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# Vegetation canopy height shapes bats' occupancy: a remote sensing approach

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## ABSTRACT

Anthropogenic activities have significantly altered land cover on a global scale. These changes often have a negative effect on biodiversity limiting the distribution of species. The extent of the effect on species' distribution depends on the landscape composition and configuration at a local and landscape level. To better understand this effect on a large scale, we evaluated how land cover and vegetation structure shape bat species' occurrence while considering species' imperfect detection. We hypothesize that intensification of anthropogenic activities in agriculture, for example, reduces heterogeneity of land cover and vegetation structure, and thereby, limits bat occurrence. To investigate this, we conducted acoustic bat sampling across 59 locations in southern Portugal, each with three spatial replicates. We derived fine-scale vegetation structural metrics by combining spaceborne LiDAR (GEDI) and synthetic aperture radar data (Sentinel-1 and ALOS/PALSAR-2). Additionally, we included land cover metrics and high-resolution climate data from CHELSA. Our findings revealed an important relationship between bat species' occupancy and vegetation structure, particularly with vegetation canopy height. Moreover, forest and shrubland proportions were the main land cover types influencing bat species responses. All species' best-ranking occupancy models included at least one climatic variable (temperature, humidity, or potential evapotranspiration), demonstrating the importance of climate when predicting bat distribution. Our acoustic surveys had a species' detection probability varying from 0.19 to 0.86, and it was influenced by night conditions. These findings underscore the importance of modeling imperfect detection, especially for highly vagile and elusive organisms like bats. Our results demonstrate the effectiveness of using vegetation and landscape metrics derived from high-resolution remote sensing data to model species distribution in the context of biodiversity monitoring and conservation.

## ARTICLE HISTORY

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Land cover; species occurrence; GEDI; bats; vegetation canopy height

## 1. Introduction

Global land cover has undergone systematic changes in recent decades, and these changes frequently exert pressure on natural habitats and biodiversity (National Research Council 2007; Peñuelas et al. 2017). To fully understand the impact of these dynamics on biodiversity, a comprehensive and detailed picture of land cover composition at a wider landscape level is required. Horizontally classifying land cover composition, in other words two-dimensional classification (e.g. agricultural land and forest), is only part of the requirement. The vertical structure of the vegetation communities, a third-dimension classification, also shapes the quality of habitats (Dubayah et al. 2010). The complexity of vegetation


strata drives distribution patterns of different species and their diversity locally and on a broader scale (Díaz et al. 2005; Guo et al. 2021; Marques et al. 2016; Moudry et al. 2023). This horizontal and vertical mapping is crucial for decision-makers to develop sustainable policies to enhance the resilience of biodiversity and ecosystem services (Lehrer et al. 2021; Starbuck et al. 2014; Weller 2008), especially in cultural landscapes where horizontal structure encompasses remnants of natural forests, croplands, agroforestry systems, and tree plantations (Shapiro et al. 2020).

Traditionally, large-scale assessments of vegetation structure relied on forest resource inventories, which typically employed systematic sampling of trees

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rendering cost, labor, and time challenges, as well as expensive spatial analyses (Barreiro and Tomé 2017; Rice et al. 2014; White et al. 2016). Remote sensing stands as a rapidly evolving set of tools that help overcome these challenges and provide systematic and consistent measurements of ecosystem structure (Guo et al. 2021; White et al. 2016). Modern spaceborne missions effectively acquire multi-source data, proving to be valuable for estimating key forest composition and structure metrics (Schulte To Bühne et al. 2018; Ustin and Middleton 2021; Valerio et al. 2023). Multispectral sensors are frequently used to horizontally map land cover remotely (*e.g.*, Chaves et al. 2020), but their limitations emerge in complex landscapes where different vegetation types exhibit similar spectral signatures (Dwiputra et al. 2023; Karra et al. 2021). Here, integrating multi-source data, including multispectral, Synthetic Aperture Radar (SAR), and Light Detection and Ranging (LiDAR), significantly enhances mapping of both horizontal and vertical vegetation components (*e.g.*, David et al. 2022; Fagua et al. 2019).

