

Using forest structural complexity and topography metrics to characterise vertical microclimatic stratification

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ARTICLE INFO

Keywords:

Terrestrial laser scanning
Microclimate monitoring
Vegetation architecture
Solar irradiation
Forest island ecosystems

ABSTRACT

Understanding how topography and forest structure drive the transformation of incoming solar energy into local microclimatic conditions is essential for predicting forest resilience under climate change. Quantifying the importance of such attributes on the stratification of microclimates requires the integration of heterogeneous ecological data streams. Here, we combined satellite-derived solar radiation and topographic data, LiDAR-derived forest structural metrics and in situ air temperature and relative humidity time series to quantify the interactions between incoming solar energy, forest structure and topography, ultimately driving microclimatic stratification.

Focusing on native and exotic forest stands on Terceira Island, Azores, Portugal, we evaluated how forest structural complexity and topography interact with incoming solar energy to jointly shape daily air temperature and vapour pressure deficit dynamics. By explicitly linking terrain complexity and three-dimensional vegetation structure with external energy inputs and sensor-derived microclimatic responses, our approach provides a data-driven basis for identifying the structural attributes that drive microclimatic variability within forests.

Our results show that forest structural complexity and topography shape the vertical gradient of air temperature and atmospheric dryness, but with responses differing among canopy, understory, and ground strata. These findings demonstrate the value of integrating remote sensing, environmental sensor networks, and statistical modelling to resolve biologically relevant microclimatic heterogeneity. More broadly, the workflow developed here offers a transferable framework for microclimate monitoring, forest restoration assessment, and the identification of microrefugia in structurally complex ecosystems.

1. Introduction

Forest ecosystems represent some of the most complex and open thermodynamic systems on Earth (Galoux, 1978; Seidel and Ammer, 2023). These organised systems continuously exchange energy and matter with their surroundings and, as they are not in thermodynamic equilibrium, they can be considered as dissipative structures in the Prigoginian sense (Nielsen et al., 2020; Prigogine and Nicolis, 1971). Forests absorb high-quality energy (solar radiation) and systematically degrade it into lower-grade energy (heat) through numerous physical and biological processes like photosynthesis, respiration and

decomposition (Nielsen et al., 2020). This energy dissipation occurs across different scales from individual leaves regulating their temperature through evaporation-based cooling, to entire canopy systems, ultimately modifying local and regional heat fluxes (Braziunas et al., 2025; Frey et al., 2016; Geiger et al., 1995). This redistribution and dissipation of energy generate vertically stratified microclimates that can diverge substantially from surrounding macroclimatic conditions (Holdaway et al., 2010; Stoy et al., 2014; Wiesner et al., 2019).

The thermodynamic behaviour of forest ecosystems emerges from the coupling between vegetation structure and incoming solar energy (Kuricheva et al., 2017; Wiesner et al., 2019). Forest structural

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<https://doi.org/10.1016/j.ecoinf.2026.104087>

Received 22 May 2026; Received in revised form 7 October 2026; Accepted 8 October 2026

Available online 10 October 2026

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complexity, encompassing horizontal distribution of stems, vertical layering, tree size variations, and internal branching patterns, fundamentally alters how incoming solar energy penetrates, reflects from, or is absorbed by forests (De Frenne et al., 2019; Ehbrecht et al., 2019; Jucker et al., 2018). Dense, multi-layered forests act as sophisticated energy dissipaters, partitioning incoming solar radiation into latent heat through evapotranspiration, sensible heat via convective exchange, and stored energy in biomass and soil (Stoy et al., 2014). Their structural complexity creates vertical gradients in temperature and relative humidity that would not exist in simpler ecosystems (De Frenne et al., 2021; Terschanski et al., 2024). The thermodynamic exchanges performed by forests become particularly evident when comparing different structural types: closed-canopy systems with high leaf area indices maintain cooler, more humid understory environments through enhanced latent heat fluxes, while open canopies with sparse vegetation often exhibit greater temperature extremes due to reduced evaporative cooling and increased sensible heat transfer to the atmosphere (Song et al., 2009; Thompson et al., 2004).

Despite the critical role of thermodynamic processes in regulating forest microclimates, a significant knowledge gap persists in our understanding of how vegetation structure interacts with incoming solar energy to govern microclimatic stratification (De Frenne et al., 2019). Microclimatic conditions within forests are inherently vertically stratified, reflecting strong gradients in radiation interception, turbulence, and energy exchange from the canopy to the forest floor (Geiger et al., 1995; Jucker et al., 2018). Consequently, the relationship between incoming solar radiation and microclimate is not uniform across the stand but varies vertically as vertical strata may differ in their exposure and coupling to atmospheric processes. While stand-level approaches provide useful integrative perspectives on forest-atmosphere energy exchange (Law et al., 2001), they implicitly assume a degree of vertical homogeneity that may obscure fine-scale variability.

Because many ecological processes and organismal responses operate at the scale of microhabitats (De Frenne et al., 2019; Scheffers et al., 2014; Zellweger et al., 2020), a stratified framework is necessary to understand which aspect of the forest structure drive microclimatic conditions. Spectral remote-sensing indices are widely used to characterise vegetation activity and canopy greenness, but they provide only indirect proxies for the biophysical properties of forests. Their sensitivity may decline in dense canopies because of spectral saturation, while the recorded signal is also influenced by canopy composition, illumination geometry, background effects and atmospheric conditions (Mutanga et al., 2023). More importantly, spectral indices generally do not resolve the three-dimensional arrangement of stems, branches and foliage, including vertical layering, gap distribution and horizontal heterogeneity, all of which influence radiation transmission, turbulent coupling and heat and moisture exchange within forests (Shugart et al., 2010). Although airborne and spaceborne LiDAR can improve the representation of forest structure, remotely sensed structural estimates remain dependent on sensor characteristics, spatial scale, model transferability and calibration data. Ground-based measurements are therefore essential for evaluating and validating remotely sensed estimates of forest attributes, particularly where fine-scale structural heterogeneity is ecologically relevant (Fassnacht et al., 2024). Terrestrial laser scanning (TLS) offers a complementary approach because it provides detailed, in situ three-dimensional measurements of forest architecture and enables the derivation of ecologically interpretable metrics of vertical and horizontal structural complexity (Calders et al., 2020). Recent applications of LiDAR have demonstrated that structural metrics can improve predictions of forest temperature buffering (Gril et al., 2023), but the extent to which specific structural attributes predict microclimatic conditions across forest strata remains insufficiently understood.

Focus on the forests of Terceira island (Azores, Portugal), we hypothesise that more structurally complex forests will exhibit greater buffering capacity, maintaining more stable microclimatic conditions in understory and ground strata through enhanced energy dissipation

across the forest vertical profiles. Also, we hypothesise that taller forests will demonstrate greater microclimatic variation in canopy and understory layers, as increased height intensifies horizontal wind effects (Freundorfer et al., 2019). Considering canopy openness, we predict reduced microclimatic stability across all forest strata for more open canopies, as diminished shading and energy interception lead to greater temperature and moisture fluctuations (Vasconcelos and Sacht, 2020). The study further explores topographic complexity, hypothesising that steeper terrain will constrain microclimatic ranges through aspect-driven variations in solar exposure and shading, while elevation will similarly reduce temperature and humidity fluctuations through combined thermodynamic effect (adiabatic cooling) and increased cloud immersion at higher altitudes.

