberts, D., 2011. Detection of subpixel treefall gaps with Landsat imagery in Central Amazon forests. Remote Sens. Environ. 115, 3322–3328. https://doi.org/10.1016/j.rse.2011.07.015

Persson, Å., Holmgren, J., & Söderman, U. (2002). Detecting and measuring individual trees using an airborne laser scanner. *Photogrammetric Engineering and Remote Sensing, 68*, 925-932.

Pimm, S.L., Askins, R.A., 1995. Forest losses predict bird extinctions in eastern North America. Proc. Natl. Acad. Sci. U. S. A. 92, 9343–9347. https://doi.org/10.1073/pnas.92.20.9343.

Plinio Sist and Amiril Saridan, 1999. STAND STRUCTURE AND FLORISTIC COMPOSITION OF A PRIMARY LOWLAND DIPTEROCARP FOREST IN EAST KALIMANTAN Author (s): Plinio Sist and Amiril Saridan Source : Journal of Tropical Forest Science, October 1999, Vol . 11, No. 4 (October 1999), Stable URL : 11, 704–722.

Polunin, N., 1980. The Sinking Ark: A New Look at the Problem of Disappearing Species, by Norman Myers. Pergamon Press, Oxford–New York–Toronto–Sydney–Paris–Frankfurt: xiii + 307 pp., 9 tables, 21.5 × 15.2 × 2 cm, US$ 8.95, 1979. Environ. Conserv. 7, 172–172. https://doi.org/10.1017/s0376892900007414.

Potapov, P., Yaroshenko, A., Turubanova, S., Dubinin, M., Laestadius, L., Thies, C., Aksenov, D., Egorov, A., Yesipova, Y., Glushkov, I., Karpachevskiy, M., Kostikova, A., Manisha, A., Tsybikova, E., Zhuravleva, I., 2008. Mapping the world's intact forest landscapes by remote sensing. Ecol. Soc. 13. https://doi.org/10.5751/ES-02670-130251.

Putz, F.E., Redford, K.H., 2010. The importance of defining "Forest": Tropical Forest degradation, deforestation, long-term phase shifts, and further transitions. Biotropica 42, 10–20. https://doi.org/10.1111/j.1744-7429.2009.00567.x.

Olson, D. M., et al. (2001). Terrestrial Ecoregions of the World: A New Map of Life on Earth. BioScience, 51(11), 933-938.

Riswan, S., Hartanti, L., 1995. Human impacts on tropical forest dynamics. Vegetatio 121, 41–52. https://doi.org/10.1007/BF00044671.

Sanchez-Azofeifa, G. A., & Hesketh, J. D. (2013). Deforestation in Costa Rica: A Quantitative Analysis Using Remote Sensing Imagery. Biotropica, 35(1), 74-78.

Schnitzer, S.A., Dalling, J.W., Carson, W.P., 2000. The impact of lianas on tree regeneration in tropical forest canopy gaps: Evidence for an alternative pathway of gap-phase regeneration. J. Ecol. 88, 655–666. https://doi.org/10.1046/j.1365-2745.2000.00489.x

Silva, C.A., Valbuena, R., Pinagé, E.R., Mohan, M., de Almeida, D.R.A., North Broadbent, E., Jaafar, W.S.W.M., de Almeida Papa, D., Cardil, A., Klauberg, C., 2019a. ForestGapR: An r Package for forest gap analysis from canopy height models. Methods Ecol. Evol. 10, 1347–1356. https://doi.org/10.1111/2041-210X.13211

Silva, C.A., Valbuena, R., Pinagé, E.R., Mohan, M., de Almeida, D.R.A., North Broadbent, E., Jaafar, W.S.W.M., de Almeida Papa, D., Cardil, A., Klauberg, C., 2019b. ForestGapR: An r Package for forest gap analysis from canopy height models. Methods Ecol. Evol. 10, 1347–1356. https://doi.org/10.1111/2041-210X.13211

Stark, S.C., Leitold, V., Wu, J.L., Hunter, M.O., de Castilho, C. V., Costa, F.R.C., Mcmahon, S.M., Parker, G.G., Shimabukuro, M.T., Lefsky, M.A., Keller, M., Alves, L.F., Schietti, J., Shimabukuro, Y.E., Brandão, D.O., Woodcock, T.K., Higuchi, N., de Camargo, P.B., de Oliveira, R.C., Saleska, S.R., 2012. Amazon forest carbon dynamics predicted by profiles of canopy leaf area and light environment. Ecol. Lett. 15, 1406–1414. https://doi.org/10.1111/j.1461-0248.2012.01864.x

Sterl, A., Severijns, C., Dijkstra, H., Hazeleger, W., Jan van Oldenborgh, G., van den Broeke, M., Burgers, G., van den Hurk, B., Jan van Leeuwen, P., and van Velthoven, P. (2008), When can we expect extremely high surface temperatures? Geophys. Res. Lett., 35, L14703, doi:10.1029/2008GL034071.

