

Short Communication

Fine-scale forest structure and natural regeneration in a mature tropical rainforest assessed using terrestrial LiDAR

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Abstract

Natural regeneration in tropical forests is influenced by fine-scale structural heterogeneity and light availability, yet these relationships remain difficult to quantify using conventional field methods. We evaluated associations between forest structure and early regeneration in a mature lowland tropical rainforest in Costa Rica using field measurements and terrestrial laser scanning (TLS). We characterized six permanent forest plots through estimates of canopy openness, overstory attributes, and TLS-derived indices describing understory complexity (UCI) and stand structural complexity (SSCI). We assessed regeneration through surveys of seedlings and saplings within subplots. Canopy openness exhibited the strongest relationship with regeneration, particularly with sapling abundance. TLS-derived metrics captured variation in forest structure and revealed positive associations between understory complexity and regeneration, whereas stand structural complexity showed no clear relationship with recruitment patterns. These findings highlighted the importance of light availability and understory structure in shaping regeneration dynamics and demonstrated the potential of TLS as a complementary tool for characterizing structural conditions associated with natural regeneration in tropical forests.

Keywords: canopy gaps, forest monitoring, plot-scale variation, sapling dynamics, understory complexity.

Introduction

Natural regeneration in tropical forests is strongly influenced by structural heterogeneity, light availability, and microsite conditions that affect seedling establishment and survival (Chazdon, 2014; Norden, 2014; De Lombaerde et al., 2021). Understanding these processes requires detailed characterization of forest structure, particularly the three-dimensional arrangement of vegetation that regulates light distribution and understory conditions (Muscolo et al., 2014). Traditional field approaches, however, often provide limited information on fine-scale structural variability, especially within the understory.

Recent advances in terrestrial laser scanning (TLS) have expanded opportunities to quantify forest structure at high spatial resolution. TLS provides accurate, non-destructive measurements of vegetation architecture and allows detailed characterization of structural attributes associated with ecological processes (Arrizza et al., 2024; Maeda et al., 2025). Although LiDAR technologies have improved the assessment of tropical forest structure, studies directly linking TLS-derived structural complexity with natural regeneration in mature tropical forests remain relatively scarce (Arrizza et al., 2024; Balestra et al., 2024). This limitation restricts our understanding of how fine-scale vegetation architecture

influences recruitment processes in structurally heterogeneous forest environments.

In this study, we evaluated how fine-scale forest structure relates to early regeneration patterns in a mature tropical rainforest in Costa Rica. By combining TLS-derived structural indices with field-based measurements of canopy openness and regeneration, we assessed whether detailed structural information could improve the characterization of recruitment processes at the plot level. We hypothesized that regeneration abundance would be positively associated with canopy openness and understory structural complexity, and that TLS-derived metrics would provide useful indicators of fine-scale conditions influencing recruitment. Understanding these relationships may contribute to improved monitoring and management of structurally complex tropical forests.

Methods

Study area. The study was conducted in six permanent forest plots (20 × 50 m) located in the Tirimbina Biological Reserve, Sarapiquí, Heredia, Costa Rica (Figure 1). Five plots were selectively logged approximately 50 years ago, while one corresponded to an abandoned