LiDAR plays a crucial role in characterizing vertical vegetation structure, providing key metrics such as canopy height, cover, and density, as heterogeneity in terms of leaf area index (LAI) and plant area index (PAI) (Dubayah and Drake 2000; Naesset 1997; Tang et al. 2012; Tang et al. 2016; Tian et al. 2021). While LiDAR deployment can be terrestrial, airborne, or spaceborne, only airborne and spaceborne platforms are suitable for large-scale studies (Melin et al. 2017; Moudry et al. 2023). Notably, the spaceborne Global Ecosystem Dynamics Investigation (GEDI) mission offers extensive LiDAR datasets for near-global coverage (Dubayah et al. 2020a). Optimized specifically for vegetation structure analysis, GEDI aims to elucidate the link between ecosystem structure and biodiversity (*e.g.*, Hakkenberg et al. 2023; Schneider et al. 2020). However, GEDI data alone does not provide spatially continuous maps of canopy structure across broad areas (Schneider et al. 2020). This limitation requires the integration of other remote sensing data sources, enabling extrapolation to regions not directly sampled by GEDI. By integrating multi-source satellite data with LiDAR information, we can develop robust models of forest structure across large spatial scales. These multifaceted remote sensing approaches ultimately enhance our understanding of the spatial distribution of wild species.

From an ecological perspective, bats are well-suited indicators for studying landscape composition and vegetation structure at large scales. Due to varied feeding strategies and adaptations, bat species are affected differently to habitat structure (Denzinger and Schnitzler 2013). Bats have been shown to respond to composition and structure (Froidevaux et al. 2016; Gehrti and Chelsvig 2003; Monadjem et al. 2007), varying by season (Taylor et al. 2013), biome (Farneda et al. 2020; Mendes et al. 2017a) and species (Fuentes-Montemayor et al. 2013; Mendes et al. 2017b). More precisely, different bat species have varied distribution patterns, ranging from locally restricted to widely distributed (Russo and Jones 2003). Moreover, bats offer the advantage of being able to be sampled using increasingly affordable autonomous ultrasound detectors, which enhances the scalability of surveying echolocating bats (Gibb et al. 2019; Hill et al. 2018). There is variability in the likelihood of acoustically detecting bats, influenced by factors such as the distance from the detector and the vegetation structure (Gorresen et al. 2008; Patriquin et al. 2003).

This study represents a significant advancement as we model species occupancy considering both horizontal and vertical habitat structures derived from a novel integration of spaceborne LiDAR (GEDI) and SAR data. We applied a modeling methodology to study bat occupancy using novel remote sensing tools while explicitly accounting for imperfect detection. Specifically, we aimed to a) assess how vegetation structure and density influence bat occupancy, and b) understand how land cover composition, as well as climate data, determines the spatial patterns of bat occupancy and detection. We anticipate species-specific variations but predict that cultural land cover will negatively affect bat species' occupancy, while areas with more complex vegetation communities will have the opposite, positive effect on occupancy. Furthermore, we hypothesize that vegetation metrics will be a determinant variable for modeling bat species occupancy.

