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Leaf Area Index variation across three forest types

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Abstract

Leaf Area Index is one of the functional traits most studied in ecology, as it is fundamental to understanding whole plant functioning, in particular related to physiological processes, namely evaporation, transpiration, CO2 exchange, and physical activities, such as radiation and water interception. This is particularly relevant in tropical forests, which are increasingly impacted by deforestation, degradation and fragmentation, and consequently affect LAI values and overall primary productivity. This study aims at quantifying LAI spatial variability across three forest types and assessing the relationship with two structural parameters, diameter at breast height and tree density. LAI values are quantified by taking pictures of the canopy through a digital camera with 35 mm focal lens and 44° field of view and processing them through the 'coveR' package in RStudio. The results show a significant difference in LAI values between forest types. In particular, the primary forest presents higher LAI values, indicating higher photosynthetic activity, compared to the other two forest types. However, no significant difference has been found between forest structural parameters (DBH and TD) and LAI. This is likely due to study limitations, namely time constraint. Further studies should consider long-term monitoring of LAI, especially considering future structural changes in the secondary and native food forests and variations between dry and wet seasons. The ability to map and characterise variation in LAI across forest types is critical for understanding how their primary productivity will respond to an increasing degree of anthropogenic disturbance.

Introduction

Leaf economics spectrum and Leaf Area Index

Plants possess functional trait values that reflect their evolutionary history and define both their physiological and physical performance (Lam et al., 2022). Functional traits are widely used in ecology as they encompass plant life history, demographics, short- and long-term responses (Sterck et al., 2006), at organ, individual, community and ecosystem scales (Ordway et al., 2022). Assessing these functional traits can help us understand plant trade-off mechanisms along a 'Leaf Economics Spectrum' (Reich, 2014), which defines the leaf morphological trade-off between resource acquisition and structural resilience. Plants at one end of the spectrum, possessing fast traits, are advantaged in high-resource environments, as they implement the 'productive strategy' for rapid light, nutrient and water uptake, but build quickly disposable tissues and are less tolerant to low resource availability (Sterck et al., 2006). Plants on the other hand of the spectrum will use the 'conservative strategy' (Paramanik et al., 2022; Sterck et al., 2006), through low respiration rates, low nutrient concentrations, slow water uptake, denser tissues, but longer leaf life-span. This conceptualisation of functional traits has offered generalisability to predict ecosystem processes (Mahowald et al., 2016), and this is fundamental for understanding plant interaction with external abiotic and biotic factors.

Watson was among the first to use the concept of Leaf Area Index (LAI), a dimensionless plant functional trait highly valued in ecology for its wide research applications (Watson, 1958). The trait equates to the one-sided cumulative leaf area of a stand per unit ground area. If the value is 0 it reflects absence of canopy, while the highest values registered so far are around 6 (thick dense canopy, no sky visible) (Clark et al., 2008; Miranda et al., 2020). Not only is it used to describe canopy density and the frequency of gaps in between the canopy, but most importantly to understand whole-plant organism functioning (Hardwick et al., 2015). LAI regulates a series of physiological processes, namely evaporation, transpiration, latent and sensible heat fluxes (Hardwick et al., 2015), CO2 exchange between terrestrial ecosystem and the atmosphere (Deb Burman et al., 2017), as well as physical processes, such as radiation and water interception (Srinet et al., 2019). Being considered an essential attribute of global vegetation, LAI has been listed as an essential climate change variable by the global climate research community (GCOS, 2011). It is positively associated with plant photosynthetic activity. In fact, it plays a crucial role in estimating Gross Primary Production (GPP) and is one of the primary parameters used in land-surface biogeochemical models and radiative transfer models (Mahowald et al., 2016; Sinha et al., 2020; Tang et al., 2012). Lastly, LAI can be linked to the evolutionary and biogeographical history of a specific vegetation form (Lam et al., 2022), as well as a community's response to abrupt changes in its surroundings (Valladares et al., 1997).

Approaches to evaluating LAI variation at a small scale

There are different methods for evaluating LAI, both directly and indirectly. Direct methods consist in harvesting leaves from the tree canopy and measuring their area on one side. With this method, precision is necessary to avoid overlapping of leaves and causing leaf area underestimation (Clark et al., 2008). A clear advantage of harvesting is the direct quantitative results obtained. On the other hand, it is expensive and logistically intensive (Clark et al., 2008; Fang et al., 2019), not to mention unsustainable especially for long-term monitoring. Indirect methods include remote sensing, ground-based light sensors, digital photography and allometric equations based on leaf harvest data or forest structure variables, such as diameter at breast height (DBH), tree height and tree density. Remote sensing involves measurement of transmitted or reflected light and calculations using inferential models, and research is increasing using this methodology (Poblete-Echeverría et al., 2015). Light Detection And Ranging (LiDAR), in particular, is very precise for estimating height and vertical structure of forests (Tang et al., 2012). However, it is not always an economically viable option, data are seldom public and require validation with ground-based data. Allometric equations are a semi-direct approach (Paramanik et al., 2022), however they are specific to site, stand age, density and climatic conditions, and can become a tenuous methodology when applied to a site with fundamentally different environmental characteristics (Wirth et al., 2001).

Digital photography has been one of the pioneering methods in forest ecology to estimate canopy cover and LAI. Indirect optical methods have been developed based on measurements of direct or diffuse light penetration through the canopy (Drever and Lertzman, 2003). Hemispherical photography acquires images with an extremely wide-angle fish lens, yielding the footprint of the canopy with a 180° Field Of View (FOV) in one photograph (Chianucci et al., 2022). The large area coverage is very advantageous, and allows determination of both leaf area and foliage angle distribution by measuring gap fraction at multiple zenith angles. However, it is very sensitive to sky conditions and camera exposure, which affects the accuracy of canopy gap retrieval (Alivernini et al., 2018). It is also very complex to process these images and theoretical formulas are necessary to infer LAI from the angular distribution of gap fraction values (Chianucci et al., 2022). Digital Cover Photography (DCP) is a more recent indirect method to quantify canopy attributes. DCP uses a narrower FOV than hemispherical photography, typically around 30°, which allows for improved image resolution close to the zenith and better distinction of crown gap sizes. Comparison with both indirect and direct LAI measurements have proven that DCP outperforms previous approaches (Poblete-Echeverría et al., 2015), such as hemispherical photography, and increases precision of LAI estimates. The main advantages include insensitivity to canopy exposure, gamma correction, canopy density and mean gap size, parameters which would typically impact hemispherical photographs (Alivernini et al., 2018; Macfarlane et al., 2007; Paramanik et al., 2022).