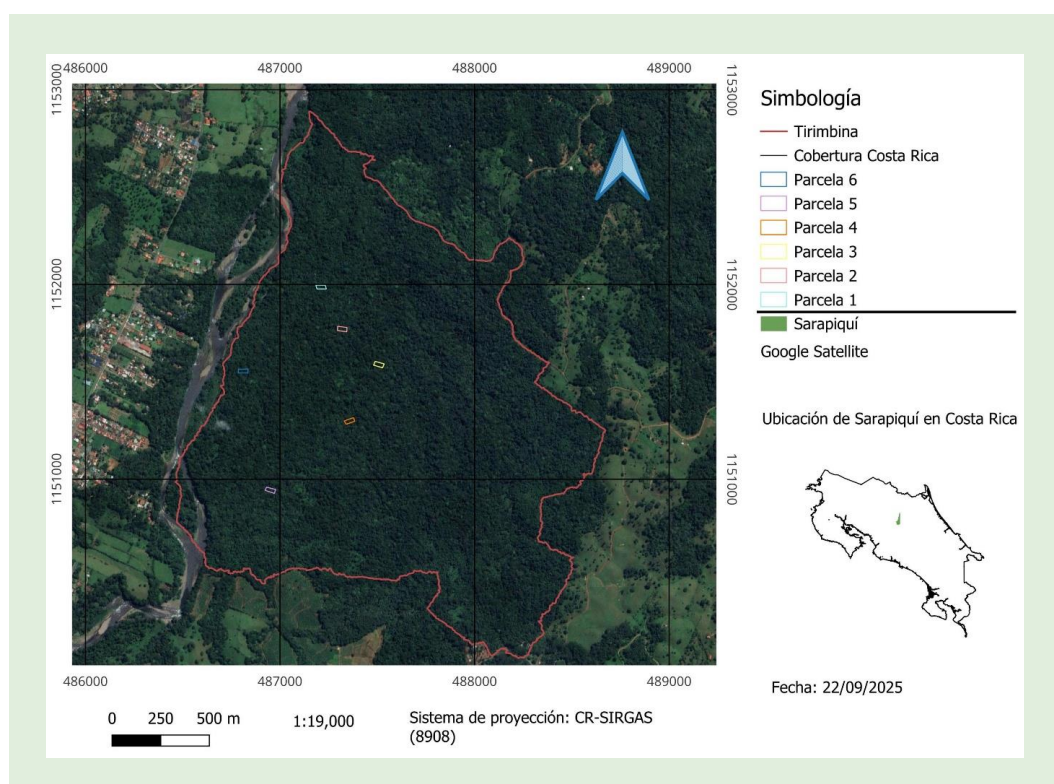


Figure 1. Location of the study plots within the Tirimbina Biological Reserve, Sarapiquí, Heredia, Costa Rica. Map prepared by Alicia Coto-Valverde.

cacao plantation last managed in the 1980s. The reserve comprises mature tropical rainforest under a humid climate, with annual precipitation exceeding 3,700 mm and mean temperatures around 25 °C (Reserva Biológica Tirimbina, s.f.).

Forest structure and canopy openness. Within each plot, all trees ≥ 10 cm DBH were measured, and tree height was estimated using a Haga hypsometer. Basal area and mean tree height were used as conventional descriptors of overstory forest structure and to provide contextual information for interpreting TLS-derived measures of structural complexity. Canopy openness was assessed with a spherical densitometer at five points along the central transect of each plot. At each point, four readings were taken facing the cardinal directions and averaged to obtain a plot-level estimate of canopy openness.

Fine-scale forest structure. Fine-scale forest structure was quantified using a terrestrial laser scanner (TLS; Faro Focus 3D S120) (Putrimas, 2013). In each plot, two single-position scans were conducted from fixed locations approximately 20 m apart, with the scanner mounted at 1.3 m above ground. This sampling design followed established protocols shown to capture representative structural attributes at the plot level (Jiménez-Méndez et al., 2024). The use of two scan positions helped reduce potential occlusion effects associated with single-scan observations. Point clouds from each scan were exported to XYZ format using CloudCompare and subsequently analyzed in RStudio (Girardeau-Montaut, 2024). Structural indices were calculated using scripts based on the workflows described by Ehbrecht et al. (2017), Frey et al. (2019), and Seidel et al. (2021), implemented through previously published R-based routines and associated packages. The Understory Complexity Index (UCI) was calculated for vegetation within the understory layer (~0.8–1.8 m height), whereas the Stand Structural Complexity Index (SSCI) was calculated from the entire point cloud following published procedures. Values obtained from the two scans conducted within each plot were averaged to generate plot-level estimates.

Natural regeneration. Natural regeneration was sampled within two 5 × 5 m subplots located in opposite corners of each permanent plot. All woody individuals ≥ 50 cm in height and < 10 cm DBH were recorded and classified as seedlings (50 cm–1.5 m height) or saplings (> 1.5 m height and < 10 cm DBH). Individuals were identified to species level.

Species richness and data analysis. Species richness was calculated separately for adult trees and regeneration. Floristic similarity was assessed using the Jaccard similarity index among plots and

between adult and regeneration layers. Relationships between forest structure and regeneration were explored using Pearson correlation analyses. Specifically, we evaluated associations between canopy openness, TLS-derived indices (UCI and SSCI), and regeneration abundance (seedlings and saplings). Additional correlations examined relationships between basal area, mean tree height, and SSCI. For each plot, TLS metrics were averaged and regeneration abundance was expressed as the total number of individuals recorded in the subplots. Analyses were performed using InfoStat v.2020 and R (Di Rienzo et al., 2020; R Core Team, 2024).