## 2. Materials and methods

### 2.1. Study area

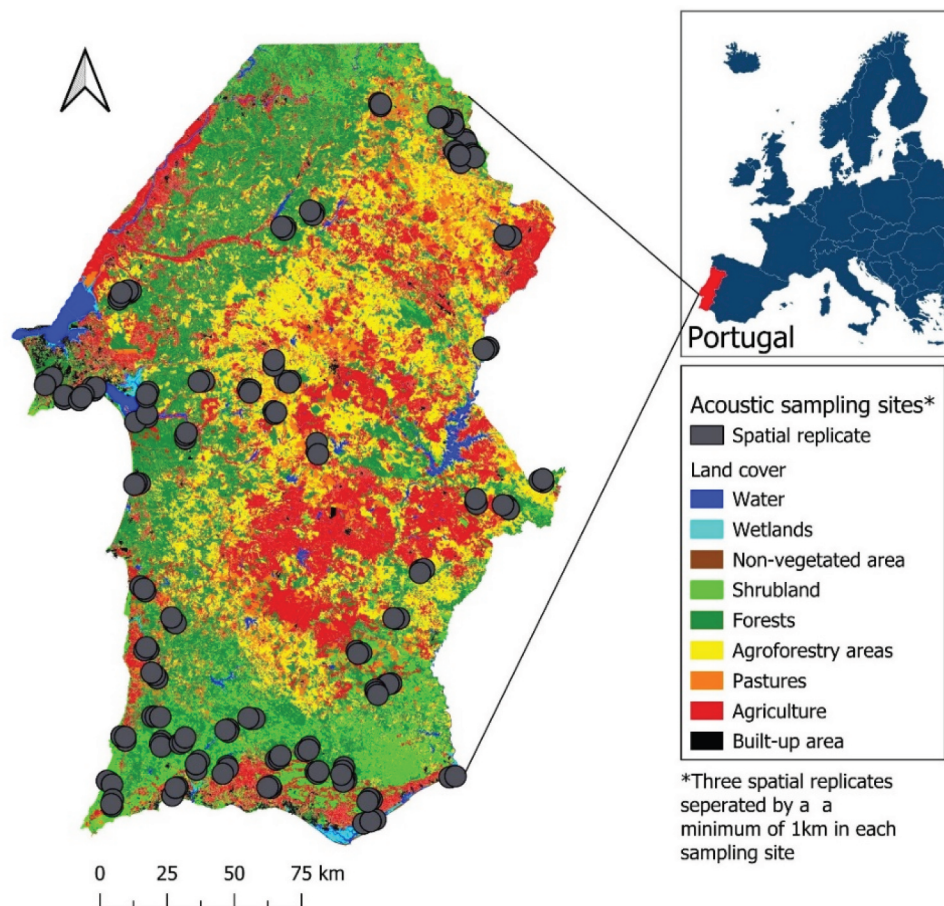
Given its diverse landscape composition and structure, the Mediterranean biogeographic region provides a favorable research context to explore the effects of land cover and vegetation structure on bat

occupancy. This study was conducted in the southern region of Portugal (Figure 1), and data collection was carried out within Natura 2000 network sites. The area is characterized by Mediterranean climate, with hot and dry summers and mild winters. The landscape exhibits a mosaic pattern comprising oak woodlands, shrublands, and human-influenced habitats, such as permanent crops (olive groves and cereal crops), pastures, and tree plantations (stone pines, eucalyptus, and maritime pines). Additionally, riparian vegetation associated with fresh-water habitats contributes to the diversity of vegetation structure in the area (Rainho 2007).

## 2.2. Bat sampling design

Bat occupancy and detection were sampled using passive and acoustic techniques during bats' annual most active period, from May to October (Mendes et al. 2014). We visited 59 sites within the study area across two years (2020–2021), and to ensure optimal

bat detectability during acoustic recording we conducted surveys only during nights with suitable weather conditions. These conditions included no rain as it can hinder bats from foraging, wind speeds below 3.5 m/s as it limits bat's capacity to fly, and nightly temperatures above 10°C, as lower temperatures reduce bat activity, compromising the detectability of the species (Amorim et al. 2012; Dixon 2012; Ford et al. 2005; Russo and Jones 2003). We implemented three spatially replicated surveys at each site, ensuring a minimum separation distance of 1 km between replicates to guarantee their independence. Given the non-territorial behavior of temperate bats during flight, any replicate location within a suitable habitat has an independent probability of detecting the target species (Rainho et al. 2011). We used Audiomoth devices, stationary automatic ultrasound recording devices (Hill et al. 2018), set up on trees or poles with a microphone perpendicular to the substrate and at a minimum height of 1.5 m to minimize signal attenuation from ground-level vegetation



**Figure 1.** Map with the location of bat acoustic sampling sites ( $n = 59$ ) and their three spatial replicates, in the study area of southern Portugal. Ten land cover categories considered to derive land cover metrics. Insert shows Portugal's location within Europe.