Leaf Area Index in the tropics

Tropical forests account for around one third of terrestrial primary productivity (Ordway et al., 2022), playing a major role as carbon sinks and in regulating regional and global climate (Clark et al., 2007). They constitute complex ecosystems of overlapping plant structures, competing for light among other resources. The existence and distribution of these plant layers has profound implications for light absorption and photosynthesis. In particular, plants that constitute the overstory of tropical forests are direct drivers of light availability within the forest (Döbert et al., 2018). Canopy density strongly influences the angle of incidence of solar radiation, and the ratio of diffuse and direct solar radiation. Previous studies have shown that tropical primary forest canopies have LAI values around 5-6, where the leaves can block up to 95% of visible light (Drever and Lertzman, 2003), affecting the understory microclimate, in terms of air and soil temperature, humidity and wind speed (Hardwick et al., 2015). Trees in nutrient-rich environments, such as the tropics, are often characterised by high leaf nutrient concentrations and invest less in structure and defence, enabling faster growth to reach for light, and rapid leaf turnover (Sterck et al., 2006). This strategy supports higher photosynthetic rates and more rapid carbon gain.

Different studies have shown that land use change is an important anthropogenic disturbance affecting the structural composition of tropical forests (Hardwick et al., 2015; Valladares et al., 1997), however not much research has been done to see how this affects LAI at community level. Deforestation is ever-increasing in the tropics, accommodating for new land uses, namely agricultural and industrial, and reducing forests to disconnected patches of land. Forests continue decreasing in size as their edges increase (Pfeifer et al., 2016), likely altering their physiological performance and their contribution as carbon sinks. The Amazon is an ecosystem deeply affected by landscape fragmentation, characterised by an alternating mosaic of agricultural concessions, gold mines, primary, secondary, and native food forests. Both ‘intact’ and regenerating tropical forests are important to the global carbon cycle and other Ecosystem Services (Clark et al., 2021), and it is important to quantify LAI values in such structurally distinct landscapes as a proxy of their primary productivity. This study aims to quantify the spatial variation of LAI values and to assess its relationship with forest structure parameters (DBH and tree density), between primary, secondary and a native food forest in the Peruvian Amazon. In particular, the research questions in this study concern i) whether LAI varies spatially between primary, secondary and native food forests; ii) whether LAI is positively related with forest structural parameters (DBH and tree density). LAI values are expected to decrease from PF to SF and NFF, respectively. With increasing DBH and TD, also LAI values are expected to increase.

Methods

Study site

This study was conducted at the Alliance for a Sustainable Amazon (ASA) research station, in Finca Las Piedras, Madre de Dios region, Peru, located in the southwestern Amazon basin. The landscape at ASA can be divided in a 50 ha primary forest, a 10 ha secondary forest and ca. 8.000 m2 native food forest. The primary forest had been selectively logged up until 20 years ago, its structural composition is very heterogeneous and rich in biodiversity. Furthermore, it is situated along the Brazil nut (Bertholletia excelsa) corridor and is one of the most abundant areas, which is very important for the Peruvian economy. The secondary forest is 7 years old, as reforestation only started in 2016 after the area was affected by a fire. Trees in the area vary greatly in size, some being taller than 10 m as part of a more established forest, while others being young treelets, some planted at the same time as this study was carried out as part of ASA's reforestation project that one day will serve as a wildlife corridor. Species include those which had previously been logged unsustainably, such as big-leaf mahogany (Swietenia macrophylla), Spanish cedar (Cedrela odorata), and ironwood (Dipteryx micrantha) (ASA Biannual Report, 2019-2020). Lastly, the native food forest is a small, experimental agroforestry system that includes Amazonian native species, namely guava (Inga edulis), cacao (Theobroma cacao) and Brazil nut (B. excelsa) (ASA Biannual Report, 2019-2020). The study was carried out during the course of two weeks between the months of September and October 2023.

