

RESEARCH ARTICLE

Active remote sensing for ecology and ecosystem conservation

UAV-Lidar reveals that canopy structure mediates the influence of edge effects on forest diversity, function and microclimate

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Grégoire Blanchard

Email: gregoire.blanchard@ird.fr**Handling Editor:** Hooman Latifi**Abstract**

1. Widespread forest loss and fragmentation dramatically increases the proportion of forest areas located close to edges. Although detrimental, the precise extent and mechanisms by which edge proximity impacts remnant forests remain to be ascertained.
2. By combining unmanned aerial vehicle laser scanning (UAV-LS) with field data from 46 plots distributed at varying distances from the edge to the forest interior in a fragmented forest of New-Caledonia, we investigated edge influence on forest structure, composition, function, above-ground biomass (AGB) and microclimate. Using simple linear regressions, structural equation modelling and variance partitioning, we analysed the direct and indirect relationships between distance to edge, UAV-LS-derived canopy structural metrics, understorey microclimate, AGB, taxonomic and functional composition while accounting for the potential influence of fine-scale variation in topography.
3. We found that the distance to the closest forest edge was strongly correlated with canopy structure and that canopy structure was better correlated to forest composition, function, biomass and microclimate than distance to the closest forest edge. This suggests that the influence of edge is mediated by changes in canopy structure. Plots located near the edge exhibited a lower canopy with more gaps, higher microclimate extremes, lower biomass, lower taxonomic and functional diversity as well as denser wood and lower specific leaf area. UAV-LS-derived canopy structural metrics were relevant predictors of understorey microclimate, biomass and taxonomic and functional composition. Overall, the influence of topography was marginal compared to edge effects.
4. *Synthesis.* Accounting for fine-scale variation in canopy structure captured by UAV-LS provides insights on the multiple edge impacts on key forest properties related to structure, diversity, function, biomass and microenvironmental conditions. Integrating UAV-LS-derived data can foster our understanding of cascading and interacting impacts of anthropogenic influence on tropical forest ecosystems and should help to improve conservation strategies and landscape management policies.

KEYWORDS

canopy structure, edge effects, forest biomass, functional traits, lidar, microclimate, tropical forest fragmentation, ultramafic soils

1 | INTRODUCTION

Tropical forests are increasingly deforested and fragmented (Hansen et al., 2020; Vancutsem et al., 2021), driving large-scale biodiversity loss and carbon emissions (Baccini et al., 2017; Haddad et al., 2015). A critical consequence of fragmentation is that a growing proportion of tropical forest habitats become closer to the forest edge, entailing a decline of biodiversity and biomass in the remaining fragments (Brinck et al., 2017; Didham et al., 2012; Fischer et al., 2021; Haddad et al., 2015; Laurance et al., 2002). Understanding the pathways through which edges influence distinct key characteristics of tropical forest ecosystems, such as their structure, diversity and functioning is crucial for predicting the current and future consequences of fragmentation and to develop appropriate conservation strategies. Recent advances in active remote sensing offer new and promising tools to address this issue (Almeida et al., 2019; MacLean, 2017).

Edge influence on tropical forests has been widely studied during the last decades. Numerous edge-induced modifications of forest biotic and abiotic characteristics have been reported, with important effects in the first hundred meters inside the forest (although some can span several kilometres from the edge) (Broadbent et al., 2008; Laurance, 2000; Laurance et al., 2002). The creation of new edges induces rapid modifications of forest micro-environmental conditions, including increasing wind disturbance and light availability, altered microclimate with generally higher temperature and drought, and potential fire incursion (Broadbent et al., 2008; Ewers & Banks-Leite, 2013; Laurance et al., 2002; Laurance & Curran, 2008). These changes lead to a series of vegetation responses, the first of which being higher evapotranspiration along with increased mortality of canopy trees near the edge (Harper et al., 2005), notably during prolonged drought periods (Qie et al., 2017). Higher tree damage and mortality following edge creation result in modifications in the physical structure of the canopy, which generally becomes both lower and more open (Harper et al., 2005). Importantly, these changes result in a loss of forest biomass, representing a decrease in local carbon sequestration which is a critical concern in the context of climate change (Chaplin-Kramer et al., 2015; Qie et al., 2017). Because understorey microclimate is intimately linked to canopy structure (Jucker, Hardwick, et al., 2018; Lenoir et al., 2017; Zellweger, De Frenne, et al., 2019; Zellweger, Coomes, et al., 2019), increasing canopy opening at the edge can, in turn, cause further alteration of forest micro-habitats (Camargo & Kapos, 1995; De Frenne et al., 2021; Didham & Lawton, 1999), along with secondary response of understorey vegetation (Harper et al., 2005).

The creation of edges not only affects forest structure and microclimate, but also impacts plant diversity and ecosystem functioning (Ewers & Didham, 2005; Harper et al., 2005; Magrach et al., 2014). Edge environments generally have lower species richness than the

forest interior (Blanchard et al., 2020; Ibanez, Hequet, et al., 2017; Magnago et al., 2014). Moreover, species facing edge influence respond differently depending on their functional strategies (Ewers & Didham, 2005). Contrasting environmental conditions along edge-to-interior gradients can thus shape tree communities with different functional composition (Laurance, Nascimento, Laurance, Andrade, Ribeiro, et al., 2006; Magnago et al., 2014). Nonetheless, edge effects are often site specific, and depend on the environmental context as well as on the rate of vegetation response since edge creation (Blanchard et al., 2020; Harper et al., 2005; Laurance et al., 2007; Ordway & Asner, 2020). Environmental gradients such as macroclimatic and topographic variation, as well as soil characteristics, are known to control tropical forest structure and composition (Blanchard et al., 2019; Jucker, Bongalov, et al., 2018; Muscarella et al., 2019), influencing their structural and compositional responses to edge creation (Ordway & Asner, 2020). Edge influence is expected to decrease over time if environmental conditions are suitable for rapid forest regeneration, while edge effects should be stronger at long-term maintained edges (Harper et al., 2005). In tropical wet forest, forest tree communities at the edge generally shift towards early successional composition, with a rapid dominance of pioneer species with high-light competitive ability (Laurance et al., 2002). However, harsher environmental conditions near the edge can also favour species with traits associated with drought resistance whereby less adapted species are filtered out (Blanchard et al., 2021; Razafindratsima et al., 2018). In contrast, cooler, wetter and shadier conditions of the forest interior are likely to favour a wider range of plant traits, from shade tolerance to fast growth rate (Blanchard et al., 2021; Chazdon, 2008).

While edge effects are known to impact different aspects of tropical forest structure, functions and microhabitat, these impacts remain often studied independently, and we lack a broader understanding of edge influence on tropical forest ecosystems (Jucker et al., 2020; Maeda et al., 2022; Ordway & Asner, 2020). In this context, the growing availability and accessibility of active remote-sensing tools such as unmanned aerial vehicle laser scanning (UAV-LS) provides opportunities to study how environmental variation and fragmentation shape forest structure and function (Almeida et al., 2019; Ordway & Asner, 2020). Combining laser scanning-derived fine-scale three-dimensional data on forest physical structure with field data on different ecosystem properties including biodiversity, function and micro-habitat has brought new insights on tropical forest functioning and potential responses to environmental changes (Chadwick et al., 2020; De Frenne et al., 2021; Jucker et al., 2020; Molina et al., 2016). Thus, UAV-LS offers relevant options to unveil and decipher the multifaceted influence of edge on tropical forest and unlocks possibilities to predict and upscale the influence of edges over large scales and with better accuracy than classical landscape metrics.