(Patriquin et al. 2003). Recordings were conducted at a mid-gain setting and with a sample rate of 256 kHz, a value at least twice as high as that of the highest sound frequency of bat species echolocation occurring in the region, whose frequency call's range from 9 kHz to 120 kHz (see Nyquist-Shannon sampling theorem, Shannon 1949). During each sampling session, the devices recorded a nine-second sound file followed by a one-second pause, employing a quasi-continuous recording approach starting 15 minutes before sunset and ending four hours after sunset. This specific time window corresponds to the period of peak bat nightly activity (Rainho 2007; Russo and Jones 2003).

### 2.3. Acoustic analysis

Due to the recording devices' substantial volume of sound files, a semi-automatic approach was employed for acoustic bat identification using Kaleidoscope Pro (Wildlife Acoustics, Massachusetts, USA). We implemented the auto-classifier algorithm within Kaleidoscope Pro to filter audio files, distinguishing those containing bat calls from those without calls. Subsequently, all files classified as containing bat calls were manually reviewed and identified using the same software to ensure the efficiency and accuracy of the file tagging process. The bat species' acoustic identification was based on Barataud (2020) and Rainho et al. (2011). In cases where multiple species' echolocation calls were present within an audio file, this was duplicated, and each copy was assigned a distinct species identification. Bat calls that could not be assigned to a species or species group were not considered for analysis. We considered a bat species as present during a survey if

its echolocation calls were recorded and positively identified at least once during the night and absent if the species was not acoustically recorded.

### 2.4. Predictors

In this study, four types of predictor covariates were employed to model bat occupancy and detection in southern Portugal: a) vegetation structure and density, b) land cover metrics, c) climate data and d) night conditions (Table 1).

#### 2.4.1. Vegetation structure and density

As a vegetation structure predictor variable, we derived from the spaceborne LiDAR system GEDI a vegetation canopy height (VCH) metric (Table 1). For this, the GEDI L2A Elevation and Height Metrics data product (Version 002) was used. The L2A product provides latitude and longitude information, quality metrics of the geolocated waveform, ground elevation, canopy height, and metrics of reflected energy (relative heights: RH0, RH10, RH20, ..., RH100) from different surfaces within the 25-m laser footprint (Dubayah et al. 2020a). As GEDI only provides samples and transects over the landscape and cannot produce spatially continuous LiDAR measurements (e.g. Ngo et al. 2023), it is crucial to extrapolate these footprint-level data to areas without GEDI coverage by integrating them with other types of remote sensing data (e.g. Ghosh et al. 2022; Liu et al. 2022; Ngo et al. 2023; Potapov et al. 2021; Sothe et al. 2022; Wang et al. 2023). Considering that Synthetic Aperture Radar (SAR) signal is sensitive to vegetation structure (e.g. Flores-Anderson et al. 2019), we developed a predictive model by integrating Sentinel-1 C-band and ALOS2/PALSAR2 L-band data. This model aimed

**Table 1.** Summary of data, sources, and usages of covariates for occupancy modeling.

Covariate	Data source	Source	Purpose	Predictor type
Vegetation Canopy height	GEDI L2A	search.earthdata.nasa.gov (GEDI02)	Occupancy and Detection	Vegetation
Enhanced vegetation Index	Sentinel-1 and ALOS2/PALSAR2	Google Earth Engine	Occupancy	Vegetation
Proportion of Land Cover	Sentinel-2	browser.dataspace.copernicus.eu (Sentinel-2)	Occupancy	Land cover
Edge density of Land cover	Orthophoto	dgterritorio.gov.pt (COS 2018)	Occupancy	Land cover
Distance to water			Occupancy and Detection	Land cover
Climatologies	CHELSA	chelsa-climate.org	Occupancy	Climate
Moon phase	NASA's Scientific Visualization Studio	svs.gsfc.nasa.gov. (Moon Phase)	Detection	Night
Land surface temperature	Sentinel-3A/SLSTR	browser.dataspace.copernicus.eu (Sentinel-3)	Detection	Night