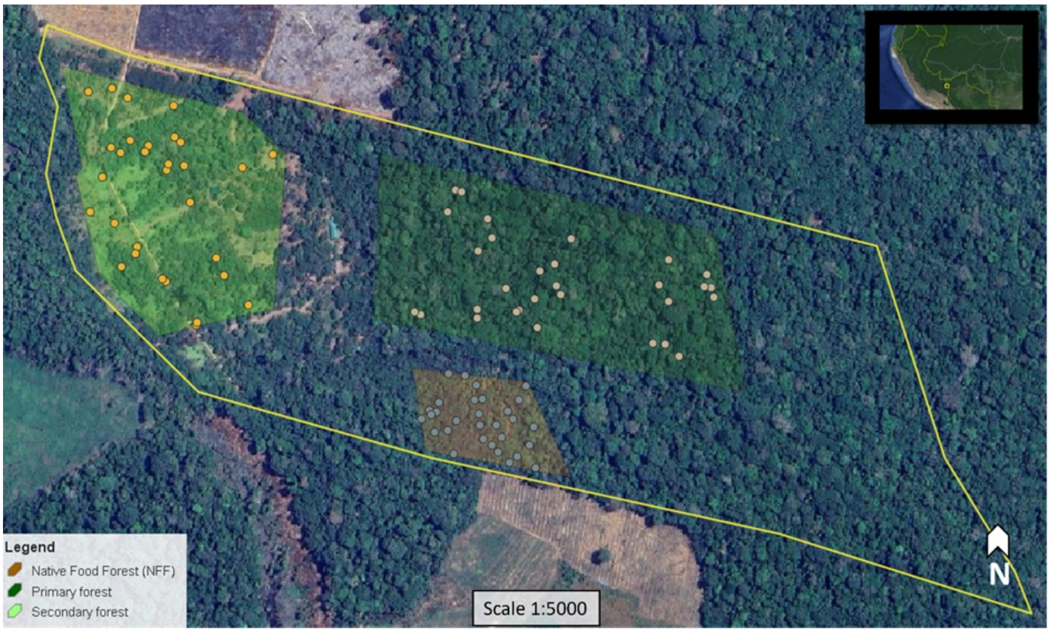


Figure 1: Aerial view of Alliance for Sustainable Amazon research station. The yellow line outlines the borders of the property. The three polygons correspond to the three study sites, which are subject to this research. The light green polygon corresponds to the Secondary Forest (SF), the dark green polygon is the Primary Forest (PF) and the brown polygon is the Native Food Forest (NFF). The points represent the plots, created through a random point generator in QGIS.

Data collection

Within each study site, 30 circular plots with 5 m radius were established through a random sampling method. In each plot, only stems of living trees with a circumference >= 5 cm were counted (Unger et al., 2013). The Diameter at Breast Height (1.3 m from ground) was calculated only for trees with a circumference >= 10 cm.

Digital Cover Photography (DCP) was the chosen method for analysing canopy cover, as it resulted relatively insensitive to sky conditions which can be attributed to a combination of high image resolution and small effective sampling of cover images. This yielded even sky illuminance and facilitated pixel classification. At the centre of each plot, a digital photograph of the canopy was taken with a Nikon D3400, at 1.5 m height from the ground and 35 mm focal length (44° FOV). The choice of focal length was made so as to correspond as closely as possible with the plot area. Some movement from the centre of the plot was considered necessary if vegetation were too close to the camera lens, cluttering the view to the canopy. Also, photographs were taken twice a day on a sunny day, early to mid-mornings and mid to late afternoons, at zenith angle of around 50°, to avoid having the sun directly overhead and affecting the quality of the photograph. This was not necessary in case of an overcast sky.

Image processing

The digital photographs of the canopy cover were imported, classified and analysed with CoveR in RStudio. The functions available in the package allowed to classify canopy gaps based on their pixel size, and to calculate forest functional attributes such as LAI, relating canopy structure to gap fraction (Macfarlane et al., 2007). Each pixel of a photo consists of three digital numbers which are light intensity quantised in the red, green and blue bands. The blue band (450 nm–495 nm) was chosen as it enables the highest contrast between sky and canopy pixels (Chianucci et al., 2022), which made image classification much easier. The pixels were then classified to get a binary image of sky (1) and canopy (0). To retrieve LAI, first the gap pixels were further classified based on their size (large gaps were considered those larger than 1.3% of the image area, following Macfarlane et al., 2007).

Data processing

The exported values equate to ‘effective LAI’ (LAIe), as the algorithm corrects LAI for woody elements, which would otherwise result in overestimation, and clumping of foliage, which would result in underestimation, with a light extinction coefficient k (Srinet et al., 2019). Light extinction coefficient indicates the light interception efficiency through the canopy. k values depend on leaf inclination and incident solar radiation represented by zenith or azimuth angles. Due to lack of in-situ measurements, k is assumed as a constant (0.85) (Chianucci, 2020).

$$\mathbf{LAIe = -\ (\log\boxed{f0}(GF))/k}$$

GF corresponds to Gap Fraction, or the fraction of gap pixels (labelled 1 in the binary image).

Tree DBH (cm) was calculated from the collected data on circumference. Tree Density (TD) was calculated by dividing the number of trees counted by the plot area.

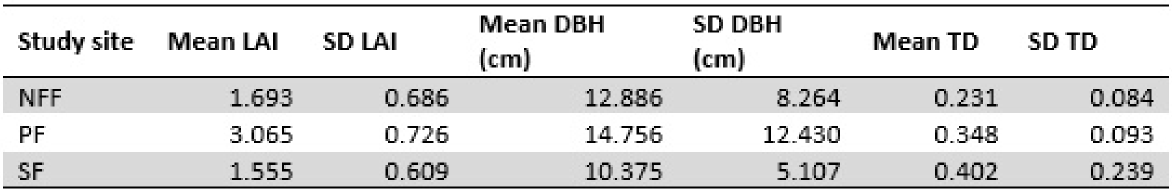
Data analysis

Mean and Standard Deviation (SD) values were calculated for LAI, DBH and TD, in each of the three forest types. Variations in LAI were observed through violin plots, which combine boxplots with density distributions. The spatial variation of LAI values was then observed with a bubble plot, which depicts the spatial coordinates of the site, and the intensity of the value through the size of the bubble. The relationship between forest structural parameters (DBH, TD) and LAI were first observed through scatterplots and calculation of R-squared from the linear trends. Finally, the significance of the effect of DBH and TD on LAI and eventual differences between forest types were statistically analysed through linear regression models.

Results

First observations

A total of 47 plots were successfully surveyed, among the three study sites (PF n = 17; SF n = 14; NFF n = 16). As shown in table 1, mean LAI values are higher in PF, and are similar between SF and NFF. Mean DBH values are consistent between the three forest types, however SD values are larger for PF, indicating greater variability. The same applies for TD values, this time also NFF presents a larger SD, compared to SF.



Study site	Mean LAI	SD LAI	Mean DBH (cm)	SD DBH (cm)	Mean TD	SD TD
NFF	1.693	0.686	12.886	8.264	0.231	0.084
PF	3.065	0.726	14.756	12.430	0.348	0.093
SF	1.555	0.609	10.375	5.107	0.402	0.239

Table 1 Mean and standard deviation values for LAI, DBH and TD at primary, secondary and native food forests.