By combining measurements of forest structural attributes, solar radiation, and vertically resolved microclimate, we aim to determine whether and how metrics of topography and forest complexity contribute to microclimatic stratification. The study provides empirical evidence for the importance of vertically explicit microclimate monitoring and offers a transferable analytical framework for understanding how variations in terrain and forest structure generate distinct microhabitats across the forest vertical profile.

2. Materials and methods

2.1. Study area and data collection

This study was conducted on Terceira Island, which is part of the Azores Archipelago (Portugal), a volcanic oceanic region located approximately 1350 km west of the Portuguese mainland (Fig. 1). The island's climate is influenced by the Gulf Stream and the Azores Current with complex wind patterns (Caldeira and Reis, 2017), resulting in mild year-round air temperatures between 16.7 and 17.5 °C and total rainfall between 775 and 1716 mm at sea level (Azevedo et al., 1999; Borges et al., 2020). The vegetation of Terceira is stratified by altitude, with low- to mid-elevation zones (≤ 500 m) dominated by pastures and non-native secondary forests, particularly stands of the invasive tree *Pittosporum undulatum* Vent. (Borges Silva et al., 2018). In contrast, higher elevations (above 500 m) support remnants of native vegetation. According to the most recent classification the native vegetation of the Azores is characterised by a variety of forest types, including *Laurus azorica*-dominated submontane forests, mixed *Juniperus brevifolia*-*Ilex azorica* montane forests, and *J. brevifolia* montane woodlands (Elias et al., 2016).

We used 19 permanent 20 × 20 m plots (400 m²), nine of which were in native forest fragments (between 590 and 899 m elevation) and ten in exotic *P. undulatum* forests (between 256 and 461 m elevation). Plots were selected to represent contrasting levels of structural complexity across the forest vertical profile, following prior characterisation in Lhoumeau and Borges (2025). The current landscape situation of the island resulted in a sampling design where forest types cannot be considered fully independent of the altitudinal gradient (Lhoumeau et al., 2025) and native forest plots exhibit greater homogeneity and structural complexity compared to the more heterogeneous and simpler secondary exotic *P. undulatum* stands. Details about the plots can be found in supplementary materials.

2.2. Forest structural complexity assessment

The structural complexity of forest ecosystems was measured in July 2024 using terrestrial laser scanning with a FARO Focus M70 scanner (FARO Technologies Inc., USA). The device utilises a phase-shift-based 3D laser scanner, capturing a field of view ranging from 305 to 360 degrees in both the vertical and horizontal dimensions with an accuracy of ± 2 mm. It captures objects up to 70 m distance that reflect the emitted laser light (1050 nm wavelength) at their surface, and to store the object's local coordinates as well as the intensity of the reflected

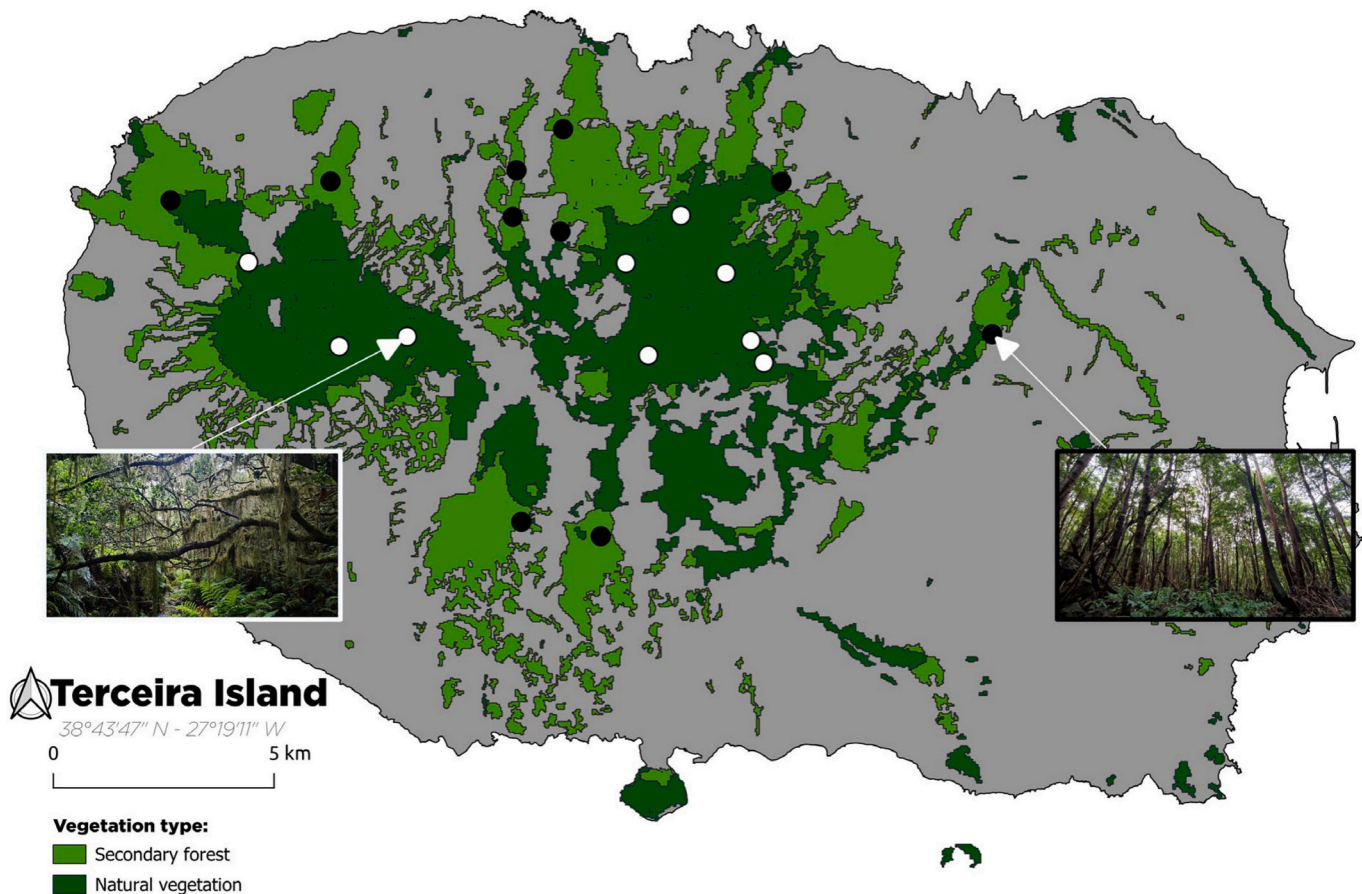


Fig. 1. Map of Terceira Island (Azores, Portugal). Spatial distribution of the 19 sampling plots used in this study: 10 in secondary exotic forest stands (black dots) and nine in native forest fragments (white dots). Inset photos show the difference in structural complexity between native and exotic forest plots.

signal. The scanner was mounted on a tripod at a height of 1.3 m, rotates and captures the entire scenery in its surroundings, thereby creating a point cloud. To ensure comprehensive coverage of each plot, five scans were performed per plot following a “five-on-a-dice” setup (Ehbrecht et al., 2021). The resulting point clouds were processed in FARO Scene (v2019) to remove noise and create a common text file for the point clouds. From these files, four established metrics were derived. For each plot, values of the metrics of five scans were averaged to produce a single representative value.