Here, we investigated the influence of edges on tropical forest structure, biodiversity, function, biomass and microclimate. We combined UAV-LS data, field data from forest plots and microclimate monitoring to study fragmented forest in the biodiversity hotspot of New Caledonia. Our goal was to evaluate how variation in canopy structure at the forest edge modulates edge effects on multiple key forest characteristics. We also accounted for the potential control of fine-scale UAV-LS-derived topographic variation. We analysed the relationships between distance to the forest edge, topography, canopy structure, forest biomass, understorey microclimate, and tree community taxonomic and functional composition. We used structural equation modelling and variance partitioning to more explicitly evaluate the direct and indirect, canopy-mediated influence of edge on forest structure, composition and microclimate. Our study highlights how the integration of appropriate UAV-LS-derived metrics in ecological studies allows a finer and more holistic understanding of the consequences of landscape fragmentation on key properties of tropical forest ecosystems, which can help to better predict and upscale the impacts of forest fragmentation.

2 | MATERIALS AND METHODS

2.1 | Study area

New Caledonia is a 18,500 km² archipelago located in the south-west Pacific (20–23°S, 164–167°E). New Caledonia's climate is tropical oceanic, with a hot (October to May) and a cool (June to September) season, overlapping with a dry season (August to November) characterized by lower rainfall and higher fire frequency, which can be intensified by the El Niño phenomenon (Ibanez et al., 2013). The study area is a 4 km² landscape located in the southern part of the main island, in the Plaine des Lacs (166.950–166.970°E, 22.215–22.235°S), at an altitude ranging between 300 m and 500 m a.s.l. Soils are mainly composed of peridotite scree and eroded ferrallitic soils with deposits of rocky ferricrete, which are particularly known to have low nutrient availability and low water retention, along with high levels of potentially toxic metals (Ibanez, Hequet, et al., 2017; Isnard et al., 2016), resulting in relatively slow vegetation growth (McCoy et al., 1999). The area receives about 3000 mm of annual rainfall and the mean annual temperature is about 20°C. Forest fragmentation mainly results from relatively recent human-driven pressure which has dramatically increased since the mid-18th century, including bush fires, logging and intensive mining prospecting (Ibanez, Hequet, et al., 2017; McCoy et al., 1999). Forest patches were delimited and georeferenced by visually interpreting recent aerial photographs (2020) at a 1:3000 scale. We also investigated the history of the studied landscape using past aerial photographs (1976) which showed that the forest area and the position of forest edges has undergone almost no change during the last 45 years. Both recent and past aerial photographs are available online (www.georep.nc). We used the QGIS software (QGIS Development Team) for forest patch delimitation and georeferencing.

2.2 | Field study design and sampling of tree communities

We surveyed a total of 46 standardized tree inventory plots. To study the influence of edges on the diversity and composition of tree communities, plots were distributed following a spatially random sampling stratified according to the distance to the closest forest edge (see S.M. 1 for a schematic representation of the study design). Based on the digitized forest patches, we generated inner-buffer lines at various distances from the digitized forest edge: 10, 20, 40, 100, 200 and 300 m. Smaller intervals were taken closer to the forest edge as we expected a non-linear relationship between edge distance and the amplitude of edge effects. A set of 100 points was then randomly drawn along each of these lines, and a subset of points was then selected with a minimum distance of 100 m between two points on the same buffer line to prevent points at the same distance from the edge from being too clustered. Among the surveyed plots, 11 plots were placed at 10 m from the edge, 11 plots at 20 m, 10 plots at 40 m, 7 plots at 100 m, 3 plots at 200 m and 4 plots at 300 m (Figure 1, see S.M. 1 for a schematic representation of the sampling design). On each selected point, we established a circular plot of 11.3 m radius (400 m²) in which all trees with a diameter at breast height (i.e. 1.30 m) greater than 10 cm were identified to the species level and measured in diameter. The centre of each plot was located in the field using multiple records spanning over a minimum of 2 h from a consumer-grade GPS device (Garmin 62S), as recommended by Duncanson et al. (2021). Each plot was considered as a distinct tree community. A total of 2093 individual trees belonging to 107 species, 69 genus and 42 families were identified.

2.3 | Microclimate monitoring

Understorey microclimate was monitored using 50 data loggers (HOBO Pro-V2U23; Onset) installed inside inventory plots. Because we expected microclimate to vary more near the forest edge (Ibanez et al., 2013), loggers were positioned at the centre of the plots located in the first 100 m from the edge (i.e. in plots located at 10, 20, 40 and 100 m from the edge). In the 11 plots whose centres were located at 10 m from the edge, we installed additional loggers right at the edge in order to evaluate the full range of microclimatic variation running from the edge to forest interior (Figure 1; S.M. 1). Loggers were placed on 1-m high poles protected from direct radiation and rainfall. Each logger recorded air temperature (°C) and relative humidity every 20 min over a period of 10 months running from 1 November 2020 to 1 September 2021. Data from four loggers were excluded due to sensor malfunction. From the temperature and relative humidity data, we calculated the vapour pressure deficit (VPD, in kPa). The VPD is defined as the difference between the amount of water that the atmosphere could contain at saturation and the amount of water present in the atmosphere ($VPD = VP_{\text{saturated}} - VP_{\text{air}}$, with $VP_{\text{saturated}} = 0.6108 \times \exp((17.27 \times T)/(T + 237.2))$ and $VP_{\text{air}} = HR/(100 \times VP_{\text{saturated}})$; Arya, 2001). VPD is known to influence water transport and transpiration in plants (Motzer et al., 2005). Specifically, prolonged periods with