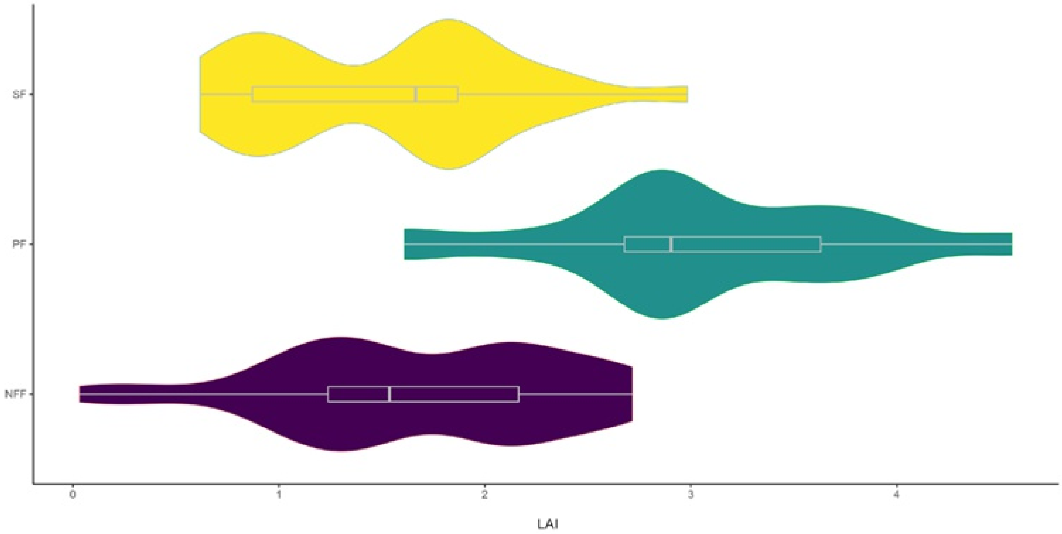


Figure 4: Violin plot showcasing data distribution for LAI across the three forest types.

Data distribution

LAI distributions are bimodal. LAI values range between 1 and 2 for SF. Distribution for PF is left-skewed and ranges between 2.5 and 3.8. It is also left-skewed for NFF, and ranges between 1.4 and 2.3. DBH data are normally distributed. The peaks fall around 10 cm for all three forest types. PF presents the largest range in values, between 5 and 65 cm. SF presents the smallest range on the other hand, between 5 and 23 cm. As for DBH, also TD data are normally distributed. SF presents the greatest variability, with TD ranging between 0.1 and 0.8.

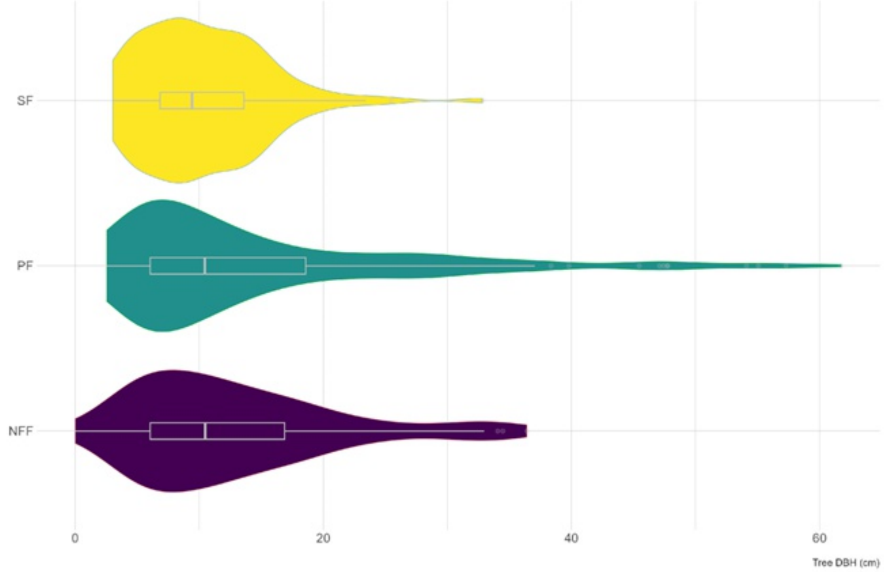


Figure 5: Violin plot showcasing DBH (cm) data distribution across forest types.

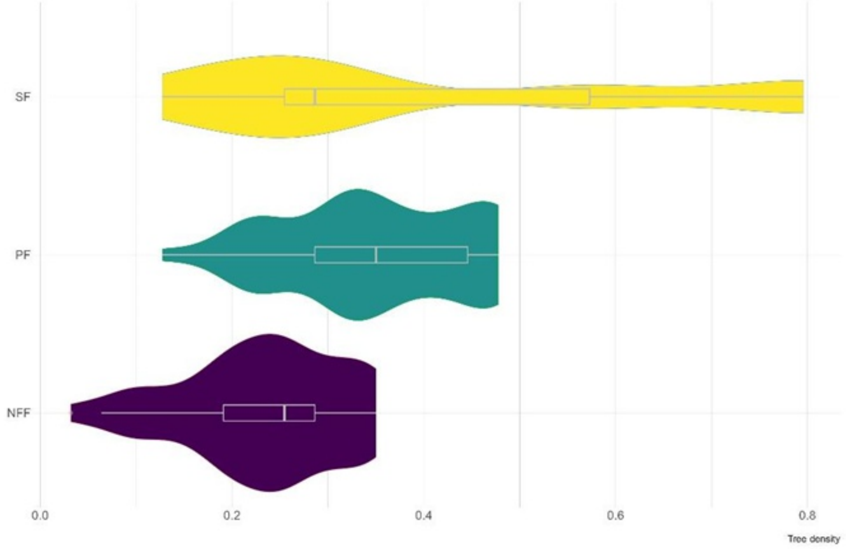


Figure 6: Violin plot showcasing tree density (n/m2) data distribution across forest types.

Figure 7 shows spatial variation of LAI values across the three study sites. SF and NFF present strong heterogeneity in LAI values, while PF is consistent with values around 3.

Figure 8 shows the frequency of large gaps (intended as > 1.3% of the image; Macfarlane et al., 2007). NFF and SF present the largest frequency (NFF = 32; SF = 27).