The structural descriptors were the Stand Structural Complexity Index (SSCI), Foliage Height Diversity (FHD), maximum canopy height (ENL0D), and canopy openness. The selected metrics are not functionally redundant, as they capture distinct mechanisms influencing light penetration, energy redistribution, and microclimatic buffering across strata. The SSCI integrates vertical and horizontal heterogeneity in the three-dimensional arrangement of vegetation and therefore provides a composite measure of stand structural organisation (Ehbrecht et al., 2017). In thermodynamic terms, greater three-dimensional heterogeneity may distribute radiation interception, sensible-heat exchange, and transpiration across a larger canopy volume, while increasing the resistance to direct radiative and turbulent coupling between the atmosphere and lower forest strata (Ehbrecht et al., 2019; Seidel and Ammer, 2023). FHD quantifies the variability in the vertical distribution of foliage and is consequently related to the number and arrangement of foliage layers involved in radiation interception and water-vapour exchange (MacArthur and MacArthur, 1961). Higher FHD may promote sequential attenuation of incoming solar radiation and distribute sensible and latent heat exchange across the vertical canopy profile. ENL0D represents the maximum vertical extent of the vegetation

and is therefore more directly related to canopy height, the distance between the forest floor and the overlying atmosphere, and the aerodynamic domain over which radiation, heat, and turbulence are modified (Ehbrecht et al., 2016; Finnigan, 2021). Canopy openness represents the radiative porosity of the stand, that is, the proportion of open sky through which direct solar radiation and atmospheric turbulence can penetrate (Zheng et al., 2013). Greater canopy openness is therefore expected to increase radiative exposure and atmospheric coupling, potentially amplifying air temperature and VPD variability. Because our objective was to assess how different dimensions of forest structure interact with energy inputs rather than to isolate the independent effect of each metric, model interpretation focuses on interaction patterns and predicted responses rather than on individual parameter estimates.

To complement data on forest structure, we use topographic data (elevation, slope and aspect) with a spatial resolution of 30 m. Elevation was sourced from the Shuttle Radar Topography Mission (OpenTopography, 2013). From this dataset, mean terrain slope and mean terrain northness and eastness were assessed. Computations were performed using QGIS software (version 3.44, Nyall Dawson et al., 2025).

2.3. Microclimate monitoring

The microclimatic conditions were recorded at three vertical strata within each plot (ground level (GRD), understory (UND), and canopy (CAN)) using easylog EL-USB-2 (Lascar Electronics, Wiltshire, UK). The loggers were attached to a central vertical rope at fixed heights: The GRD was established at 2 cm above the forest floor, the UND was positioned at the midpoint between GRD and CAN, and the CAN was located

at approximately 75% of the plot's maximum canopy height. These placements ensure that the dataloggers are not exposed to direct sunlight and are protected against strong winds in the upper canopy. This effectively minimises potential biases due to radiation absorption by the equipment itself. To provide additional protection against the island's frequent rainfall and high humidity, they were secured in a downward position using elastic bands and plastic ties and sealed with extra waterproofing to ensure the sensors remained exposed (Fig. 2).

The recording of air temperature (potentially ranging from -35 to 80 °C, with an accuracy of ± 0.45 °C) and relative humidity (0–100% RH, with an accuracy of $\pm 3\%$) was conducted at hourly intervals from August 2023 to June 2025. However, due to adverse weather conditions and occasional equipment failures, continuous time series were not available for all strata and plots. The raw data were subjected to a screening process to eliminate anomalies. Unrealistic observations, including air temperatures exceeding 35 °C, were removed because such values are highly unlikely in the shaded ground, understory, and canopy environments monitored on Terceira Island and may indicate sensor displacement, direct solar exposure, or equipment malfunction. Only days with complete 24-h records were retained for analysis.

From these data, we calculated daily mean value and range for air temperature and vapour pressure deficit (VPD in kPa), the latter derived as follows from Allen et al. (1998):

$$VPD = e_s - e_a$$

Equation 1: Computation of vapour pressure deficit (VPD).
With

$$e_s = 0.6108 * e^{\frac{17.27 * T}{T + 237.3}}$$

The saturation vapour pressure at a given air temperature T (in °C) and

$$e_a = \frac{RH}{100} * e_s$$

The actual vapour pressure at a given T and a given relative humidity (RH in %).

2.4. Remote sensing data of incoming solar energy

To account for external input of energy, we obtained hourly Global Horizontal Irradiation data (GHI in Wh m^{-2}) from the Copernicus Atmosphere Monitoring Service (CAMS) for the same period (Copernicus Atmosphere Monitoring Service, 2020). These model-derived reanalysis data were sourced using the API from Climate Data Store (package



Fig. 2. Configuration of a data logger at ground level (GRD). Note the supplementary protection against adverse weather conditions. The sensor heads are positioned in a downward direction to prevent the accumulation of rain.

cdsapi, Python 3.12). GHI is defined as the solar downward irradiation integrated over the entire spectrum (285–2800 nm) that is available at ground level on a horizontal surface. In the present study, the variable was employed as a proxy for incoming short-wave solar radiations. The hourly data were then summed to derive the total daily incoming energy.

2.5. Statistical modelling framework

We used mixed-effects models to evaluate how forest structure and topography modified the response of forest microclimates to incoming solar energy across vertical strata. Separate models were fitted for each stratum (GRD, UND, CAN) and for each microclimatic response variable: daily mean air temperature, daily mean VPD, daily temperature range (DTR), and daily VPD range (DVPDR). In each model, total daily incoming solar energy was included as a main effect, together with the main effects of canopy openness, ENL0D, SSCI, FHD, elevation, slope, northness and eastness. We included interactions between total daily incoming solar energy and each predictor to test whether structural and topographic attributes modified microclimatic sensitivity to energy input. All predictors were centred and scaled prior to model fitting using the function *scale* from the base package in R. Site identity was included as a random intercept to account for repeated measurements within sites and persistent among-site differences. Multicollinearity among metrics was assessed using variance inflation factors, which ranged from 1.04 to 4.39. This indicated that there was no substantial multicollinearity among the predictors.

Model selection focused on identifying the most appropriate model structure. For each response variable, the inspection of their distribution allowed the selection of the best suitable model. Therefore, linear mixed-effects models (LMMs) were retained to model the response of the mean air temperature where gamma generalised mixed-effects model (GLMMs) were retained for the other microclimatic response variables. Response distribution plots are available in supplementary materials. All models were fitted with a temporal autoregressive correlation structure to account for temporal autocorrelation among successive daily observations. Models explicitly consider the seasonality of the response variables and were compared with a simpler model lacking temporal autocorrelation structure using information criteria (AIC). These comparisons lead to the systematic inclusion of the temporal autoregressive correlation structure and seasonality (see supplementary materials). We further inspected model performance metrics (marginal and conditional R^2) to assess explanatory power. To control for multiple testing, p -values were adjusted using the Benjamini & Hochberg method (Benjamini and Hochberg, 1995).