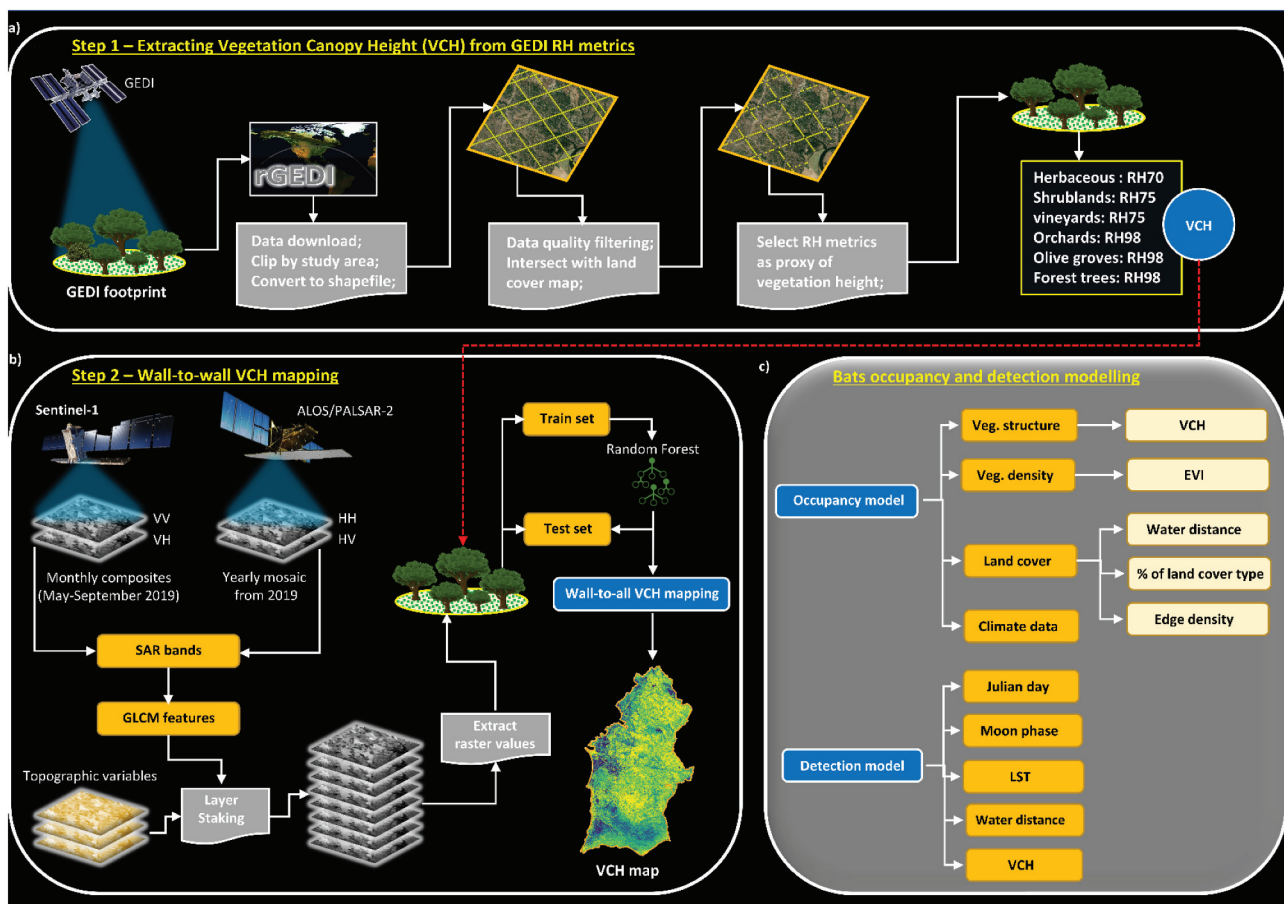
to generate a spatially continuous GEDI-derived VCH metric. In addition to SAR data, three topographical variables – elevation, slope angle, and slope aspect – were computed and employed as predictor variables for VCH, resulting in a total of 51 analyzed variables (Table S1). The relative importance of each predictor variable in estimating vegetation canopy height was assessed by calculating the percentage increase in mean squared error (%IncMSE), where higher % IncMSE values indicate high importance of the predictor variable. Based on this integrated model that estimates the VCH, a map representing the continuous vegetation height for each  $25 \times 25$ -meter pixel was generated across the study area (Figure 2).