Relationship between forest structural attributes and LAI

A significant difference is observed between forest types (p-value < 0.0001). Figure 8 shows results from the correlation between DBH (cm) and LAI. No significant difference was found between DBH (cm) and LAI (p-value = 0.137). Figure 9 shows results from the correlation between TD (n/m2) and LAI. A weak negative correlation can be observed for PF ($R2 > 0.09$). A weak significant difference was found between TD (n/m2) and LAI (p-value = 0.019).

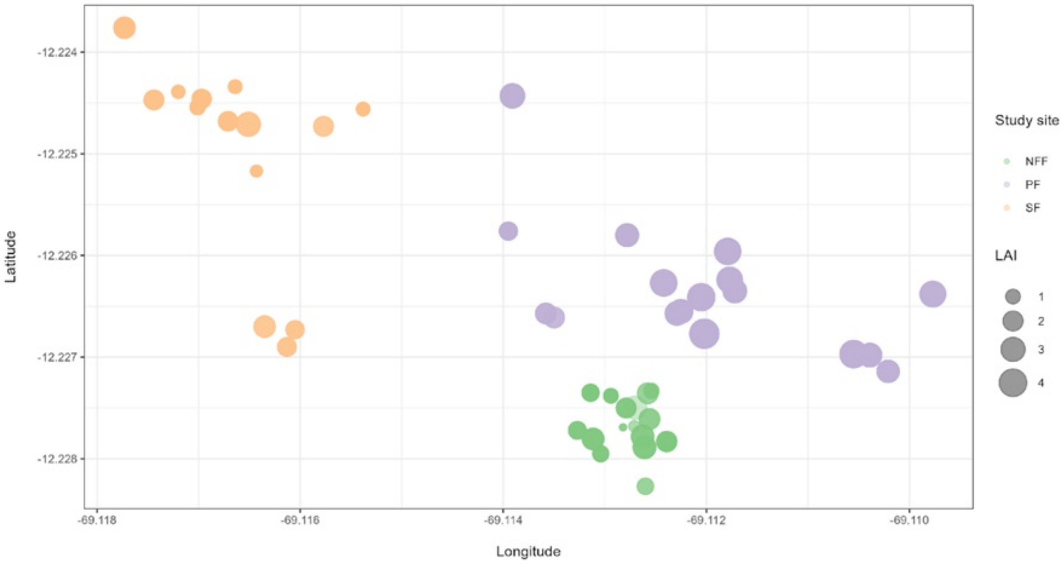


Figure 7: Spatial variation of LAI on site, depicted at the location of the plots. The value of LAI is represented with dots, the size variation corresponding to the value of LAI. The data points are subdivided by

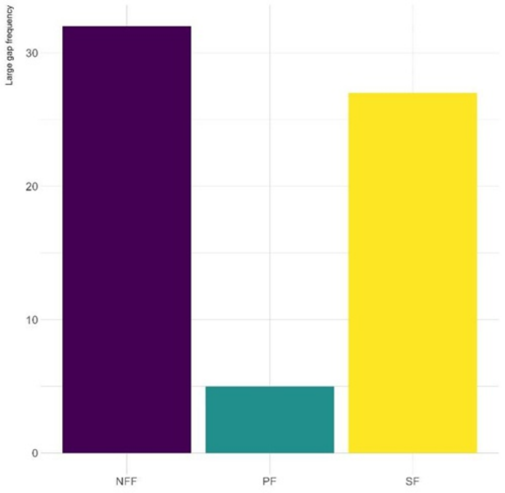


Figure 8: bar plot showing frequency of large gaps in the canopy (considered as > 1.3% of the image size; Macfarlane et al., 2022).

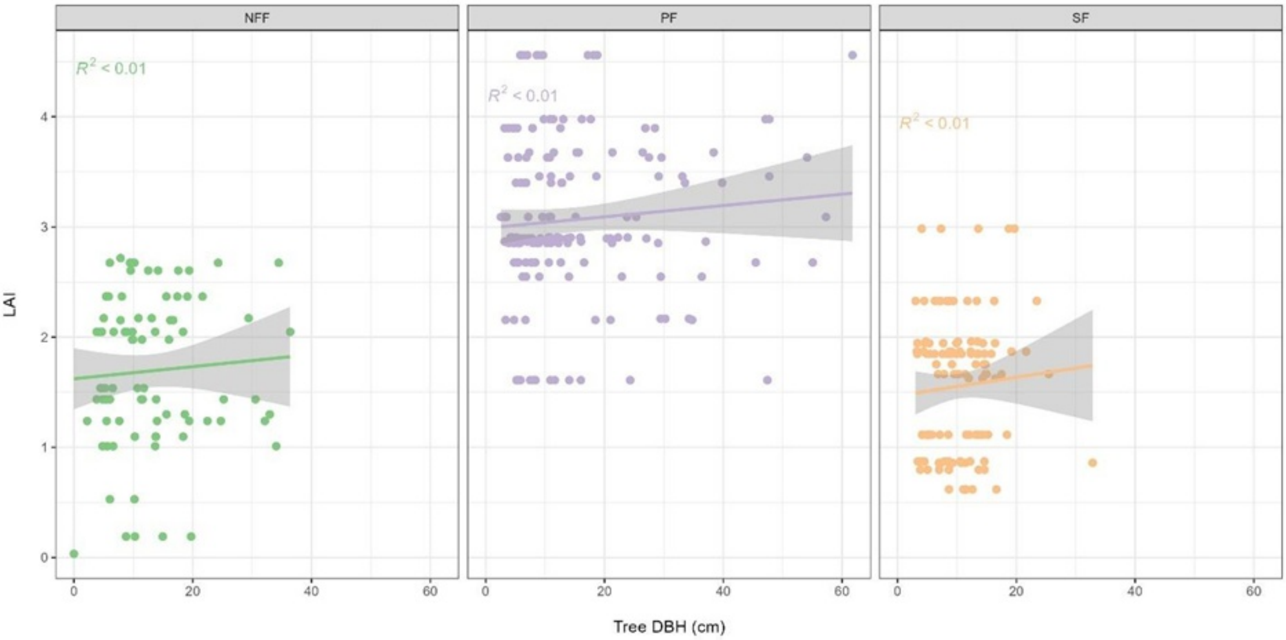


Figure 9: Scatterplot of Tree DBH (cm) on LAI. The plot is divided by forest type.