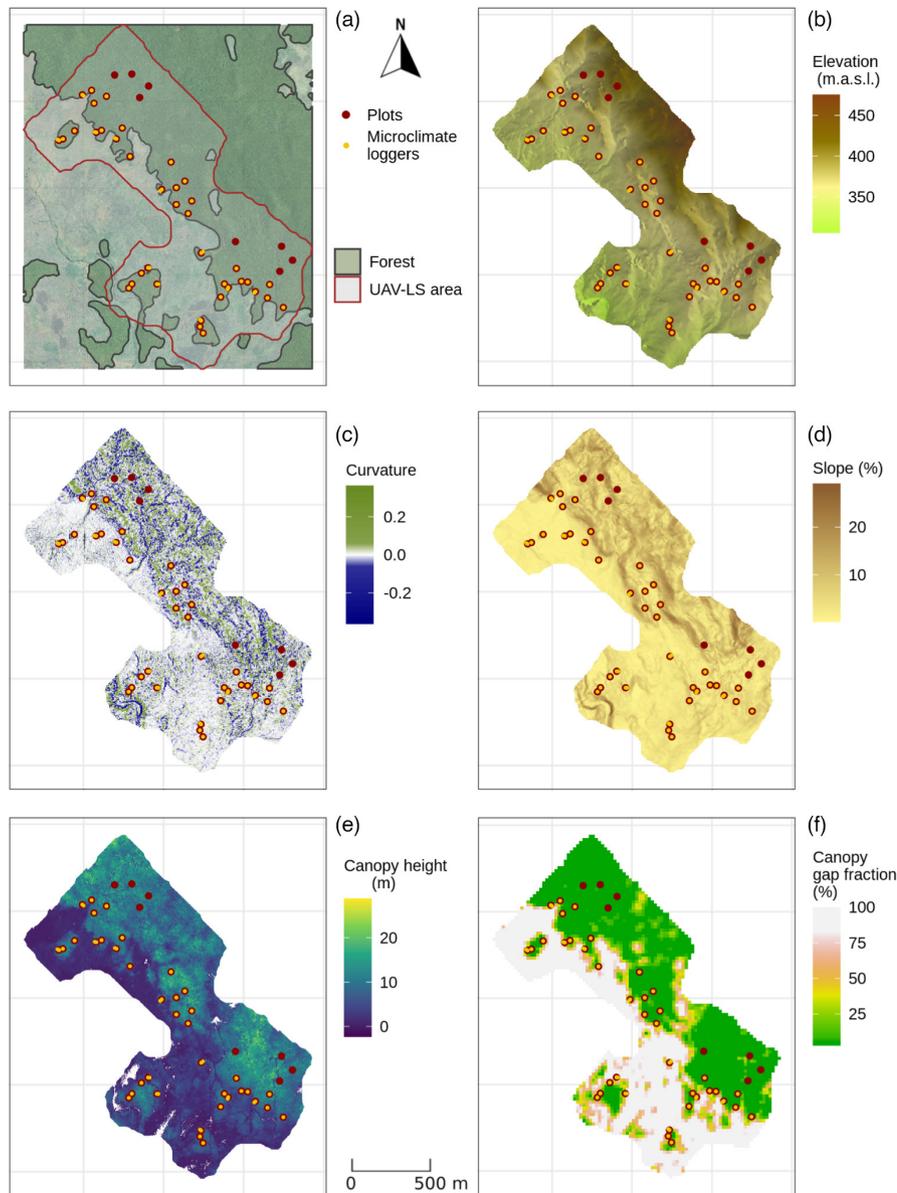


FIGURE 1 Maps of the study site and Lidar-derived characteristics. (a) Map showing the design, with the digitized forest areas, the Lidar-surveyed area, and the position of forest plots and microclimate loggers. (b) Digital elevation model, (c) curvature and (d) slope at 5-m resolution. (e) Canopy height model at 1-m resolution, and (f) the proportion of canopy gaps (gap fraction) at 20-m resolution, all derived from UAV-LS data.

high VPD have been shown to impact tropical tree survival (McDowell et al., 2018). VPD also correlates with litter moisture content and fire spread rate in tropical wet forest (fires spread are strongly inhibited for $VPD < 0.75$ kPa) (Ray et al., 2005). As we expected spatial variation in VPD to be stronger during daytime, we focused only on day temperature (8am–5pm, S.M. 2). Microclimate extremes (min, max) are expected to vary more strongly between forest edge and interior than other microclimate indices (Tuff et al., 2016). Thus, we calculated the average monthly VPD for each data logger and extracted the maximum monthly VPD, corresponding to the driest month (i.e. November 2020).

2.4 | Unmanned aerial vehicle laser scanning data

The UAV-LS data were acquired using a YellowScan Surveyor (<https://www.yellowscan-lidar.com/products/surveyor-ultra>) in July

2021. The sensor emits pulses at a frequency of 300kHz over 360°. The sensor was airborne by a drone (Matrice 600 DJI) at an elevation of 60m above ground level (i.e. about 50m above the canopy on average) with a speed of 5 m s^{-1} . A lateral overlap of neighbouring flight lines of 50% for a maximum scan angle of 45° was implemented. The surveyed area covered about 140ha with an average point density or $67.7\text{ points m}^{-2}$ (Figure 1). Eight flights were necessary to cover the area. The obtained point clouds were processed using the LAStools software (<http://rapidlasso.com/lastools>, see details below). Data from the different flights were first merged using *lasmerge*. The resulting point cloud was classified in ground and non-ground returns using the *lasground* tool. Ground returns were used to fit a 5 m resolution digital elevation model (DEM) using the *las2dem* tool. From the DEM, we also derived a 5 m resolution terrain slope (in degrees) and a 5 m resolution topographic index of curvature describing the concavity of the terrain. Negative values of curvature indicate a concave topography (i.e. ‘valleys’) while a positive curvature indicates

terrain convexity (i.e. ridges) using the *rsaga.slope.asp.curv* function from the *RSAGA* R-package (Brenning, 2008). A normalized point cloud was produced by subtracting the DEM to the non-ground returns using the *lasheight* tool. Then a 1 m resolution Canopy Height Model (CHM) was fitted by taking the maximum return heights in each grid pixel using the *lasgrid* tool. Canopy gaps were then mapped from the CHM based on canopy areas lower than a threshold height of 5 m, using the *getForestGaps* function from the *FORESTGAPR* R-package (Silva et al., 2019). For the centre of each forest plot as well as for the 11 microclimate loggers located on the forest edge, we extracted the average values of canopy height, slope and curvature within a circular area corresponding to the tree community sampling plots (i.e. 11.3 m radius). We also computed a local index of gap fraction representing the proportion of gaps in the plot canopy from the map of canopy gaps. These different values were considered as representing the local conditions in terms of micro-topography and canopy structure at the position of the inventories and around the microclimate loggers.

2.5 | Species functional traits

For all sampled species, we measured wood density and three leaf functional traits involved in resource-use strategies and stress resistance, following standardized protocols (Pérez-Harguindeguy et al., 2013). Traits were collected during the years 2020 and 2021 in the same months (between November and December). We measured the wood density of one wood sample (5.15 mm diameter core at breast height) per individual and five individuals per species. Wood density is a key trait of the wood economic spectrum, from high hydraulic conductivity and high growth rate to lower growth rate and higher drought resistance (Chave et al., 2009). For leaf traits, we collected five sun-exposed leaves per individual and sampled five individuals per species. For compound leaves, we considered a leaflet as the laminar unit. Petioles and petiolules were removed from leaves before measurement. We measured leaf area (LA; the area of a leaf in cm²), specific LA (SLA; the LA per dry mass in cm²g⁻¹) and leaf dry-matter content (the leaf dry mass per fresh mass in mgg⁻¹). SLA and leaf dry-matter content capture species investment in leaves and represent a trade-off between acquisitive (high SLA) and conservative (high leaf dry-matter content) strategies (Wright et al., 2004). LA represents the light-capturing and transpiration surface and is thus related to water-use efficiency (Moles, 2018). For 47 species, some trait data were already available from the New Caledonian plant inventory and permanent plot network (NC-PIPPN) database (this was the case for 47 species), in which trait measurements were carried out in the same region and using identical protocols (Blanchard et al., 2019, 2020, 2021; Ibanez, Chave, et al., 2017) so that field collections were only used to complement the database with the objective of five individuals per species. Data for the four functional traits were finally available for 101 of the 107 identified species, representing 99.7% of all recorded individuals in the dataset. SLA and LA values were log-transformed before analyses to correct for strong skewness of their distribution.

2.6 | Community functional composition

For each plot, we computed the community-weighted mean (CWM), that is the mean trait value of all species present weighted by species abundances. CWM is a widely used trait-based statistic which is expected to reflect trait–environment relationships (Ackerly & Cornwell, 2007). As CWM of different traits can covary among communities, we computed a principal component analysis (PCA) on CWM traits values (i.e. CWM of the four measured traits). The strength of correlation between CWM traits and PCA axes was evaluated and tested based on Spearman's rho rank correlation coefficients. The first axis of the PCA explained a high percentage of CWM variation (64%, S.M. 3) and was significantly correlated with all CWM variation of each individual trait (Spearman's rho between 0.58 and 0.92). This first principal component was positively correlated with SLA and LA, and negatively correlated with wood density and leaf dry-matter content. It thus represented a synthetic axis of functional variation among tree communities, running from communities with denser, smaller leaves and denser wood to communities with larger, thinner leaves and softer wood. We then considered the first PCA axis as a synthetic variable representing variation in CWM traits values in further analyses. We also estimated the plot-level functional diversity based on the functional divergence index proposed by Villéger et al. (2008), using the *FD* R-package (Laliberté et al., 2014). Based on the multidimensional trait space, functional divergence defines how species with high abundances deviate from the centre of the functional space. It is strictly constrained between 0 and 1.