The general model structure was:

$$g(\mathbb{E}(Y_{jt})) = \beta_0 + \beta_1 E_{jt} + \sum_{k=1}^p \beta_{k+1} X_{jk} + \sum_{k=1}^p \gamma_k (E_{jt} \times X_{jk}) + \beta_{\sin} \sin\left(\frac{2\pi DOY_t}{365.25}\right) + \beta_{\cos} \cos\left(\frac{2\pi DOY_t}{365.25}\right) + b_j$$

where $\mathbb{E}(Y_{jt})$ is the expected microclimatic response variable for a stratum, site j , and day t ; E_{jt} is the total daily incoming solar energy; X_{jk} represents the k^{th} structural or topographic predictor; β and γ are fixed-effect coefficients; b_j is the random intercept for site j .

Equation 2: General model structure for testing interactions between solar energy and forest structure on microclimate.

For mean temperature, we fitted a Gaussian LMM with the identity link g function and normally distributed residuals. For the other response variables, we fitted Gamma GLMMs with a log link.

To account for annual seasonality, we included sine and cosine transformations of day of year (DOY) as covariates in each model. These paired harmonic terms represent a smooth cyclic annual pattern while avoiding a discontinuity between the end and beginning of the calendar year. DOY was scaled to an annual cycle using $\frac{2\pi DOY}{365.25}$.

All data management and pre-processing were conducted in Julia language v1.11.6 (Bezanson et al., 2017) with use of *Psychrometrics.jl* (Umpierre and c-ortbauer, 2024) for the computation of the VPD. Statistical analyses were conducted in R v4.4.1, (R Core Team, 2024) using the *nlme* and *glmmTMB* packages for model fitting and diagnostics (Bates et al., 2015; Pinheiro et al., 2026). Model goodness of fit (R^2 marginal and conditional) using *performance* package (Lüdtke et al., 2021). Visualisations were designed using *ggplot2* (Wickham, 2016) and *patchwork* (Pedersen, 2025).

2.6. Material limitations

Several material limitations should be considered.

First, although the EL-USB-2 loggers provide high-frequency measurements, sensors were not individually calibrated, which may introduce small systematic offsets among devices; however, manufacturer specifications indicate high long-term stability ($<0.02^\circ\text{C year}^{-1}$), and our analyses focus primarily on within-site temporal dynamics and daily ranges.

Second, weather-related sensor failures produced uneven temporal coverage across sites and strata; to minimise bias, analyses were restricted to days with complete 24-h records. It is important to note that certain periods may be under-represented. Nonetheless, it should be noted that not all data loggers ceased to function simultaneously for the same duration. Consequently, microclimatic data was successfully obtained for the entire study period at a minimum of one stratum of one site.

Also, forest structural complexity was quantified from terrestrial laser scanning conducted in July 2024, whereas microclimate monitoring spanned August 2023–June 2025; we therefore assume that plot-level structural attributes (SSCI, ENL0D, canopy openness, FHD) were broadly stable across the study window, although storm damage or vegetation dynamics could introduce mismatch. Nevertheless, no significant alterations to the vegetation structure were visually observed during the monitoring period, either because of extreme weather events or the phenology of species that are evergreen (Dias et al., 2021).

To contextualise the interpretation of these structural attributes further, it is important to consider their relationship with elevation and forest type. This reflects the history of land use change on Terceira, where much of the native lowland forest below 500 m was converted for other uses, primarily pasture and orchards. Subsequent abandonment has allowed secondary forests dominated by exotic and invasive species to develop (Lhoumeau and Borges, 2025). Therefore, elevational turnover in plant communities is closely associated with differences in forest structure, partly due to variations in tree architecture among species. While elevation can influence forest structure directly and indirectly, similar elevational gradients occur in forests worldwide (see for example McNichol et al., 2024). The distribution of forest types in our study area means that the effects of elevation and structural complexity cannot be fully separated and must be considered together.

Finally, although a more precise digital elevation model (DEM) would be preferable for capturing fine-scale topographic variation potentially relevant to microclimatic heterogeneity, such data were not consistently available for Terceira Island nor possible to collect without dramatically disturbing the three-dimensional forest structure. We therefore used the 30 m SRTM DEM, which provided complete and spatially consistent island-wide coverage. This spatial resolution may underestimate or smooth fine-scale features such as small depressions, microsites, ravines, and local exposure differences.

3. Results

3.1. Data description

Across all sites, we recorded a median of 290 days (6960 h) in the

ground stratum, 310 days (7440 h) in the understory strata, and 297 days (7128 h) in the canopy strata. More detailed descriptions of the data recorded per stratum are available in the supplementary material.

During this period, the summed daily GHI data sourced ranged from 280 Wh m^{-2} to 9005 Wh m^{-2} , with an average of 3515 Wh m^{-2} (Fig. 3). Meanwhile, our field measurements showed a mean air temperature ranging from 3 to 23°C in the ground strata, from 3 to 24°C in the understory strata, and from 3 to 24°C in the canopy strata (Fig. 4). The VPD ranged from 0 to 0.70 kPa in the ground strata, from 0 to 0.81 kPa in the understory strata, and from 0 to 0.74 kPa in the canopy strata (Fig. 5).

3.2. Temporal patterns in solar radiation and microclimate

Incoming solar energy displayed a clear annual cycle, with highest values in summer (June–September) and lowest in winter (December–March, Fig. 3).

Microclimatic conditions varied across the 22-month study period (August 2023–June 2025).

The mean air temperature followed strong seasonal trends, with summer maxima and winter minima (Fig. 4). The stratification of mean air temperature was inconsistent over time, with few differences between August 2023 and March 2024, followed by warmer temperatures in the upper strata ($+1.3^\circ\text{C}$ in CAN and UND comparing to GRD) until September 2024. This was then reversed, with higher temperatures in the ground stratum until February 2025 ($+0.5^\circ\text{C}$ compared to CAN and $+0.1^\circ\text{C}$ compared to UND).

The mean VPD followed a similar seasonal pattern, peaking in the summer months (June–August) and reaching a minimum in the winter months (December–February; Fig. 5). The ground stratum consistently exhibited the lowest VPD throughout the year. The greatest differences between strata occurred during periods of high irradiance (e.g. July 2024), whereas stratification was less pronounced in winter.

3.3. Interacting effects of forest structure and incoming solar energy on microclimatic variables

Topography and forest structure were interacting with incoming solar energy to shape microclimatic conditions, the effects of which varied among vertical strata (Fig. 6). In terms of topography, elevation was of particular significance for most of the forest strata. It tended to reduce energy-driven increases in air temperature and VPD-related responses in all strata. Moreover, the interaction between elevation and incoming solar energy was only positive for DVPDR in CAN, indicating that increasing elevation increased the effect of incoming solar energy on the daily variability of the atmospheric dryness. Terrain exposure only has a limited impact on driving the response of VPD in UND and DTR in CAN while slope did not have any significant interaction in our study plots. Considering the forest structure metrics, results showed that canopy openness frequently amplified moisture variability in UND and CAN and DTR in GRD. SSCI increased the effect of the solar energy on thermal conditions in UND and GRD while FHD constantly decreased the effect of incoming solar energy on the atmospheric dryness in the lower strata (UND and GRD). The stand height (ENL0D) reduced the variability of moisture in CAN, but increased the response of VPD to solar energy in GRD.