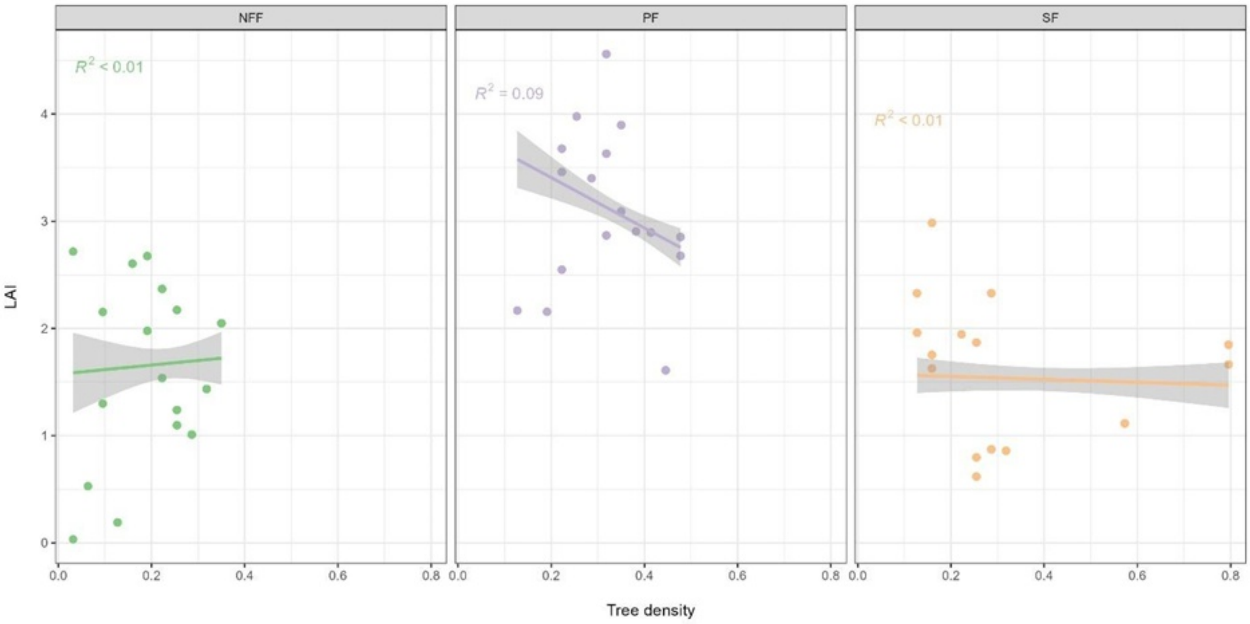


Figure 10: Scatterplot presenting the relationship between tree density and LAI. The plot is divided by forest type.

Discussion

LAI varies in space within and between forest types

From initial observations of LAI values and visual observations of its spatial variation, it is possible to say that there is a clear difference in LAI between forest types (p-value < 0.0001). The three sites present inherent structural differences, in terms of age, species composition and diversity, and stand structural heterogeneity. Also, as expected, PF presented the highest values of LAI (mean ca. 3), in accordance with other studies on tropical forests (Tang et al., 2012). This reflects the maturity of the forest (20+ years old), its nutrient-rich environment and the high level of primary production that occurs. Contrary to expectations, mean LAI values were similar for NFF and SF, around 1. According to similar studies, any LAI =< 1 allows some light energy to fall onto the soil (Lam et al., 2022). This reflects the structural characteristics of NFF and SF, which in fact present large canopy gaps (fig. 8). However, this result is in disagreement with other studies, which have found a greater similarity between SF and PF (Aragão et al., 2005; Miranda et al., 2020), rather than with agroforestry systems (Liu and Pattey, 2010; Macfarlane et al., 2007). This could be due to the fact that agroforestry systems are generally more structured and managed than SF. However, this does not apply for this specific research site, and the similarity could be explained by the fact that both SF and NFF projects started around the same time and are still in development (ASA Biannual Report, 2017-2018).

Relationship between LAI and forest structural parameters

The scatterplots (fig. 9 and 10) highlighted a lack of relationship between forest structural parameters and LAI, with a weak exception for TD in the PF. In fact, the negative trend visible in fig. 10 for PF is tenuous, as only 9% of LAI variability is explained by the model (R2 = 0.09). Differently from other studies, which found strong coupling of stem traits – including DBH and TD – with LAI across forested environments (Clark et al., 2021; Ordway et al., 2022), this study didn't find statistical significance between either structural parameter and LAI. The null hypothesis is therefore accepted, inferring that these two parameters do not influence variations in LAI. This is likely due to presence of confounding factors, as high plant biodiversity (Xie et al., 2023), topographic (Pfeifer et al., 2016; Valladares et al., 1997) and edaphic heterogeneity (Villegas, 2019) are known to influence LAI variability in Amazonian ecosystems. Other studies have also included tree height in their measurements (Paramanik et al., 2022). This could improve the accuracy of results significantly, especially considering the high vertical heterogeneity of PF forests.

Study limitations and observations for future studies

A variety of limitations should be pointed out to support the results obtained. Time was a big constraint for data collection. Because of this, only 47 plots were successfully collected, out of the 90 which had been planned originally. A greater sample size will likely allow better accuracy in depicting the spatial variation of LAI across the three sites. This will be especially significant for PF, also to detect presence of large light gaps, which were not considered in this study. Large gaps play a prominent role in determining the composition and structure of forest communities, and consequently LAI values (Liu and Pattey, 2010; Montgomery and Chazdon, 2002). Future studies should also consider long-term temporal variation of LAI values and its relationship to forest structural parameters (Wirth et al., 2001), as there will likely be interesting differences between the dry and the wet season. It also needs to be pointed out that Brazil nut trees were not measured during this study, both due to instrument limitations for DBH measurements and the random plot allocation design. The canopy would have also been very hard to capture digitally, considering their height, and would have provided inaccurate LAI estimates. However, they are present at high density, and their inclusion would certainly have an impact on the results. Using remote sensing, and LiDAR technology in particular, would certainly improve the accuracy of these estimates.