Stork, N.E., Coddington, J.A., Colwell, R.K., Chazdon, R.L., Dick, C.W., Peres, C.A., Sloan, S., Willis, K., 2009. Vulnerability and resilience of tropical forest species to land-use change. Conserv. Biol. 23, 1438–1447. https://doi.org/10.1111/j.1523-1739.2009.01335.x.

St-Onge, B., Vepakomma, U., Sénécal, J.-F., Kneeshaw, D., Doyon, F., 2014. Canopy Gap

Detection and Analysis with Airborne Laser Scanning 419–437. https://doi.org/10.1007/978-94-017-8663-8_21

St-Onge, B., Treitz, P., Wulder, M.A., 2003. Tree and canopy height estimation with scanning lidar. In: Wulder, M.A., Franklin, S.E. (Eds.), Remote Sensing of Forest Environments: Concepts and Case Studies. Kluwer Academic Publishers, Boston, pp. 489–509.

Sun, C., Cao, S., Sanchez-Azofeifa, G.A., 2019. Mapping tropical dry forest age using airborne waveform LiDAR and hyperspectral metrics. Int. J. Appl. Earth Obs. Geoinf. 83, 101908. https://doi.org/10.1016/j.jag.2019.101908

Tilman, D., 1999. The Ecological Consequences of Changes in Biodiversity: A Search for General Principles Author (s): David Tilman Published by : Wiley Stable URL : http://www.jstor.org/stable/176540 REFERENCES Linked references are available on JSTOR for this article : Ecology 80, 1455–1474.

Van Breugel, M., 2007. Dynamics of secondary forests.

Wallace, L., Lucieer, A., Watson, C., Turner, D., 2012. Development of a UAV-LiDAR system with application to forest inventory. Remote Sens. 4, 1519–1543. https://doi.org/10.3390/rs4061519

Watts, J., 2019. Human society is under urgent threat from the loss of Earth’s natural life. Guard. 1–7.

White, E.P., Enquist, B.J., Green, J.L., 2008. On estimating the exponent of power-law frequency distributions. Ecology. https://doi.org/10.1890/07-1288.1

White, J.C., Coops, N.C., Wulder, M.A., Vastaranta, M., Hilker, T., Tompalski, P., 2016. Remote

Sensing Technologies for Enhancing Forest Inventories: A Review. Can. J. Remote Sens. 42, 619–641. https://doi.org/10.1080/07038992.2016.1207484.

Whitmore, T.C., 2011. Canopy Gaps and the Two Major Groups of Forest Trees Author (s): T. C. Whitmore Published by: Ecological Society of America Stable URL: http://www.jstor.org/stable/1940195. CANOPY GAPS AND THE TWO MAJOR GROUPS OF FOREST TREES. America (NY). 70, 536–538.

Wright, J.S., 2017. The Uncertain Future of Tropical Forest Species Author (s): S . Joseph Wright and Helene C. Muller-Landau Published by: Association for Tropical Biology and Conservation Stable URL: http://www.jstor.org/stable/30044025 38, 443–445.

Wright, S.J., 2005. Tropical forests in a changing environment. Trends Ecol. Evol. 20, 553–560. https://doi.org/10.1016/j.tree.2005.07.009.

Wright, S.J., Muller-landau, H.C., 2006. The Future of Tropical Forest Species 1 Amazon Basin and Guiana Shield, or the Congo Basin and western Given the importance of habitat loss to estimates of future. Biotropica 38, 287–301.

Yamamoto, S.I., 1992. The gap theory in forest dynamics. Bot. Mag. Tokyo 105, 375–383. https://doi.org/10.1007/BF02489426

Yang, J., Jones, T., Caspersen, J., He, Y., 2015. Object-based canopy gap segmentation and classification: Quantifying the pros and cons of integrating optical and LiDAR data. Remote Sens. 7, 15917–15932. https://doi.org/10.3390/rs71215811

Yavitt, J.B., Battles, J.J., Lang, G.E., Knight, D.H., 1995. The canopy gap regime in a secondary neotropical forest in Panama. J. Trop. Ecol. 11, 391–402.

https://doi.org/10.1017/S0266467400008853

Zeppel, M.J.B., Anderegg, W.R.L., Adams, H.D., 2013. Forest mortality due to drought: Latest insights, evidence and unresolved questions on physiological pathways and consequences of tree death. New Phytol. 197, 372–374. https://doi.org/10.1111/nph.12090.

Zhao, G., Sanchez-Azofeifa, A., Laakso, K., Sun, C., Fei, L., 2021. Hyperspectral and full waveform lidar improve mapping of tropical dry forest's successional stages. Remote Sens. 13. https://doi.org/10.3390/rs13193830