2.7 | Community taxonomic composition

We used species richness as an indicator of taxonomic α -diversity. Because the number of individuals per plot was highly variable (ranging from 18 to 79 with a mean of 45 individuals), we used standardized species richness for equal sample size to limit bias in comparison of species richness among plots (Chao & Jost, 2012). For each plot, standardized species richness was estimated for 20 sampled individuals from sample-size-based rarefaction curves estimated from 50 iterations of random sampling of individuals using the *iNEXT* R-package (Hsieh et al., 2016). We also estimated the variation in taxonomic composition between plots (i.e. taxonomic β -diversity) based on pairwise Bray–Curtis dissimilarity matrix using the *vegdist* function of the *VEGAN* R-package (Oksanen et al., 2020). To account for the difference in number of individuals per plot, we computed the mean pairwise Bray–Curtis dissimilarity from 50 iterations of random sampling of 20 individuals per plots in the community matrix (using the *rrarefy* function from the *RAREFY* R-package). Then, we used a principal coordinate analysis (PCoA; Legendre & Legendre, 1998) to project the taxonomic dissimilarity matrix along a limited number of dimensions. The dissimilarity matrix was transformed using the Cailliez (1983) procedure to prevent negative eigenvalues. The first axis of the PCoA was then used in further analyses as representing

the one-dimensional variation of taxonomic β -diversity among forest plots, including 22% of the total variation in taxonomic dissimilarity.

2.8 | Above-ground biomass estimation

Above-ground biomass (AGB) was calculated for each forest plot using the framework proposed in the `BIOMASS` R-package (Réjou-Méchain et al., 2017). First, we fitted a height–diameter allometry model using regional data from the New Caledonian Plant Inventory and Permanent Plot Network (NC-PIPPN) database (Ibanez et al., 2014), including diameter and height data for 3582 individual trees belonging to 387 species. We used a log–log model [$\log(H) = a + b \times \log(D)$] as it resulted in the lowest residual standard error for our dataset compared to the other models proposed in Réjou-Méchain et al. (2017). Then, we used the resulting height–diameter allometric model to estimate the height of all individual trees from our dataset. We used individual diameter, estimated height and species-level average wood density measured in the field to estimate the AGB (Mg) of each tree based on the generic allometric model of Chave et al. (2014). For the five individuals with no trait data, we used plot-level average wood density. Plot-level AGB was finally estimated by summing individual AGB within each plot and dividing it by the area of the plots in hectare (Mg ha^{-1}).

2.9 | Statistical analyses

First, we used simple linear regressions (`lm` function from the `STAT` R-package) to evaluate the influence of distance to the closest edge, topography (i.e. curvature and slope) and UAV-LS-derived canopy structure (i.e. canopy height and gap fraction) on all measured forest attributes (i.e. tree community taxonomic and functional α -diversity, β -diversity, CWM of each trait, synthetic CWM trait variation, AGB and understorey microclimate). Distance to edge was log-transformed to correct for non-linearity of the relationships. The simple regressions were additionally computed for the CWM of each trait (see S.M. 4). We also used simple linear regressions to test the influence of distance to edge and topography on canopy structure, either using data extracted from plot position or data extracted from all cells from a 20×20 grid representing aggregated UAV-LS-derived metrics (i.e. mean curvature, slope, canopy height and the proportion of canopy gaps). The goodness of fit of the models were evaluated using the coefficient of determination (R^2). The correlations between the different predictors (i.e. distance to forest edge, topography and canopy structure) were evaluated using Pearson's correlation coefficient (see S.M. 5). Elevation was removed from the list of predictors used hereafter because it was strongly correlated with distance to forest edge in the study site (i.e. Pearson's correlation coefficient = 0.74). There was only a 80 m elevation difference between the lowest and highest forest plots and therefore we did not expect a strong independent influence of elevation.

Second, we used structural equation models (SEMs), a statistical method designed to model multivariate relationships based on several structural equations, to investigate the direct and indirect influence of edge and topography on forest attributes. We expected canopy structure to depend on distance to edge and topography and to mediate the influence of edge vicinity on forest composition, AGB and understorey microclimate. Based on the relationships evaluated using linear models, we fitted separate SEMs representing the direct and indirect (i.e. mediated by canopy structure) influence of distance to edge and topography on each measured forest attribute (S.M. 6). The slope was excluded from SEMs as it has systematically non-significant contribution, so that topography was only represented by curvature. Next, we constructed two more complex SEMs. The first model included all previous components except those related to canopy structure, representing the joint influence of distance to forest edge and topography on all forest attributes as well as their residual covariation. The second model included all variables and measured attributes, representing the indirect influence of distance to edge and topography mediated by canopy structure. SEMs were fitted using the `LAVAN` R-package (Rosseel, 2012). All variables were standardized to mean zero and unit variance to help model convergence. The `lavaan` algorithm can handle missing data (missing at random) through full information maximum likelihood (FIML) estimation. For the two complex models, FIML was thus used to estimate missing values of maximum VPD for the 12 plots with no microclimate data. The two models were adjusted using stepwise removal of non-significant relationships until all relationships represented significant contributors to the final model. However, the non-significant effect of curvature on canopy structure was kept in the second model for an easier comparison between the two models. Model parameters were estimated using maximum likelihood estimation with robust standard errors (MLR), which provides scaled test statistics in case of non-normality or incomplete data (Savalei & Rosseel, 2021). Global fit of SEM was assessed using chi-squared statistic and p -value ($p > 0.05$ indicates a good fit), root mean square error of approximation (< 0.08 indicates a good fit), standardized root mean square residual (< 0.08 indicates a good fit) and comparative fit index (> 0.9 indicates a good fit) and non-normed fit index (> 0.9 indicates a good fit).

Third, we performed variance partitioning and hierarchical partitioning analyses to evaluate the relative importance of shared and independent effects of distance to edge, canopy structure and topography on the different forest attributes. For this last analysis, we estimated missing VPD data as the median values from 50 multiple imputations, using the `MICE` R-package (van Buuren & Groothuis-Oudshoorn, 2011). We then used the recent method proposed by Lai et al. (2022) in the `RDACCA.HP` R-package, which provides a generalized framework for evaluating the relative importance and individual effects of different predictors in multi-response regression models based on canonical redundancy analysis (RDA; Rao, 1964). We used this method to evaluate the relative influence and individual effect of distance to edge and topography (i.e. curvature and slope) on canopy structure (i.e. canopy height and gap fraction), and the relative

influence and individual effect of distance to edge, topography (i.e. curvature and slope) and canopy structure together on taxonomic composition (i.e. rarefied species richness and β -diversity), functional composition (i.e. CWM traits and functional diversity) and AGB and microclimate.

3 | RESULTS

3.1 | Direct influence of edge and topography on forest characteristics

Linear regression models indicated strong relationships between UAV-LS-derived canopy structure and distance to edge, with both an increase in canopy height and a decrease in gap fraction as log-transformed distance to edge increases (Figure 2). Distance to edge alone explained 51% of the variation in canopy height and 32% of the variation in gap fraction measured on forest plot location, and the analysis of the whole landscape showed consistent results. In contrast, we found only weak influence of topography (i.e. curvature and slope) on canopy structure (Figure 2). The analysis of the whole landscape showed that curvature had a weak negative influence on canopy height ($R^2=0.06^{***}$) and no influence on gap fraction. Likewise, the same analysis showed that slope had only a very weak influence on forest canopy height and gap fraction (Figure 2). When considering only forest plots, the influence of curvature and slope on canopy height and gap fraction was not significant anymore.