The Digital Cover Photography (DCP) method presents inherent assumptions and inaccuracies. Scattering effects might have influenced the calculation of LAI values (Alivernini et al., 2018), especially as the sun was moving closer to zenith during the time of each survey. The main disadvantage of DCP is that it would require knowledge of leaf angle distribution to improve accuracy of LAI estimates (Wirth et al., 2001). Estimates of LAI were calculated with a light extinction coefficient (k) at a constant (0.85). Such extinction coefficient implies a spherical distribution of foliage, which rarely occurs in real forest canopies (Wirth et al., 2001). It is recommended to collect estimates of k at the site of interest (Srinet et al., 2019), however this was not feasible for this study as it would have impacted the nature conservation objectives of the research station. A study also suggests to take multiple photographs per plot to improve spatial representation (Pfeifer et al., 2016), and the number should be chosen based on the structural heterogeneity of the forest under study. Further studies should focus on increasing the number of photographs especially for PF, considering the vertical heterogeneity and canopy layering of the forest.

Conclusion

This study constitutes the first attempt to estimate LAI values and assess whether their variation was influenced by forest structural parameters. The results were not matching expectations, and this was likely due to experimental design limitations. However, it is fundamental to continue studying this parameter, especially in the long-term, being considered an essential climate change variable. Establishment of appropriate relationships between leaf area and other predictor variables, such as DBH, TD, and tree height, are essential in plant physiology research. The ability to map and characterise variation in LAI across forest types is critical for understanding how their primary productivity will respond to an increasing degree of anthropogenic disturbance. Accurate estimates of LAI will also be fundamental for modelling processes concerning energy balance, gas exchange and light distribution at different spatiotemporal scales.

Bibliography

Alivernini, A., Fares, S., Ferrara, C., Chianucci, F., 2018. An objective image analysis method for estimation of canopy attributes from digital cover photography. Trees 32, 713–723. https://doi.org/10.1007/s00468-018-1666-3

Aragão, L.E.O.C., Shimabukuro, Y.E., Espírito Santo, F.D.B., Williams, M., 2005. Landscape pattern and spatial variability of leaf area index in Eastern Amazonia. Forest Ecology and Management 211, 240–256. https://doi.org/10.1016/j.foreco.2005.02.062

Chianucci, F., 2019. An overview of in situ digital canopy photography in forestry. Can. J. For. Res. 227–242. https://doi.org/10.1139/cjfr-2019-0055

Chianucci, F., Ferrara, C., Puletti, N., 2022. coveR: an R package for processing digital cover photography images to retrieve forest canopy attributes. Trees 36, 1933–1942. https://doi.org/10.1007/s00468-022-02338-5

Clark, D.B., Oberbauer, S.F., Clark, D.A., Ryan, M.G., Dubayah, R.O., 2021. Physical structure and biological composition of canopies in tropical secondary and old-growth forests. PLOS ONE 16, e0256571. https://doi.org/10.1371/journal.pone.0256571

Clark, D.B., Olivas, P.C., Oberbauer, S.F., Clark, D.A., Ryan, M.G., 2008. First direct landscape-scale measurement of tropical rain forest Leaf Area Index, a key driver of global primary productivity. Ecology Letters 11, 163–172. https://doi.org/10.1111/j.1461-0248.2007.01134.x

Deb Burman, P.K., Sarma, D., Williams, M., Karipot, A., Chakraborty, S., 2017. Estimating gross primary productivity of a tropical forest ecosystem over north-east India using LAI and meteorological variables. J Earth Syst Sci 126, 99. https://doi.org/10.1007/s12040-017-0874-3

Döbert, T.F., Webber, B.L., Sugau, J.B., Dickinson, K.J.M., Didham, R.K., 2018. Logging, exotic plant invasions, and native plant reassembly in a lowland tropical rain forest. Biotropica 50, 254–265. https://doi.org/10.1111/btp.12521

Drever, C.R., Lertzman, K.P., 2003. Effects of a wide gradient of retained tree structure on understory light in coastal Douglas-fir forests. Can. J. For. Res. 33, 137–146. https://doi.org/10.1139/x02-167

Fang, H., Baret, F., Plummer, S., Schaepman Strub, G., 2019. An Overview of Global Leaf Area Index (LAI): Methods, Products, Validation, and Applications. Reviews of Geophysics 57, 739–799. https://doi.org/10.1029/2018RG000608

GCOS, 2011. Systematic Observation Requirements for Satellite-based Products for Climate Supplemental details to the satellite-based component of the Implementation Plan for the Global Observing System for Climate in Support of the UNFCCC [WWW Document]. URL https://library.wmo.int/records/item/48411-systematic-observation-requirements-for-satellite-based-products-for-climate-supplemental-details-to-the-satellite-based-component-of-the-implementation-plan-for-the-global-observing-system-for-climate-in-support-of-the-unfccc (accessed 10.12.23).