In CAN, microclimatic conditions were jointly driven by topography and forest structure. Elevation and northness showed significant interactions with incoming solar energy. Higher elevation tended to reduce the warming and drying effect of incoming solar energy while increasing the DVPDR. Northness was reducing the response of the DTR induced by incoming solar energy, meaning that north-exposed plots showed a reduction in their daily thermal variations. Finally, the interaction between solar energy and ENL0D showed that the greater the stand height, the lower the drying resulting from the action of incoming

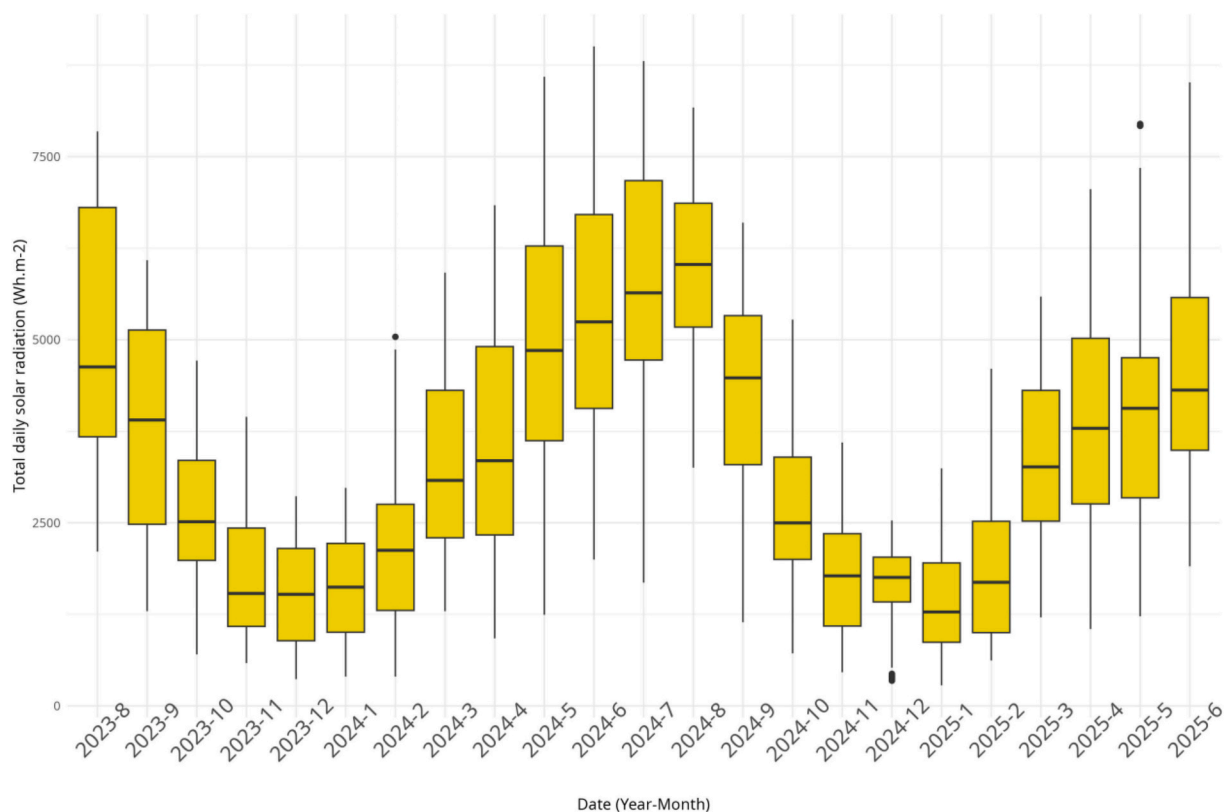


Fig. 3. Time series of the total daily incoming solar energy for all the 19 study sites aggregated per month.

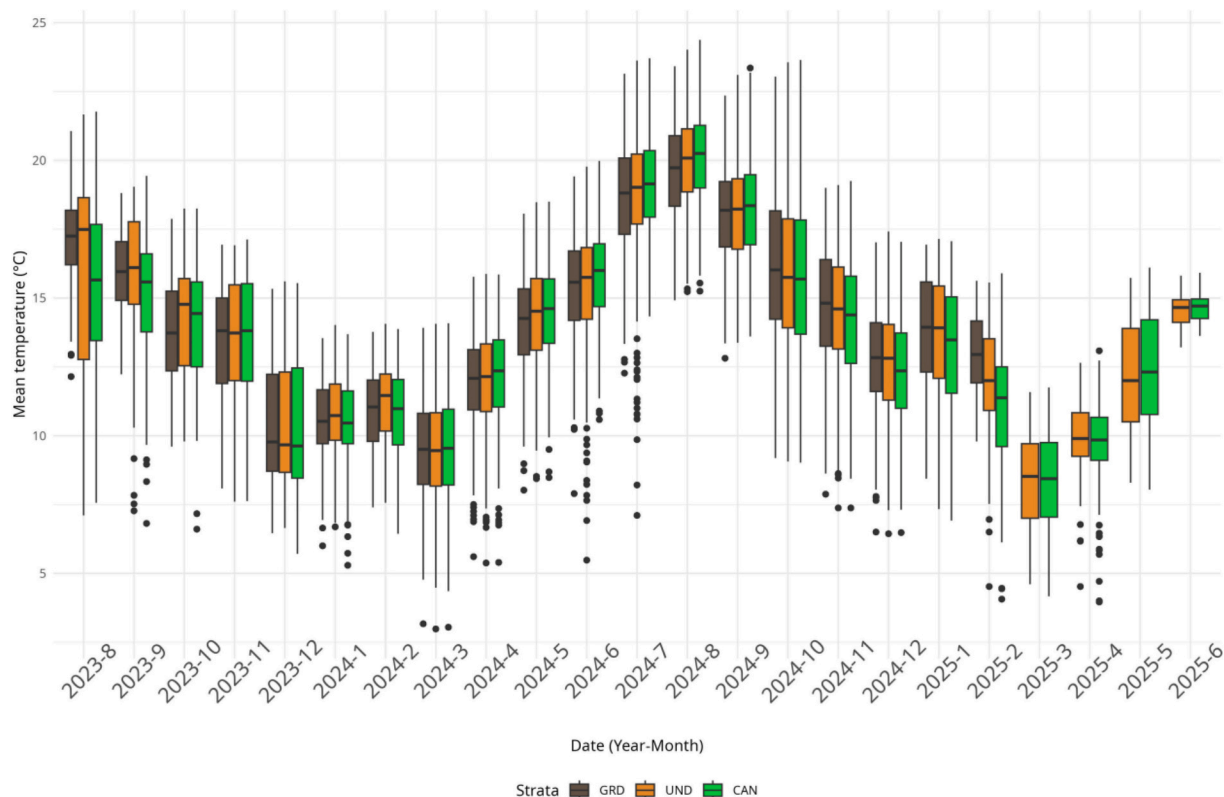


Fig. 4. Time series of the mean daily temperature for all the 19 sites, aggregated by month. Colours are according to the strata, green = canopy, orange = understory, brown = ground. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