Our results revealed consistent relationships between distance to forest edge and most variables measured in the field. First, we found strong associations between microclimate and distance to the forest edge. Daily mean temperature oscillated between 18 and 24°C at 100m from the edge and from 20 to 27°C at the edge depending on the season (S.M. 2). The hottest month was February 2021, with some individual daily records exceeding 30°C at the edge. On average, daily VPD oscillated between 0.1 and 0.2 kPa at 100m from the edge, and from 0.2 to 0.9 kPa at the edge, with the driest month being November 2020. This maximum monthly VPD showed a strong non-linear negative relationship with distance to edge, decreasing from values exceeding 1 kPa at the edge to less than 0.5 kPa at 100m in forest interior and indicating sharp microclimate changes in the first meters from the edge (Figure 3). AGB showed a strong negative relationship with distance to edge. AGB increased from around 100Mg/ha on plots located at 10m from the edge to around 300Mg/ha on plots located at 300m. Synthetic CWM variation and species richness both significantly increased with increasing distance to edge, while functional diversity was not influenced by edge distance (Figure 3). Taxonomic β -diversity also significantly depended on distance to the forest edge. In addition, functional diversity and taxonomic β -diversity showed weak negative relationships with curvature. Slope had a weak positive influence on synthetic CWM variation, species richness and taxonomic β -diversity, as well as a weak negative influence on maximum monthly VPD (Figure 3).

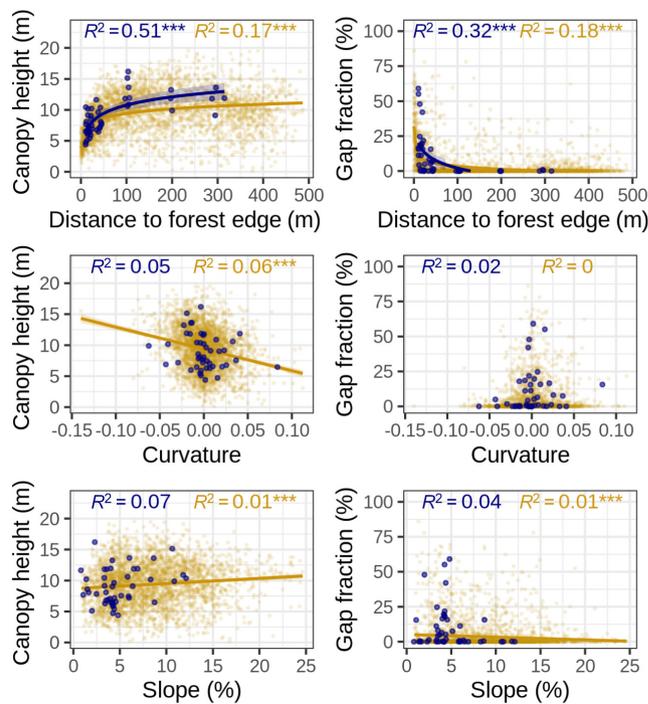


FIGURE 2 Linear regressions showing the relationships between the distance to the nearest forest edge, the topography (curvature and slope) and the structure of the canopy. These relationships were tested for either data from plots ($n=46$, blue) or all raster cells (20m resolution) located in the studied forest patches ($n=3201$, yellow). Distance to forest edge was log-transformed but predictions are plotted on a regular scale for easier interpretation, resulting in non-linear relationships. Variance explained (R^2) and significance of the models are reported (* p -value < 0.05; ** p -value < 0.01; *** p -value < 0.001).

3.2 | Edge effects mediated by canopy structure

Linear regression models revealed stronger influence of UAV-LS-derived canopy metrics than distance to edge on forest attributes measured in the field (Figure 3). Canopy height and gap fraction had significant and opposed influence on all attributes (Figure 3), including CWM of individual traits (S.M. 2). Maximum monthly VPD showed a strong negative relationship with canopy height ($R^2=0.64$) and a strong positive relationship with gap fraction ($R^2=0.66$). AGB, synthetic CWM traits, functional diversity, rarefied species richness and β -diversity were all positively related to canopy height and negatively related to gap fraction.

SEMs highlighted the direct and indirect influence of edge on all forest attributes as well as the associations between them (Figure 4). The SEM excluding UAV-LS-derived canopy structure indicated an overall combined influence of distance to edge and topography on functional composition (CWM traits and functional diversity) and taxonomic composition (rarefied species richness and β -diversity) (Figure 4a, S.M. 7a). In this model, AGB and microclimate were only influenced by distance to edge, with no accounted effect of topography. This first SEM also displayed important residual covariation between different attributes, with positive