Details on the methodological steps employed to generate the VCH metric can be found in the Supplementary Material. As a proxy of vegetation density, we computed the Enhanced Vegetation Index (EVI) from the Sentinel-2 multispectral data (Table 1). Both VCH and EVI metrics were produced

at a resolution of  $25 \times 25$  m. To enhance our ability to capture fine-scale information within both VCH and EVI and understand their influence on bat occupancy patterns, we calculated the mean, median, variance, standard deviation, minimum, and maximum values for these variables at four different buffer sizes (500, 1000, 1500, and 2000 m).

#### 2.4.2. Land cover metrics

We derived landcover metrics from the 2018 Land Cover Map of Portugal (Table 1). This land cover map covers the entire geographic extent of mainland Portugal and has a minimum cartographic resolution of 1 hectare per polygon and a minimum of 20 m between lines (Direção-Geral do Território, 2019). In this study, we considered ten land cover categories: “Built-up area,” “Agriculture,” “Pasture,” “Agroforestry areas,” “Forests,” “Forests excluding Eucalyptus spp.,” “Shrubland,” “Non-vegetated area,” “Wetlands,” and “Water bodies” (Figure 1). These categories were



**Figure 2.** Methodological workflow to estimate the VCH values in a two-step process. LiDAR GEDI data acquisition a) and Sentinel-1 C-band and ALOS2/PALSAR2 L-band data integration b); Predictor variables used for occupancy and detection model building c). VCH – vegetation canopy height; EVI – enhanced vegetation index; LST – land surface temperature.

vectorized and classified based on visual interpretation of orthophotos with four spectral bands (blue, green, red and near-infrared) (Direção-Geral do Território, 2019). Buffers of two sizes (500 m and 2000 m) were selected to examine the scale dependence of bat occupancy concerning land cover variables (Ferreira et al. 2022; Smith et al. 2021) and were established around each of the 177 sampling points. Within these buffers and at the two focal scales, we calculated the proportion of land cover for each of the ten categories mentioned above (Table 1). We also calculated the edge density of the respective land cover categories (Pauli et al. 2017) (Table 1). The proportion of land cover classes was computed in QGIS v3.30.0 software (QGIS.org 2021) by quantifying the area of land cover within the buffer in square meters, while the edge density was calculated using the R package “landscapemetrics” (Hesse et al. 2012). Edge density quantifies the configuration of a land cover category within a buffer zone. It is calculated dividing the total length of the land cover category’s edge (in meters) by the total area of that land cover category within the buffer (in square meters) as defined by Hesse et al. (2012). As we conducted the occupancy analysis at the site level with three replicates, we obtained the average value from the three sampling points to represent the site. We included the distance to rivers and water bodies as covariates to account for spatial heterogeneity between the spatial replicates, as water availability has been demonstrated to have a strong influence on bat distribution and diversity in a drought-prone Mediterranean landscape (e.g. Amorim et al. 2018).

#### 2.4.3. Climate data

We obtained 12 bioclimatic indicators from CHELSA (Climatologies at high resolution for the earth’s land surface areas) (Version 1.2, Karger et al. 2017) (Table 1). These included variables of temperature, precipitation, humidity, and primary productivity (Table S3). The climatic variables were used to model occupancy as they have been reported as determinant to assess bat species’ range (Amorim et al. 2014; Rebelo et al. 2010; Tuan et al. 2023) We conducted a normality test to detect strong deviations from the normal distribution and a correlation analysis to verify multicollinearity between indicators. Among the variables that exhibited Pearson’s correlations of higher than 0.7 with others, we selected those

that held ecological relevance to bat occupancy. These indicators, with a resolution of approximately  $1 \times 1$  km, have demonstrated good predictive capacity when used in Species Distribution Models, including models of bat distributions (Karger et al. 2017; Tuan et al. 2023). We averaged the value of each climatic indicator at the two previously mentioned buffers (500 and 2000 m) for the 59 sites.