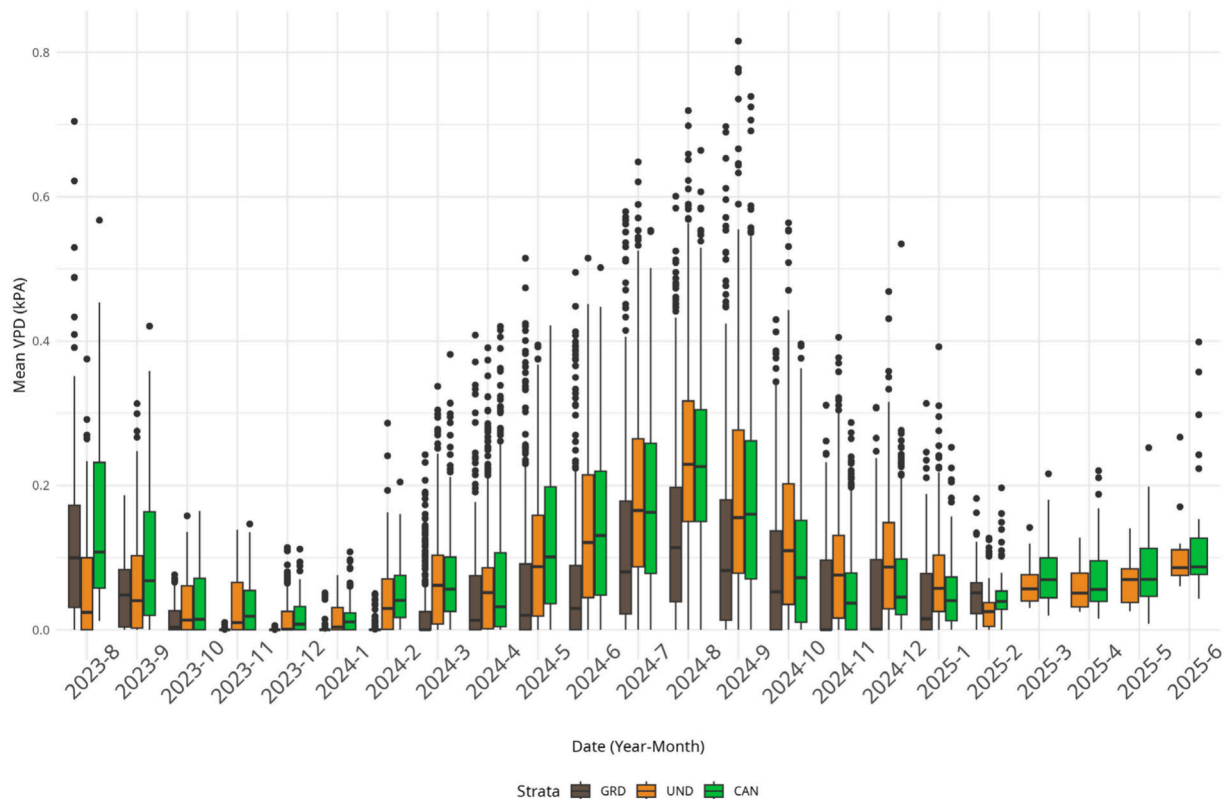


Fig. 5. Time series of the mean daily VPD (Vapour Pressure Deficit) for all the 19 sites, aggregated by month. Colours are according to the strata, green = canopy, orange = understory, brown = ground. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

solar energy. VPD response was also mediated by canopy openness and SSCI, showing an increase of dryness in more open canopies, but a decrease in more complex plots.

Within UND, the interplay between solar energy topography and vegetation structure produced a different pattern of microclimatic conditions and interestingly, no measured metrics were interacting with incoming solar energy to drive the DTR. Regarding the interaction between topography and incoming solar energy, and elevation was still of significant interactions in mean VPD and temperature, similarly to CAN. Eastness decreased the VPD induced response: more east exposed sites tended to exhibit a more constantly humid microclimate. Regarding forest structure-related metrics, canopy openness was of particular significance to moisture conditions. Increase in openness was related to increase in the effect of incoming solar energy on the VPD and DVPDR, meaning that more canopy opened habitats constantly exhibited drier microclimate. Also, FHD had the strongest effect on the reduction of the impact of the incoming solar energy on the increase of the mean VPD within plot: more layered plots were generally more humid. Finally, SSCI was positively interacting with incoming solar energy to amplify the raising of temperature.

At GRD, microclimatic conditions were strongly shaped by interactions between solar energy and topography features. Elevation consistently reduced warming effect of the incoming solar energy and the associated variability: higher plots were cooler and more stable, regardless the terrain exposure. Concerning the forest structure metrics, both canopy openness and SSCI increased the response of the DTR to incoming solar energy: more open or more complex plots showed a greater solar induced thermal variability. Finally, FHD reduced the mean VPD and DVPDR response to solar induced drying: more layered forest plot showed lower and less variable VPD. This interaction was in the opposite direction when it came to ENLOD with an increase of the drying effect of solar energy in higher stand.

4. Discussion

Our results show that microclimatic stratification, forest structural complexity and topography are closely correlated across strata in Terceira Island's forests. Although we did not directly measure the physical mechanisms at work (such as wind speed, turbulent fluxes, or evapotranspiration rates), this observational study highlights different sensitivities of canopy, understory and ground layers to incoming solar energy. Overall, the findings broadly support our initial hypotheses, but they also reveal important nuances across the canopy, understory, and ground layers. The combined patterns highlight that no single structural attribute universally shaped microclimatic variations; instead, the strength and direction of energy–structure interactions differ across the vertical profile, likely reflecting distinct physical mechanisms dominating each stratum. Topography-related metrics showed a more consistent effect across all strata, whereas forest structure metrics had a more specific impact in each stratum. These results point to a more subtle influence of forest structure on the vertical stratification of the microclimate, whereas topography has a broader impact on the vegetation stand.

4.1. Structural complexity as a driver of microclimate at a fine scale

The structural complexity of forest stand is a significant factor in driving microclimate. Global evidence corroborates that diverse and multi-layered forests moderate thermal and moisture conditions. Research conducted in China (Schnabel et al., 2025), the Pacific Northwest (Davis et al., 2019), and boreal regions (Zhang et al., 2024) has demonstrated that enhancing structural complexity through species diversity, canopy cover, or basal area leads to a reduction in maximum air temperatures and VPD close to the forest floor. Our findings align with the broader pattern outlined and with data obtained earlier on Terceira Island (Gabriel, 2000), though the magnitude of its effect vary