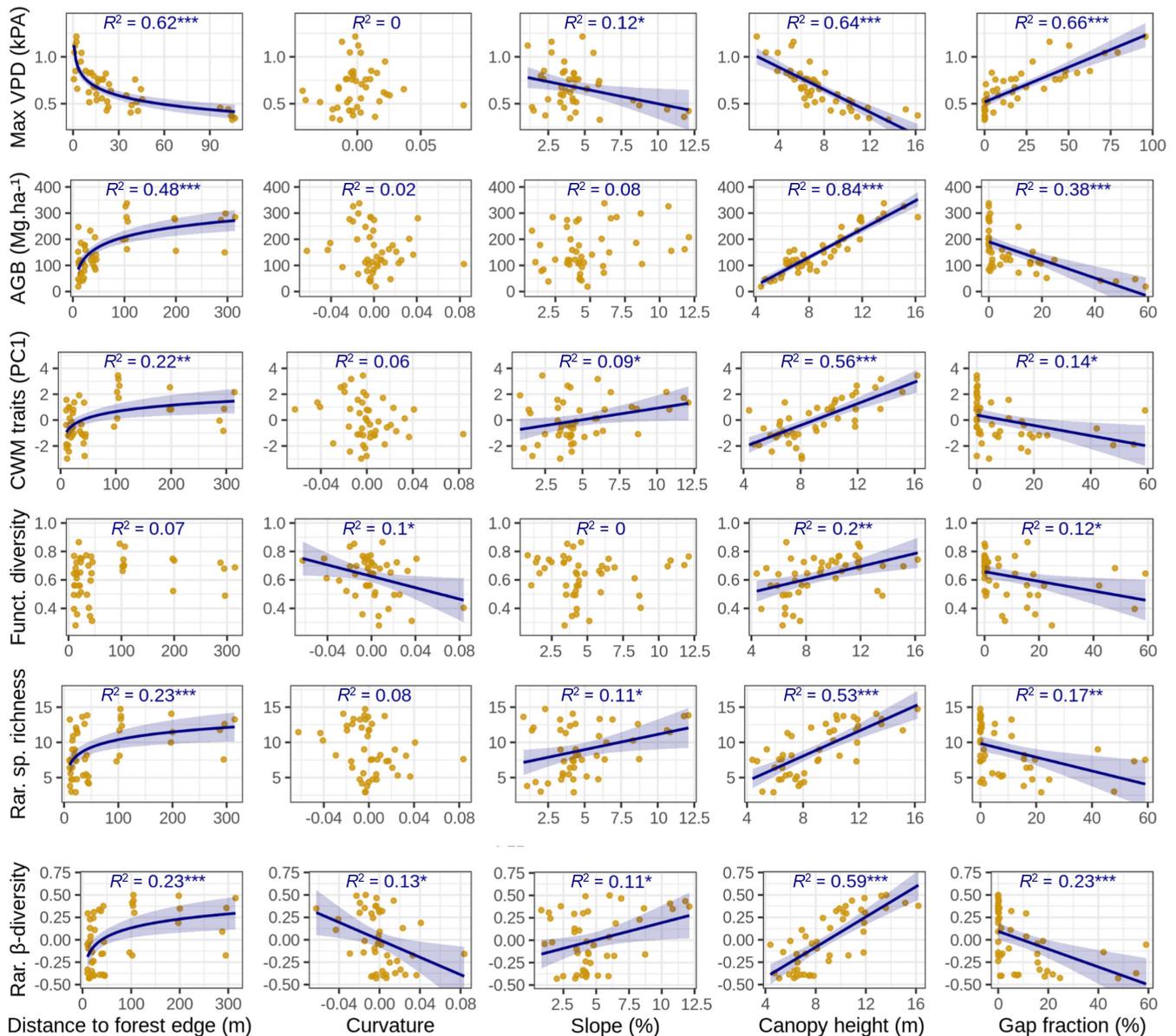


FIGURE 3 Linear regressions showing the influence of distance to forest edge, topography (curvature and slope) and UAV-LS-derived canopy structure (canopy height and gap fraction) on different forest attributes: maximum monthly VPD (max VPD), above-ground biomass (AGB), synthetic community weighted-mean traits (CWM traits on PCA axis 1), functional diversity, rarefied species richness and β -diversity. Distance to forest edge was log-transformed but predictions are plotted on a regular scale for an easier interpretation, resulting in non-linear relationships. Shaded areas represent 95% confidence intervals of predicted values. Variance explained (R^2) and significance of the models are reported (* p -value < 0.05; ** p -value < 0.01; *** p -value < 0.001). The model for maximum VPD was fitted using available data from microclimate loggers (i.e. placed on plots located from 10m to 100m from the forest edge, including 11 loggers placed on the edge), while other models were fitted using data from the 46 plots (i.e. located from 10 to 300m from the forest edge).

association between functional, taxonomic composition and AGB, and negative association between the latter and maximum VPD. Integrating UAV-LS-derived canopy metrics in the SEM revealed both the strong, direct influence of distance to edge on canopy structure and the pervasive influence of canopy structure on AGB, microclimate, taxonomic and functional composition (Figure 4b; S.M. 6 and 7b). Accounting for UAV-LS-derived canopy structure substantially increased the variance explained by the model for all forest attributes. This second SEM thus provides insight on the

indirect influential pathway of distance to edge on forest structure, composition and microclimate.

The variance and hierarchical partitioning analyses brought complementary insights about the relative independent contribution of distance to edge, topography, and UAV-LS-derived canopy structure on groups of forest attributes representing functional composition, taxonomic composition, and AGB and microclimate (Figure 5). In accordance with SEM, hierarchical partitioning analysis indicated that distance to edge explained about 40% of the

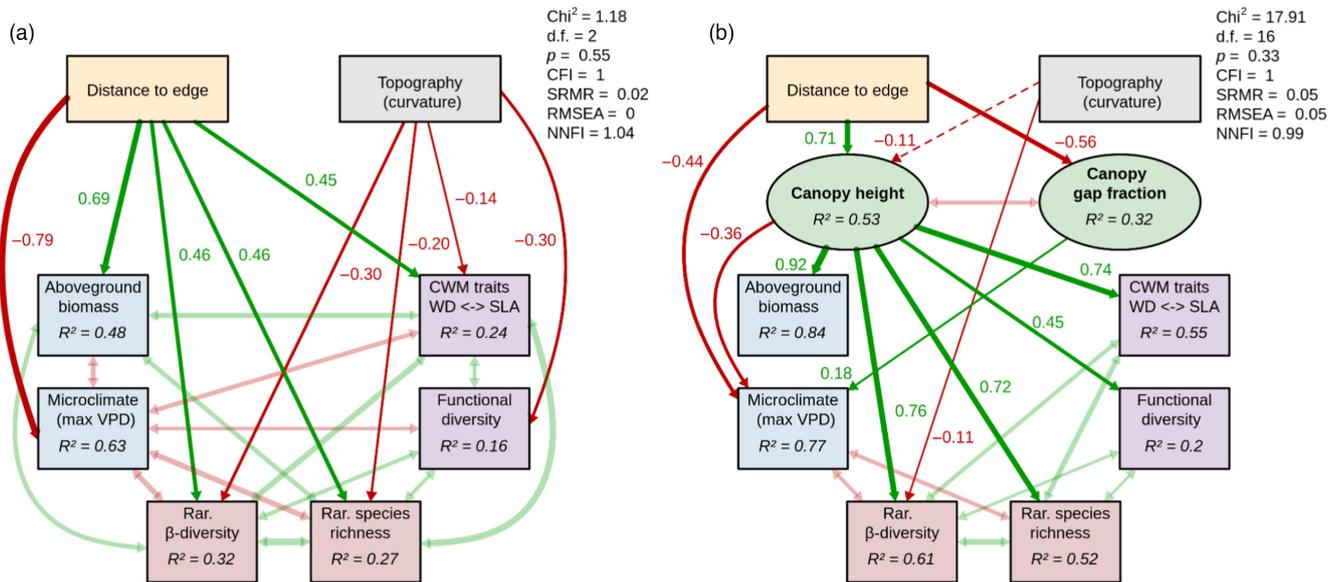


FIGURE 4 Structural equation models indicating the direct (a) and indirect (i.e. mediated by canopy structure) (b) influence of distance to forest edge and topography on understorey microclimate, aboveground biomass, functional diversity and mean trait values, species richness and β -diversity of tree communities. All significant pathways ($p < 0.05$, solid arrows) were reported, except the influence of topography on canopy height (dashed arrow). Standardized parameter estimates are indicated for each path. Significant residual covariances are represented by transparent arrows. Global fit statistics of SEMs are indicated on the top right of each model: Chi-squared statistic and p -value ($p > 0.05$ indicates a good fit), root mean square error of approximation ($RMSEA < 0.08$ indicates a good fit), standardized root mean square residual ($SRMR < 0.08$ indicates a good fit), comparative fit index and non-normed fit index ($CFI > 0.9$ and $NNFI > 0.9$ indicate a good fit).

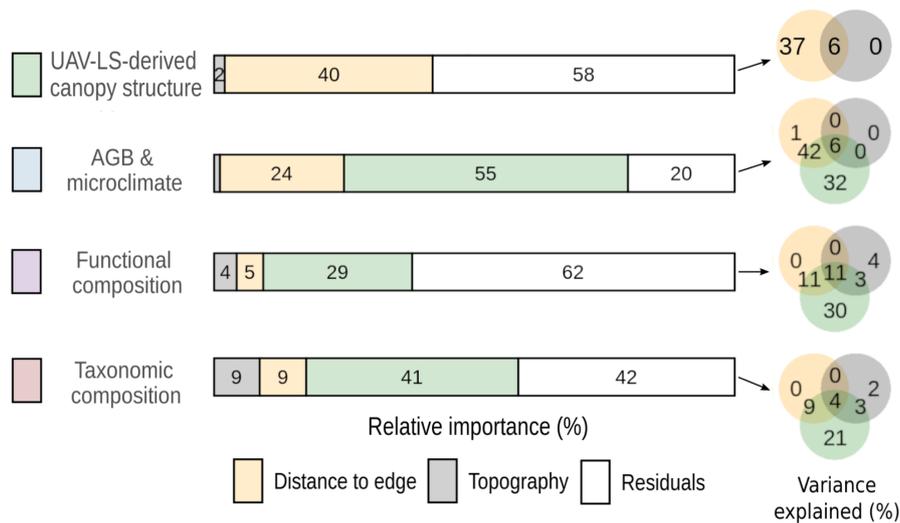


FIGURE 5 Relative importance (stacked bars) and variance explained (Shared and independent effect represented by Venn diagrams, right side) of distance to edge, topography and UAV-LS-derived canopy structure (canopy height and gap fraction) on groups of variables representing forest structure and microclimate (AGB and maximum monthly VPD), functional composition (CWM traits and functional diversity), taxonomic composition (rarefied species richness and β -diversity). Groups of response importance and variance explained by predictors, are represented using the same colours as in Figure 4.

variation in canopy structure, with only a weak influence of topography. Hierarchical partitioning also showed that UAV-LS-derived canopy structure had a strong influence on AGB, microclimate and functional and taxonomic composition, indicating a dominance of indirect effects of distance to edge mediated by canopy structure. The variance partitioning analysis revealed that the influence of

canopy structure on AGB, microclimate, taxonomic and functional composition encompassed most of the influence of distance to edge (Figure 5). Furthermore, this analysis showed that canopy structure always had important individual effects on the measured forest characteristics, allowing to explain much more variance than distance to edge alone.