Results

Forest structure. Basal area and mean tree height varied among the six permanent forest plots, reflecting structural heterogeneity within the study area. Neither basal area ($r = 0.15$, $P = 0.77$) nor mean tree height ($r = 0.28$, $P = 0.59$) was associated with stand structural complexity (SSCI).

Fine-scale forest structure (TLS). TLS-derived indices revealed substantial variability in understory and stand structure among plots. The Understory Complexity Index (UCI) was positively associated with seedling abundance ($r = 0.27$) and showed a stronger relationship with sapling abundance ($r = 0.78$, $P = 0.07$) (Figure 2). In contrast, the Stand Structural Complexity Index (SSCI) showed no clear relationship with seedling abundance ($r = 0.59$, $P = 0.21$) or sapling abundance ($r = 0.53$, $P = 0.92$).

Canopy openness. Canopy openness showed positive associations with regeneration abundance. The relationship was moderate for seedlings ($r = 0.66$, $P = 0.15$) and stronger for saplings ($r = 0.83$, $P = 0.04$) (Figure 3).

Natural regeneration. Regeneration density varied among plots. Seedlings and saplings exhibited different patterns of abundance across the study area.

Species richness and floristic similarity. Adult tree richness ranged from 19 to 30 species per plot. Floristic similarity among adult plots was low (Jaccard index = 0.11–0.34). The proportion of species shared between adult and regeneration layers ranged from 11% to 29%.