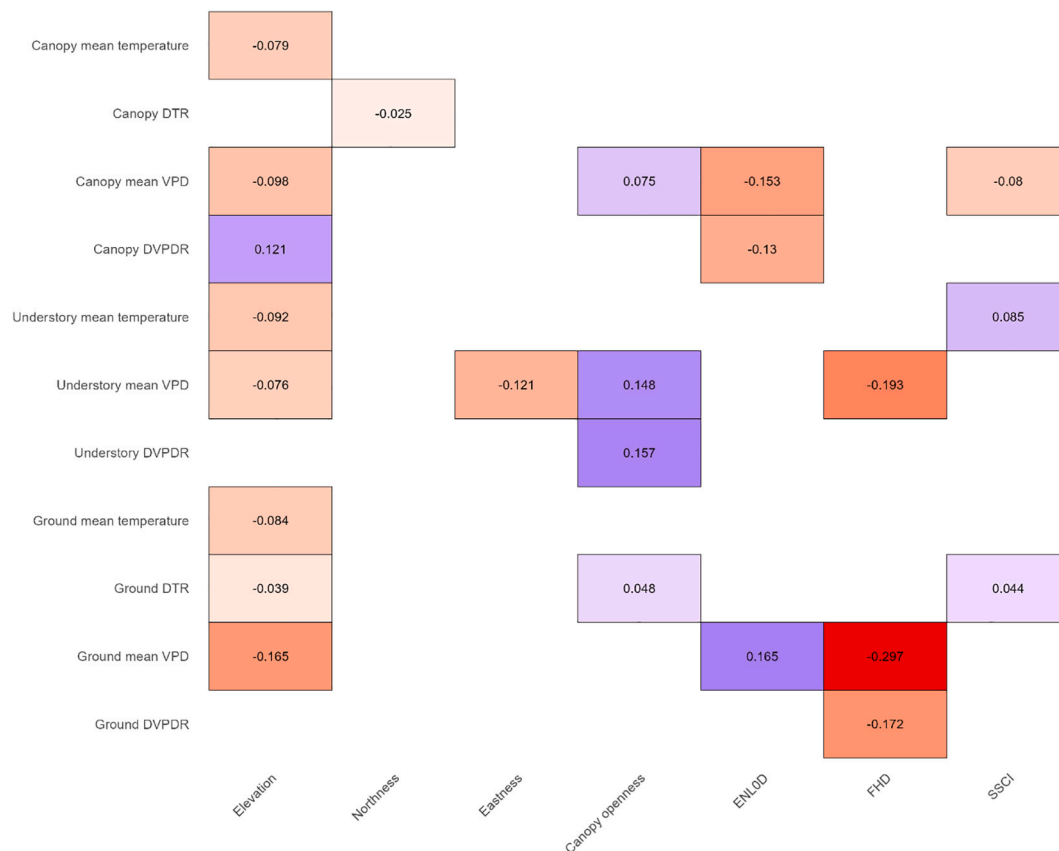


Fig. 6. Heatmap of model estimates for the interaction between total daily incoming solar energy and structural or topographic predictors across three forest strata: canopy, understory and ground. Response variables include daily mean temperature, daily temperature range (DTR), daily mean vapour pressure deficit (VPD), and daily vapour pressure deficit range (DVPDR).

Blue cells indicate positive interactions, meaning that the predictor strengthened the effect of incoming solar energy on the response variable. Red cells indicate negative interactions, meaning that the predictor attenuated the effect of incoming solar energy and therefore contributed to microclimatic buffering. White cells indicate non-significant interaction terms at $p \geq 0.05$. Values inside cells are model estimates.

Full model outputs and goodness-of-fit statistics are provided in the supplementary material. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

by stratum. We found that higher structural complexity (i.e. stands with higher SSCI) decrease the influence of incoming solar energy on the mean VPD in the canopy, while increase its interaction with temperature in the understory and thermal variability in the ground stratum. Also, greater forest layering (i.e. greater FHD) resulted in lowering the drying effect of the incoming solar energy. Together these results are showing that management actions aimed at increasing complexity may yield the greatest microclimatic impacts in these specific strata.

These patterns are consistent with the idea that increased vertical distribution and layering of foliage, which intercept direct beam radiation, can modify coherent airflow, and promote the conversion of sensible heat into turbulent fluxes. However, direct energy-flux and wind measurements would be required to confirm the underlying physical pathways. Banerjee and Linn (2018) demonstrated that even forests with identical leaf area index can differ markedly in physiological and energy-exchange behaviour when leaf area density varies across the profile. Similarly, Chen et al. (2019) showed that incorporating vertical foliage density into turbulence models substantially strengthens estimates of thermal turbulent transfer, emphasising the role of structural layering in enhancing energy dissipation. Also, Law et al. (2001) found that realistic three-dimensional canopy architectures transmit substantially less radiation than simplified random-distribution models, further supporting the idea that complex, heterogeneous canopies reduce radiative load and alter turbulent mixing. Recent theoretical work provides further evidence by linking structural complexity with growth efficiency (Seidel and Ammer, 2023). While a physical mechanistic approach is out

of the scope of this study, our findings illustrate that forest architectures are linked to strata specific microclimates likely by attenuating energy penetration (i.e. shading effect) and modifying the aerodynamic environment that governs heat and moisture exchange.

4.2. Forest height and microclimate buffering

We initially predicted that taller forests would generate greater microclimatic variability if increased height would intensify horizontal wind penetration and amplify thermal fluctuations. However, our results did not support this prediction: stand height only affected the interaction between moisture and incoming solar energy. Canopy height reduced the VPD response and variability to solar energy in the canopy, while also having a strong positive impact on the mean VPD on the ground but no impact in the understory.

Taller stands often form dense windbreaks (Finnigan, 2021), where the forest edge or upper crown surface deflects horizontal airflow and reduces wind penetration and subcanopy turbulence (Heisler and Dewalle, 1988). As a result, the space below the canopy becomes a “quiet zone” decoupled from external atmospheric conditions (McNaughton, 1989), allowing lesser thermal variability because it is less subject to wind-driven cooling and greater shading effect. In contrast, the canopy top remains directly exposed to strong horizontal winds, especially important in the Azores (Caldeira and Reis, 2017), limiting such decoupling. It is also important to note that top canopies in cloud-forest ecosystems (like most of the native forests patches in the

Azores) may be strongly coupled with free-air conditions due to frequent cloud interception (Johnson and Smith, 2008), further reducing the influence of forest height on the lower strata. The absence of significant relationship observed between canopy-height and solar-radiation interactions on the other strata may also reflect a structural consequence: in our system, taller forests often have sparser understories (Lhoumeau and Borges, 2025), which retain less heat and cool more rapidly (De Frenne et al., 2019). Moreover, in the Azores, where strong maritime winds can maintain tight atmospheric coupling at canopy height, we therefore expect weaker buffering at the canopy top than in the understory and near the forest floor.

4.3. Canopy openness amplifies microclimatic instability in less complex forest structure

Across lower strata, our results strongly support the hypothesis that canopy openness acts as a consistent amplifier of microclimatic instability. Globally solar heating intensifies in open or sparsely structured areas (Zellweger et al., 2020), whereas greater vertical and horizontal complexity moderated this response by increasing both aerodynamic resistance and radiative shielding (De Frenne et al., 2019). Our results showed an amplification effect of canopy openness on the mean VPD and range in the understory, underlining an increase in dryness and instability under more open systems. However, this structural metric did not strengthen the influence of solar energy on mean air temperature while remains weak predictor of thermal variability on the ground strata. These patterns likely arise from the combination of more direct radiative penetration and higher light-fleck frequency under discontinuous canopies (Canham et al., 1990; Chazdon and Pearcy, 1991; Durand and Robson, 2023), which together increase thermal and humidity heterogeneity. In more complex forests, the impact of the canopy openness is limited by important radiative shielding from the understory crown material.