Hardwick, S.R., Toumi, R., Pfeifer, M., Turner, E.C., Nilus, R., Ewers, R.M., 2015. The relationship between leaf area index and microclimate in tropical forest and oil palm plantation: Forest disturbance drives changes in microclimate. Agricultural and Forest Meteorology 201, 187–195. https://doi.org/10.1016/j.agrformet.2014.11.010

Lam, W.N., Chan, P.J., Ting, Y.Y., Sim, H.J., Lian, J.J., Chong, R., Rahman, N.E., Tan, L.W.A., Ho, Q.Y., Chiam, Z., Arora, S., Lai, H.R., Ramchunder, S.J., Peh, K.S.-H., Cai, Y., Chong, K.Y., 2022. Habitat Adaptation Mediates the Influence of Leaf Traits on Canopy Productivity: Evidence from a Tropical Freshwater Swamp Forest. Ecosystems 25, 1006–1019. https://doi.org/10.1007/s10021-021-00697-7

Liu, J., Pattey, E., 2010. Retrieval of leaf area index from top-of-canopy digital photography over agricultural crops. Agricultural and Forest Meteorology 150, 1485–1490. https://doi.org/10.1016/j.agrformet.2010.08.002

Macfarlane, C., Hoffman, M., Eamus, D., Kerp, N., Higginson, S., McMurtrie, R., Adams, M., 2007. Estimation of leaf area index in eucalypt forest using digital photography. Agricultural and Forest Meteorology 143, 176–188. https://doi.org/10.1016/j.agrformet.2006.10.013

Mahowald, N., Lo, F., Zheng, Y., Harrison, L., Funk, C., Lombardozzi, D., Goodale, C., 2016. Projections of leaf area index in earth system models. Earth System Dynamics 7, 211–229. https://doi.org/10.5194/esd-7-211-2016

Miranda, R. de Q., Nóbrega, R.L.B., Moura, M.S.B. de, Raghavan, S., Galvíncio, J.D., 2020. Realistic and simplified models of plant and leaf area indices for a seasonally dry tropical forest. International Journal of Applied Earth Observation and Geoinformation 85, 101992. https://doi.org/10.1016/j.jag.2019.101992

Montgomery, R., Chazdon, R., 2002. Light gradient partitioning by tropical tree seedlings in the absence of canopy gaps. Oecologia 131, 165–174. https://doi.org/10.1007/s00442-002-0872-1

Ordway, E.M., Asner, G.P., Burslem, D.F.R.P., Lewis, S.L., Nilus, R., Martin, R.E., O’Brien, M.J., Phillips, O.L., Qie, L., Vaughn, N.R., Moorcroft, P.R., 2022. Mapping tropical forest functional variation at satellite remote sensing resolutions depends on key traits. Commun Earth Environ 3, 1–11. https://doi.org/10.1038/s43247-022-00564-w

Paramanik, S., Behera, M.D., Dash, J., 2022. Symbolic regression-based allometric model development of a mangrove forest LAI using structural variables and digital hemispherical photography. Applied Geography 139, 102649. https://doi.org/10.1016/j.apgeog.2022.102649

Pfeifer, M., Kor, L., Nilus, R., Turner, E., Cusack, J., Lysenko, I., Khoo, M., Chey, V.K., Chung, A.C., Ewers, R.M., 2016. Mapping the structure of Borneo’s tropical forests across a degradation gradient. Remote Sensing of Environment 176, 84–97. https://doi.org/10.1016/j.rse.2016.01.014

Poblete-Echeverría, C., Fuentes, S., Ortega-Farias, S., Gonzalez-Talice, J., Yuri, J.A., 2015. Digital Cover Photography for Estimating Leaf Area Index (LAI) in Apple Trees Using a Variable Light Extinction Coefficient. Sensors 15, 2860–2872. https://doi.org/10.3390/s150202860

Reich, P.B., 2014. The world wide 'fast–slow' plant economics spectrum: a traits manifesto - Reich - 2014 - Journal of Ecology - Wiley Online Library [WWW Document]. URL https://besjournals.onlinelibrary.wiley.com/doi/full/10.1111/1365-2745.12211 (accessed 10.11.23).

Sinha, S.K., Padalia, H., Dasgupta, A., Verrelst, J., Rivera, J.P., 2020. Estimation of leaf area index using PROSAIL based LUT inversion, MLRA-GPR and empirical models: Case study of tropical deciduous forest plantation, North India. International Journal of Applied Earth Observation and Geoinformation 86, 102027. https://doi.org/10.1016/j.jag.2019.102027

Srinet, R., Nandy, S., Patel, N.R., 2019. Estimating leaf area index and light extinction coefficient using Random Forest regression algorithm in a tropical moist deciduous forest, India. Ecological Informatics 52, 94–102. https://doi.org/10.1016/j.ecoinf.2019.05.008

Sterck, F.J., Poorter, L., Schieving, F., 2006. Leaf Traits Determine the Growth Survival Trade Off across Rain Forest Tree Species. The American Naturalist 167, 758–765. https://doi.org/10.1086/503056

Tang, H., Dubayah, R., Swatantran, A., Hofton, M., Sheldon, S., Clark, D.B., Blair, B., 2012. Retrieval of vertical LAI profiles over tropical rain forests using waveform lidar at La Selva, Costa Rica. Remote Sensing of Environment 124, 242–250. https://doi.org/10.1016/j.rse.2012.05.005

Unger, M., Homeier, J., Leuschner, C., 2013. Relationships among leaf area index, below-canopy light availability and tree diversity along a transect from tropical lowland to montane forests in NE Ecuador. Tropical Ecology 54, 33–45.

Valladares, F., Allen, M.T., Pearcy, R.W., 1997. Photosynthetic responses to dynamic light under field conditions in six tropical rainforest shrubs occuring along a light gradient. Oecologia 111, 505–514. https://doi.org/10.1007/s004420050264

Villegas, S.E., 2019 Ecological Succession in Tropical Forests: The Role of Edaphic Factors, Initial Conditions and Competition.

Watson, D.J., 1958. The Dependence of Net Assimilation Rate on Leaf-area Index. Annals of Botany 22, 37–54. https://doi.org/10.1093/oxfordjournals.aob.a083596

Wirth, R., Weber, B., Ryel, R.J., 2001. Spatial and temporal variability of canopy structure in a tropical moist forest. Acta Oecologica 22, 235–244. https://doi.org/10.1016/S1146-609X(01)01123-7

Xie, X., Yang, Y., Li, W., Liao, N., Pan, W., Su, H., 2023. Estimation of Leaf Area Index in a Typical Northern Tropical Secondary Monsoon Rainforest by Different Indirect Methods. Remote Sensing 15, 1621. https://doi.org/10.3390/rs15061621