4 | DISCUSSION

Our study revealed pervasive edge effects on multiple key characteristics of New Caledonian forest, providing insights on the complex association between structure, biomass, microclimate, diversity and functioning in fragmented tropical forests. This concurs with previous studies on edge effects in South America and South-East Asia (Benchimol & Peres, 2015; Ewers & Banks-Leite, 2013; Laurance et al., 2002, 2011; Ordway & Asner, 2020; Qie et al., 2017). However, our work provides a more comprehensive assessment of the influence of multifaceted edge effects which remain rarely addressed together, unveiling direct and canopy-mediated edge influence on different essential properties of tropical forest ecosystems. Importantly, we show that UAV-LS-derived canopy metrics are reliable predictors of these fundamental characteristics under edge influence, emphasizing the usefulness of UAV-LS for evaluating and predicting the impacts of fragmentation on tropical forest biodiversity, function and services.

4.1 | Canopy-mediated edge effects on forest composition, function, structure and microclimate

In the studied landscape, canopy metrics varied consistently with distance to edge, reflecting the strong edge influence on the physical structure of tropical forest (Laurance et al., 1997, 2002), which has been recently highlighted by other studies based on laser scanning (Almeida et al., 2019; Maeda et al., 2022; Ordway & Asner, 2020). Both canopy height and gap fraction displayed continuous but non-linear responses to edge influence, with exponentially decreasing height and increasing gaps towards the forest edge. This is consistent with the well-documented rise in large tree mortality driven by increasing drought and wind exposure as well as possible fire incursion following edge creation, resulting in abrupt changes in canopy profiles and morphology (Brando et al., 2014; Laurance, Nascimento, Laurance, Andrade, Ribeiro, et al., 2006; Smith et al., 2018). Moreover, wind-related changes in canopy structure near the edge may be more intense in cyclone-prone regions such as New Caledonia (Catterall et al., 2008; Ibanez et al., 2019; Pohlman et al., 2007). This canopy pattern was associated with sharply decreasing AGB towards the edge, with a biomass per unit area three times higher in the interior than at the edge. This emphasizes the negative impact of edge effects on the pantropical carbon stock (Brinck et al., 2017; Magnago et al., 2017; Qie et al., 2017).

Jucker, Bongalov, et al. (2018); Jucker, Hardwick, et al. (2018) have shown that understorey microclimate maxima mainly depended on canopy structure in Borneo. Likewise, our results exhibit a strong control of edge-related changes in canopy structure on understorey microclimate, with strong contrasts in VPD between the edge and forest interior during drought periods (here, the driest month of the surveyed period). Both decreasing canopy height and increasing gap fraction entailed rising values of maximum monthly VPD near the edge. While microclimatic edge effects have been documented in

both tropical (Didham & Lawton, 1999; Ewers & Banks-Leite, 2013; Ibanez et al., 2013; Magnago et al., 2015; Pohlman et al., 2007) and temperate forest (Baker et al., 2013; Meeussen et al., 2021), our work explicitly illustrates that edge influence on microclimate is mainly modulated by canopy structure. Gradual reduction in canopy height and increasing gap fraction near the edge entail increasing radiation input along with wind incursion, resulting in lower microclimate buffering and elevated evaporated demand (De Frenne et al., 2021; Ewers & Banks-Leite, 2013; Laurance & Curran, 2008; Nunes et al., 2022). In our study, extreme daily VPD values measured up to 20m in forest interior (>1.5 kPa, S.M. 2) exceed thresholds above which tropical tree growth and survival can be impeded (Jucker, Hardwick, et al., 2018; Motzer et al., 2005), and increases the risk of fire incursion (Ibanez et al., 2013; Ray et al., 2005). Moreover, increasing frequency and strength of extreme climatic events such as prolonged droughts (Cai et al., 2014) and cyclones (Kang & Elsner, 2015) may trigger synergistic effects with positive feedback between altered canopy structure and change in understorey microclimate, further increasing drought-induced tree mortality (Laurance & Curran, 2008; McDowell et al., 2018; Nunes et al., 2022; Silvério et al., 2019).

Our results highlight intertwined edge effects on tree community functional and taxonomic composition, which were mostly mediated by changes in canopy structure. Decreasing canopy height towards the forest edge was associated with marked shifts in both wood and leaf traits (i.e. denser wood, smaller and denser leaves) along with reduced functional diversity, indicating a convergence towards drought resistance and resource conservation strategies. This functional pattern depicts consistent environmental filtering of species in relation with tree physiological functioning induced by harsher conditions near the edge (Blanchard et al., 2020, 2021; Matos et al., 2017; Razafindratsima et al., 2018; Santos et al., 2010; Swenson & Enquist, 2009). Higher wood density reduces the risk of drought-induced embolism (Chave et al., 2009; Markesteijn & Poorter, 2009; Poorter et al., 2010), and small leaves with dense tissue minimize transpiration (Moles, 2018; Poorter et al., 2009; Wright et al., 2017), enabling species with this set of traits to establish and persist under dryer conditions such as those measured close to the forest edge. Importantly, this filtering of species with edge-adapted traits could, in turn, entail a feedback on local canopy structure and openness near the edges. In contrast, wetter conditions towards forest interior allow species communities with a wider range of traits to establish. Higher canopies with buffered microclimate may also favour the recruitment of species with traits associated with faster resource acquisition and growth as well as higher light-competing ability, including lower wood density, larger and thinner leaves (Chave et al., 2009; Díaz et al., 2016; Givnish, 1987; Moles, 2018). This pattern contrasts with the rapid proliferation of fast-growing pioneer species after edge creation in neotropical forests (Benchimol & Peres, 2015; Ewers et al., 2017; Laurance, Nascimento, Laurance, Andrade, Fearnside, et al., 2006; Magnago et al., 2015). In our study, the strong preponderance of species with stress resistance strategies in communities adjacent to the forest

edge may reflect the particular characteristics of New Caledonian ultramafic soils, which could contribute to environmental filtering by allowing only long-lived light-demanding species to establish in open environments (McCoy et al., 1999). Indeed, ultramafic soils are generally nutrient poor and subject to seasonal water deficits, while greater abundance of litter and closed canopy can make water and nutrients less limiting in forest interior (Ibanez, Hequet, et al., 2017; Isnard et al., 2016; Read et al., 2006).

In addition, species richness strongly decreased along with canopy height towards the edge, in combination with a marked taxonomic turnover (i.e. β -diversity). Thus, as revealed by other works, edge effects not only lead to a decrease in species diversity (Blanchard et al., 2020; Magnago et al., 2014; Razafindratsima et al., 2018), but also to a divergence in taxonomic composition (i.e. β -diversity) between edge and interior habitats (Arroyo-Rodríguez et al., 2013; Krishnadas et al., 2019). Important association between functional and taxonomic composition indicated by our SEM analysis suggests that changes in species composition result from environmental filtering involving wood and leaf traits. Nonetheless, other trait-based mechanisms which cannot be assessed here, such as species-specific dispersal dynamics and seed predation, or resistance to fire, may also play a role in compositional changes along the edge-to-interior gradient (Magnago et al., 2014; Rocha-Santos et al., 2017; Ibanez, Hequet, et al., 2017; Ibanez, Chave, et al., 2017).