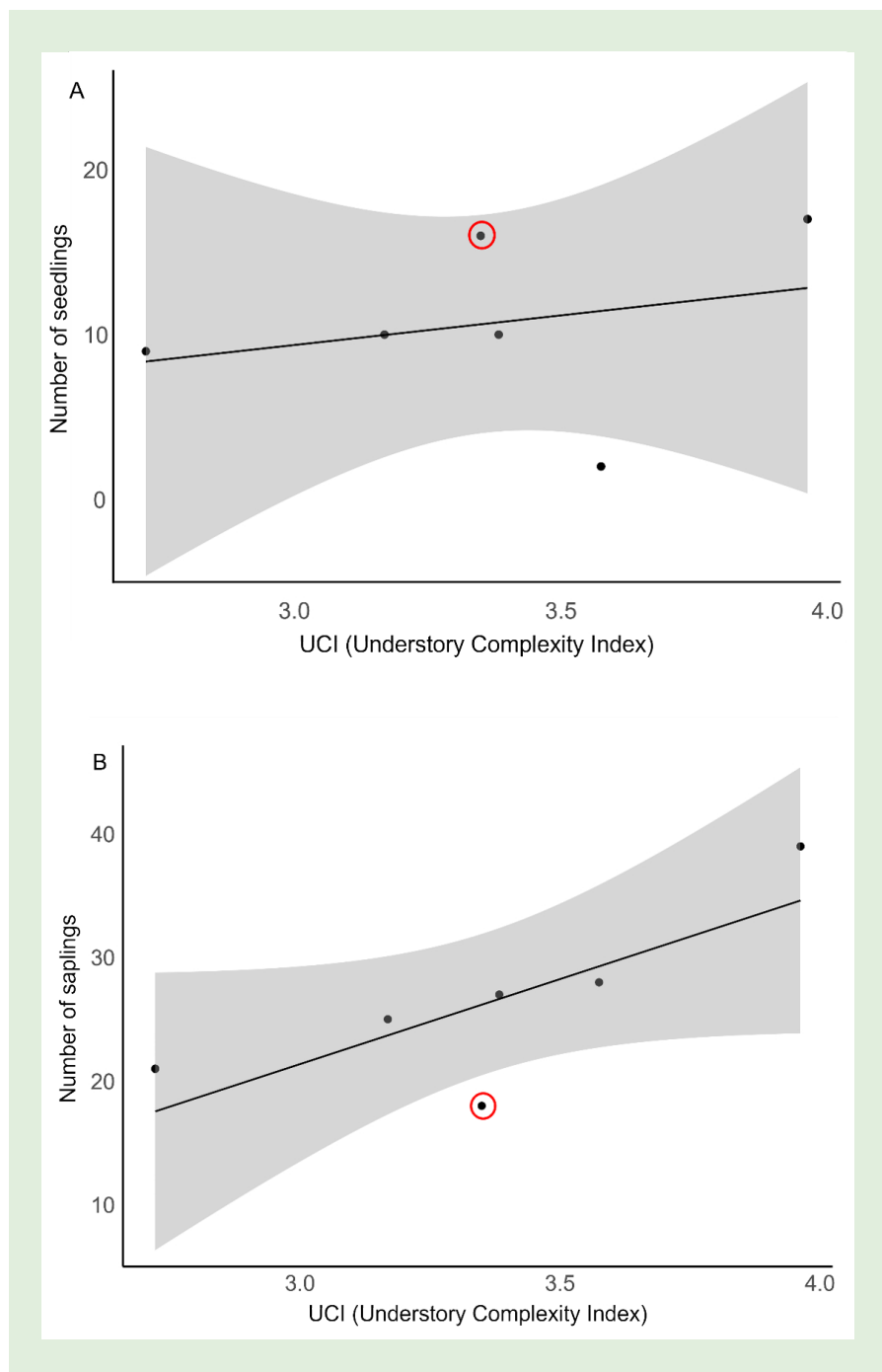


Figure 2. Relationship between the Understory Complexity Index (UCI) and the number of seedling (A) and sapling individuals (B). The red-circled point represents the abandoned cacao plantation plot.