#### 2.4.4. Night conditions

We hypothesized that nightly variables would impact bat detectability during acoustic sampling (Smith et al. 2021). Thus, we incorporated julian day of the sampling night into the detection component of our models to capture the seasonal variability of bat activity. To account for variability in night temperature, we extracted, at each sampling point, land surface temperature (LST) data for the surveyed night provided by the Sentinel 3 mission (Sentinel-3 team 2013) (Table 1). We also examined the influence of the moon phase on bat species detection, obtaining the percentage of disk illumination data from NASA’s Scientific Visualization Studio (Blanco and Garrie 2020) (Table 1).

#### 2.5. Statistical analysis

We assessed the effects of land cover, vegetation structure, and climate on bat occupancy and detection using single-species occupancy models under a Bayesian approach. We used the R package spOccupancy (Doser et al. 2022) in R version 4.1.2 (R Core Team 2023), which follows a data augmentation strategy for an improved parameter estimation (Polson et al. 2013). In this statistical approach, two sets of latent auxiliary variables follow a Pólya-Gamma distribution, resulting in occurrence and detection regression parameters in occupancy models. We individually tested the effect of each covariate on the estimated parameters by building univariable models with linear and quadratic terms to uncover possible unimodal relations. Before the analysis, all variables were scaled in the model specification. We summarized univariate models, and if the 95% Bayesian credible interval of the logit link function did not overlap zero, we considered this variable as having unequivocal meaning and so considered it for the next step of the multi-variable model construction (Burnham and Anderson 2002). Once the meaningful variables

were selected, we built a multi-variable model for detection, followed by a multi-variable model for occupancy. We adopted a backward elimination strategy where all the meaningful predictor variables were initially included in the multi-variable model and were removed one at a time. This method is preferred over forward variable selection (Heinze et al. 2018) and allowed us to better select covariates based on biological meaning while avoiding over-fitted models. Model selection was based on comparing the relative support of candidate models using Widely Applicable Information Criterion (wAIC) (Burnham and Anderson 2002) and predictive performance from using k-fold cross-validation (Hobbs and Hooten, 2015) as wAIC may not always be reliable for occupancy models (Broms et al. 2016). Using posterior predictive checks, we applied the goodness-of-fit test to the candidate models. Models with a  $\Delta wAIC$  value of less than two units from the top-ranked model were accounted as plausible alternatives, as this difference is not considered statistically significant according to  $\Delta wAIC$  scoring (Kéry and Royle 2016). Using the best candidate model of each species, we tested the residual spatial autocorrelation in species distributions. Residual autocorrelation is tested through the Nearest Neighbor Gaussian Process that accounts for unexplained spatial variation in species occurrence across the region of interest (Datta et al. 2016). The best candidate models resulting from this selection process were used to generate posterior predictive samples and occupancy probability species maps.