Topographic control on forest properties was marginal compared to the strong influence of edge effects. This is likely due to relatively small topographical variations in the study sites and to the fact that our study was primarily designed to investigate the influence of edge effects and not topographic variations. However, our results indicate that tree communities located on convex parts of the landscape (e.g. ridges) displayed lower canopy, higher wood density, lower SLA as well as reduced taxonomic and functional diversity. This is consistent with recent works indicating that topography, by controlling water and nutrient availability, is an important factor of tropical forest composition (Blanchard et al., 2019; Jucker, Bongalov, et al., 2018). It is also important to note that edge-related changes are gradual over time (Harper et al., 2005; Ordway & Asner, 2020), so the effect of recent edges on forest properties can appear weaker (Razafindratsima et al., 2018). The prevailing effects of edges observed in our study probably result from long-term maintained edge influence and associated alteration of canopy structure, as suggested by the absence of major landscape change over the past decades. In this, the neo-Caledonian fragments studied here could represent a textbook case, with well-stabilized edge effects.

4.2 | Deciphering and predicting the multiple impacts of forest fragmentation and disturbance using UAV-LS data

Edge effects have historically been investigated through relationships between field-measured forest characteristics and distance to edge, or through binary comparisons of these attributes between the

edge and in the forest interior (Broadbent et al., 2008; Krishnadas et al., 2019; Magnago et al., 2017; Pohlman et al., 2007). Although our study showed substantial influence of edge distance on forest structure, composition, function and microclimate, accounting for changes in fine-scale canopy structure obtained from UAV-LS shed more light on the pervasive influence of edge effects. Both AGB and understorey microclimate were tightly linked to UAV-LS-derived canopy profiles running from the edge to the forest interior. Our results also demonstrated that UAV-LS-derived canopy metrics were reliable predictors of edge-induced variations in forest diversity and function. Thus, our work emphasizes the promising use of remote sensing tools such as UAV-LS to accurately assess the influence of forest fragmentation on tropical forest biomass, microclimate, diversity and function (Almeida et al., 2019; Broadbent et al., 2014; Ordway & Asner, 2020).

Beyond underlining the relevance of UAV-LS-data to assess the variability of edge influence on tropical forest, our study also emphasizes how local canopy structure determines forest microhabitat and influences species composition. Recent studies have revealed how airborne LiDAR surveys can help to unveil the intimate links between canopy structure and various dimensions of forest micro-environmental conditions as well as historical perturbations (Lenoir et al., 2022; Tymen et al., 2017). Our work suggests that simple and meaningful LiDAR-derived metrics such as local canopy height and gap fraction are able to capture this structural control on forest microhabitat and composition. However, the basic structural metrics used in our study do not account for local variations in LiDAR sampling intensity or scan angle for instance (Brede et al., 2022). Laser power and wavelength, footprint size or flight altitude are also known to impact lidar penetration in the canopy. A better accounting for these effects could allow deriving quantitative estimates of plant area within 3D voxels (Vincent et al., 2017). Radiative transfer models based on these estimates and integrating sun angle and sky light (Ebengo et al., 2021; Gastellu-Etchegorry, 2008) would then provide more precise estimates of micrometeorological variables at any given time. Moving towards such approaches should help to understand and predict the current and future responses of forest microclimate and functioning to changes in disturbance regimes driven by ongoing climate and land-use changes (De Frenne et al., 2021; Zellweger et al., 2020).

The increasing use of UAV-LS approaches provides new opportunities to study and monitor the impacts of anthropogenic disturbances on tropical forest ecosystems, and allows to make predictions at spatial scales that were not previously accessible. Interactive impacts of forest fragmentation and climate change can be forecasted by upscaling UAV-LS-based microclimate models to evaluate the future consequences on forest functioning (Corlett, 2016; De Frenne et al., 2021; Jucker, Hardwick, et al., 2018; Zellweger, De Frenne, et al., 2019). Repeated UAV-LS surveys can also be used to track the recovery or dieback of fragmented tropical forest and to identify the underlying factors (Milodowski et al., 2021; Nunes et al., 2021). In addition, the ongoing rapid development of space-borne passive and active

remote-sensing tools should offer further options for extrapolating insights from UAV-LS-based surveys and could help to more accurately monitor changes in forest biomass, biodiversity and functioning at regional and global scales (Asner, 2009; Bustamante et al., 2016; Chaplin-Kramer et al., 2015; Jucker, 2022; Ordway & Asner, 2020). Future studies should also investigate the relevance of UAV-LS-derived data for evaluating and predicting the consequences of forest fragmentation on different trophic groups (Harrison & Banks-Leite, 2020; Krishnadas et al., 2018; Püttker et al., 2020). This further encourages the use of airborne LiDAR studies to foster our understanding of multifaceted impacts of forest fragmentation and to guide adapted conservation strategies.

AUTHOR CONTRIBUTIONS

Grégoire Blanchard: Conceptualization, Methodology, Investigation, Data Curation, Formal analysis, Writing—Original Draft, Supervision. Thomas Ibanez: Conceptualization, Methodology, Investigation, Writing—Review & Editing. Nicolas Barbier: Conceptualization, Methodology, Formal analysis, Writing—Review & Editing. Ghislain Vieilledent: Conceptualization, Methodology, Writing—Review & Editing. Thomas Ibanez: Conceptualization, Methodology, Writing—Review & Editing. Vanessa Hequet: Conceptualization, Methodology, Investigation, Data Curation. Stéphane McCoy: Conceptualization, Investigation. Philippe Birnbaum: Conceptualization, Methodology, Funding acquisition, Writing—Review & Editing.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14105>.

DATA AVAILABILITY STATEMENT

Data used in this study are archived in an open access repository on Zenodo <https://doi.org/10.5281/zenodo.7787640> (Blanchard et al., 2023).

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SUPPORTING INFORMATION

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

S.M. 1: Schematic representation of the study design. 46 standardized tree inventory plots (400 m²) distributed following a spatially random sampling stratified according to the distance to forest edge (10, 20, 40, 100, 200 and 300 m).

S.M. 2: Annual variation of understory microclimate: mean daily temperature and vapor pressure deficit (VPD) during daytime (8h a.m. to 5h p.m.), as measured by the 50 sensors distributed on forest plots located at different distances from the forest edge.

S.M. 3: Covariation in community weighted-mean (CWM) traits.

S.M. 4: Linear regressions showing the influence of distance to forest edge, topography (curvature and slope) and canopy structure (canopy height and gap fraction) on community weighted-mean of each measured trait.

S.M. 5: Correlation matrix showing the Pearson correlation coefficients between the different predictors of forest attributes (i.e., distance to forest edge, curvature, slope, elevation, canopy height and gap fraction).

S.M. 6: Separate structural equation models indicating the direct influence of distance to forest edge and topography on canopy structure, and indirect influence on understory microclimate, aboveground biomass, functional diversity and mean trait values, species richness and β -diversity of tree communities. Significant ($p < 0.05$) and

insignificant pathways and covariances are indicated by solid and dashed arrows, respectively.

S.M. 7a: Raw and standardized parameter estimates for SEM including all variables except canopy structure (* p -value < 0.05 ; ** p -value < 0.01 ; p -value < 0.001).

S.M. 7b: Raw and standardized parameter estimates for SEM including all variables with canopy structure (* p -value < 0.05 ; ** p -value < 0.01 ; *** p -value < 0.001).

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