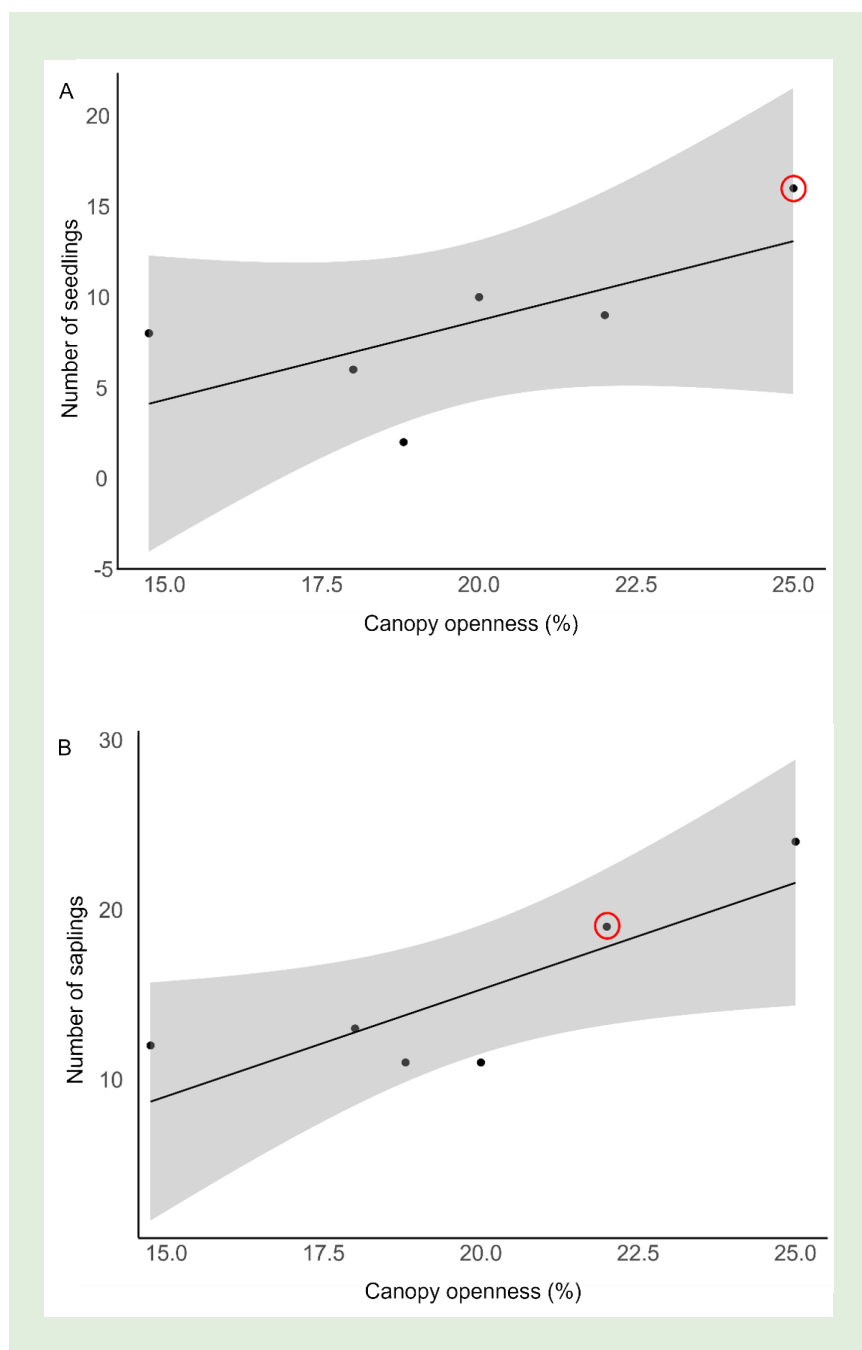


Figure 3. Relationship between canopy openness and seedling (A) and sapling (B) abundance. The circled point represents the abandoned cacao plantation plot.

Discussion

The results highlight the importance of fine-scale structural heterogeneity and light availability in shaping regeneration patterns in mature tropical forests. Among the variables evaluated, canopy openness showed the strongest association with regeneration, particularly with sapling abundance, reinforcing the role of light as a key driver of growth and survival during early forest development (Moretti et al., 2024; Baul et al., 2025). The weaker associations observed for seedlings suggest that establishment may be influenced by additional microsite factors operating at smaller spatial scales (Stone et al., 2025; Seidel et al., 2021).

Overall, canopy openness showed the strongest association with regeneration, particularly with sapling abundance, whereas TLS-derived metrics provided complementary information on fine-scale structural variation. Among these metrics, UCI showed stronger relationships with regeneration than SSCI, suggesting that understory conditions may be more closely linked to recruitment processes than broader stand-level structural attributes.

TLS-derived metrics provided complementary information on structural variability. The positive relationship between the Understory Complexity Index (UCI) and sapling abundance supports the idea that heterogeneous understory environments contribute to regeneration by creating diverse microsites and resource conditions (Ehbrecht et al., 2017; Seidel et al., 2021). Because UCI specifically characterizes vegetation density and heterogeneity within the understory layer, it is more directly linked to the environmental conditions experienced by establishing seedlings and saplings. In contrast, the lack of a clear relationship between the Stand Structural Complexity Index (SSCI) and regeneration suggests that broader structural descriptors may be less sensitive to processes operating at the scale of recruitment and establishment. Similarly, the absence of clear relationships between SSCI and conventional overstory descriptors such as basal area and mean tree height suggests that TLS-derived metrics capture structural attributes that are not adequately represented by traditional stand measurements. The abandoned cacao plantation plot did not exhibit a consistently distinct pattern relative to the selectively logged plots, suggesting that present structural conditions may be more influential than historical land-use differences in explaining the observed variation among plots. These findings emphasize the importance of considering spatial scale when evaluating forest structure–regeneration relationships, as stand-level indicators may fail to capture microsite variability critical for seedling establishment and sapling development.

Low floristic similarity among plots and between adult and regenerating layers reflects the high compositional turnover typical

of tropical forests and supports the role of dispersal processes and local environmental filtering in shaping recruitment dynamics (Chazdon, 2014; Norden, 2014; De Lombaerde et al., 2021). Despite the limited number of intensively characterized plots, the observed patterns were ecologically consistent and demonstrate the value of TLS for capturing fine-scale structural attributes associated with regeneration. Combined with conventional field measurements, TLS offers a promising approach for improving the assessment and monitoring of regeneration processes in structurally complex tropical forests.

Conclusions

Canopy openness was the structural attribute most strongly associated with regeneration, particularly at the sapling stage, highlighting the importance of light availability in mature tropical forests. TLS-derived metrics provided complementary information on fine-scale structural heterogeneity, demonstrating their usefulness for characterizing conditions associated with regeneration. The integration of TLS and conventional field measurements offers a practical approach for improving regeneration assessment and forest monitoring in structurally complex tropical ecosystems.

Author contributions

BH conceived and designed the study, conducted field data collection, performed data analysis, and led the interpretation of results and manuscript writing. LNM contributed to field data collection, data analysis, and interpretation of the results. PHV and RQM contributed to field data collection and assisted in the discussion and interpretation of the findings. All authors contributed to drafting and revising the manuscript and approved the final version.

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AI use declaration

Artificial intelligence (AI) tools were used exclusively for language editing and improvement of English writing. All AI-assisted text was carefully reviewed, verified, and revised by the authors. All scientific content, data analyses, interpretations, and conclusions were developed by the authors, who take full responsibility for the accuracy and integrity of the manuscript.

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