4.4. Topographic complexity as a broad driver of energy–microclimate interactions

Elevation emerged as strong and consistent drivers of temperature and VPD responses likely arising from mechanisms such as adiabatic cooling, cloud immersion, wind exposure and reduced net radiation. We found our elevated sites having systematically more stable microclimate characterised by cooler and wetter conditions. Comparable dynamics have been reported elsewhere: Pepin and Lundquist (2008), found that summit environments maintain more stable temperatures due to free-air advection and Montejo-Kovacevich et al. (2020) documented enhanced thermal buffering with elevation in forested habitats. In contrast to our expectations, slope did not impact microclimate while terrain exposure only drives DTR in the canopy and VPD in the understory. These phenomena are attributable to various physical and compositional aspects of the terrain. Specifically, sun-exposed orientations are known to generate stronger warm-dry cycles, while shaded aspects have been observed to reduce diurnal extremes (Desta et al., 2004; Fan et al., 2020; Seyfried et al., 2021). Also, in the Azores, this pattern may reflect the greater exposure of west-facing terrain to moist Atlantic air masses and prevailing westerly to northwesterly winds, which can enhance ventilation, cloud formation and orographic moisture inputs while strong south winds (locally known as “Carpenter winds”) can have a drying effect. Persistent low-cloud and fog conditions may further reduce incoming radiation while maintaining high relative humidity.

4.5. Ecological importance of the microclimate stratification in Azorean forests

Vertical microclimatic stratification is not only a physical property of forests but also a fundamental ecological axis along which species partition habitat. Our stratum-specific microclimate results reveal the

vertical environmental gradients that may influence habitat use: the interaction between incoming solar energy and forest structural attributes generates contrasting thermal and moisture regimes across layers, reinforcing vertical niche differentiation as predicted by classical niche theory. In this framework, niche partitioning may emerge because species sort along fine-scale environmental the vertical gradients of energy flux, evaporative demand, and radiative exposure that differ from the ground to the canopy and are highly relevant for multiple forest organisms.

This partitioning may filter plant species, which may contribute to microclimatic variation in a feedback loop, since tree species differ in their canopy characteristics and how they regulate energy exchange. Forest vegetation structure and canopy traits, including leaf area, are associated with variation in understory temperatures, partly through shading and evapotranspiration (Perot et al., 2025; Wang et al., 2025). However, our study did not test for species-specific effects; consequently, our results describe relationships with measured structural attributes rather than effects attributable to plant species.

Moreover, in Azorean forests, arthropods are vertically structured and respond differently to habitat degradation across forest layers (Costa et al., 2023; Lhoumeau and Borges, 2025). For example, adults and juveniles of the same spider species often differ in vertical breadth, with adults occupying broader portions of the gradient (Costa et al., 2025). Such patterns align with the idea that individuals exploit the strata where microclimatic conditions maximise fitness while minimising physiological stress. Also, bryophytes are fixed organisms both constrained by moisture availability (Coelho et al., 2023a) and contributing to the microclimatic environment (Coelho et al., 2023b). Even subtle shifts in vapour pressure deficit or solar exposure across strata can therefore create distinct microhabitats that promote fine-scale niche separation.

Arthropod-based biotic integrity indices developed for the Azores show that canopy, intermediate and epigeal communities can provide different signals of forest condition, and that pooling strata may obscure biologically meaningful responses (Tsafack et al., 2023). Recent trait-based analyses also show that vertical occupancy is linked to both abundance trends and extinction risk, with endemic ground-dwellers often more vulnerable than canopy-associated species (Oyarzabal et al., 2024).

From a monitoring perspective (see e.g. Borges, 2025), these results highlight that single-height microclimate measurements overlook biologically relevant conditions. Canopy, understory and ground environments respond differently to incoming solar energy and structural complexity, meaning that ecologically meaningful niches for organisms like arthropods and bryophytes cannot be inferred from a single stratum. Consequently, restoration planning and microrefugia assessments will benefit from stratum-specific microclimate indicators aligned with the vertical layers most used by focal taxa and life stages.

5. Conclusion

This study shows that forest structural complexity and topography are related to vertical microclimatic stratification by quantifying how canopy, understory, and ground layers respond to incoming solar energy. By integrating terrestrial laser scanning, high-frequency microclimate sensor data, remotely derived solar radiation estimates, and mixed-effects modelling, we provide a data-driven framework for quantifying structure–energy–microclimate relationships in forest ecosystems.

Our findings demonstrate that different forest strata respond differently to external energy inputs and that these responses are mediated by multiple dimensions of vegetation structure. Structurally complex forests can alter microclimatic variability, but the strength and direction of these alterations depend on the vertical layer considered and on the specific structural attributes involved. These results emphasise the need for vertically explicit microclimate monitoring and for analytical

approaches that integrate structural and climatic data streams.

More broadly, the workflow presented here links three-dimensional forest structure with dynamic microclimatic observations and external environmental forcing. Such integrative approaches can be coupled with biodiversity survey to improve restoration evaluation and the identification of microrefugia under climate change. In island ecosystems and other environmentally sensitive landscapes, combining structural complexity metrics with sensor-based microclimate monitoring offers a promising pathway for understanding and managing fine-scale habitat conditions.

CRedit authorship contribution statement

Sébastien Lhoumeau: Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Dominik Seidel:** Resources, Methodology, Data curation. **Rui B. Elias:** Writing – review & editing, Resources. **Rosalina Gabriel:** Writing – review & editing. **Paulo A.V. Borges:** Supervision, Project administration, Funding acquisition, Conceptualization.

Fundings

This research was funded by Biodiversa+, the European Biodiversity Partnership, in the context of the BioMonI – Biodiversity monitoring of island ecosystems project under the 2022–2023 BiodivMon joint call. It was co-funded by the European Commission (GA No. 101052342) and by FCT – Fundação para a Ciência e a Tecnologia, BiodivMon/0003/2022 to BioMonI members R.E., R.G. and P.A.V.B. Sensors were funded by the project FCT-UIDB/00329/2020–2024 (DOI [10.54499/UIDB/00329/2020](https://doi.org/10.54499/UIDB/00329/2020)) and APC was supported by FCT-UID/00329/2025 - Centre for Ecology, Evolution and Environmental Changes (CE3C) DOI <https://doi.org/10.54499/UID/00329/2025>. S.L. is funded by the Azorean Government Ph.D. grant numbers M3.1.a/F/012/2022.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We thank Dirk Böttger, Michael Unger and Paul Konrad Seidel for their help during the LiDAR fieldwork and Kerstin Pierick for her helpful guidance and suggestions during the modelling phase. We also acknowledge the use of ChatGPT and DeepL during the writing phase of the manuscript to enhance the clarity of the wordings.

The fieldwork was conducted under permits issued by the Natural Park of Terceira (Permits CCIR-RAA/2023/28; CCIR-RAA/2024/7; CCIR-RAA/2025/54).

We are very grateful to all the nine anonymous referees, whose comments substantially improved the paper clarity.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecoinf.2026.104087>.

Data availability

Data and code are available on GitHub repository: https://github.com/SebEyes/Microclimate_structure_interaction

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