### 3. Results

#### 3.1. Predictive model for VCH

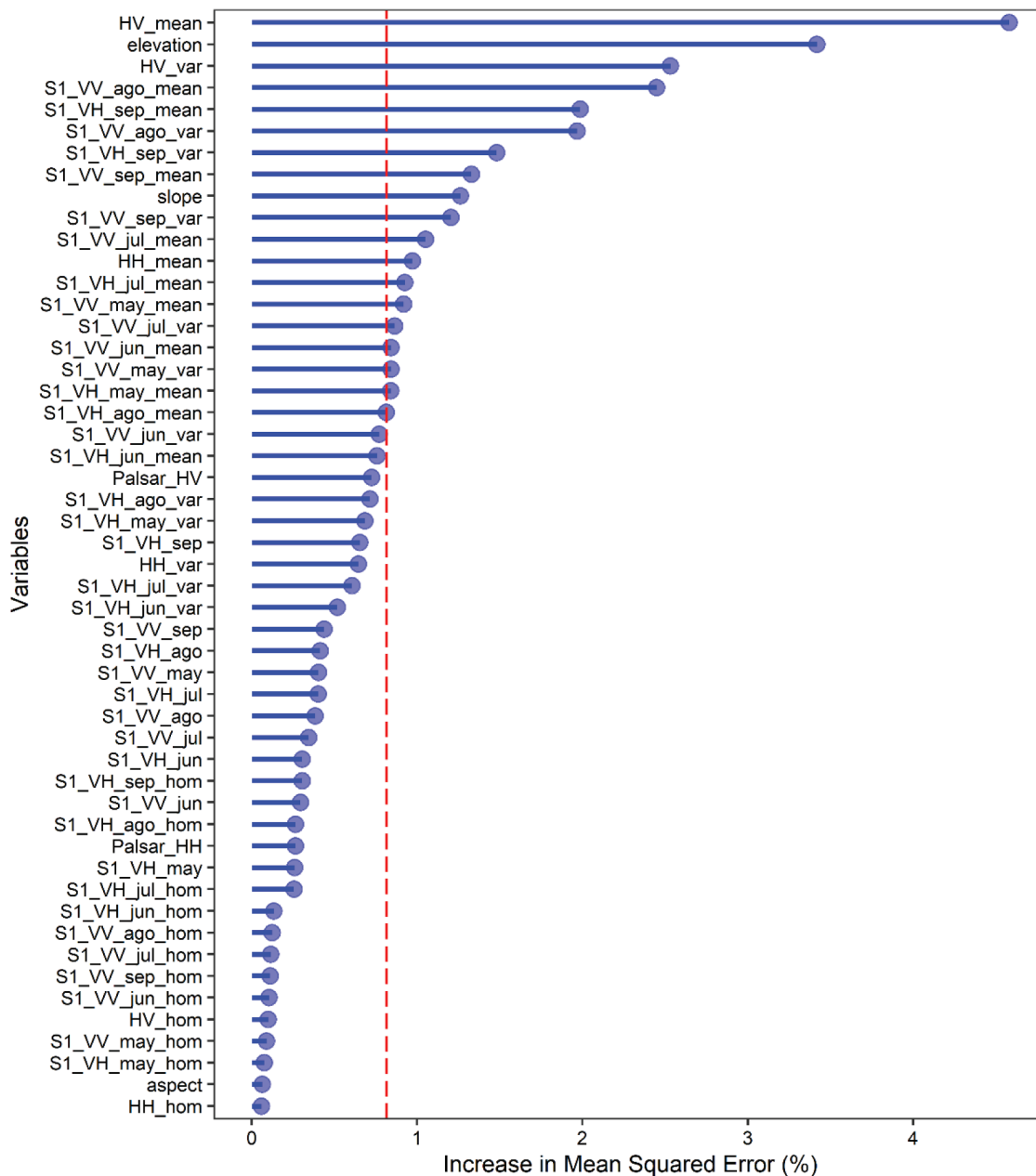
Among the relative heights (RH) metric combination tests made (Table S2), it was observed that the combination of RH98 for trees (forests, orchards, and olive groves), RH75 for shrubs (scrubland and vineyards), and RH70 for pastures achieved the highest coefficient of determination ( $R^2 = 0.69$ ) (Figure S1). The model that uses the RH98 metric for all types of vegetation resulted in lower performance with an  $R^2$  of 0.66, suggesting that RH98 may not be the best option to represent vegetation height for low-stature vegetation types, such as shrubs, vineyards, and pastures. We ranked the relative importance of 51 independent variables for estimating vegetation canopy

height. This ranking showed the mean texture of Horizontal-Vertical polarizations (HV\_mean) derived from ALOS2/PALSAR2 as the most important among the tested variables, followed by elevation (3.41%) and the texture variance of HV polarizations (HV\_var) (2.53%) (Figure 3). The list of the top 6 most important variables is completed with the mean and variance texture variables calculated from Sentinel-1 August Vertical-Vertical (VV), Vertical-Horizontal (VH), and September VV polarizations, with relative importance of 2.44%, 1.98%, and 1.96%, respectively (Figure 3). From the group of the top 6 most important variables, information derived from the L-band of ALOS2/PALSAR2 had a combined relative importance of 7.11%, while those derived from the C-band of Sentinel-1 represented 6.38%. This indicates that the L-band produces better results than the C-band, which can be explained by its greater penetration capacity through the canopy (Huang et al. 2018; Naidoo et al. 2015). Overall, these results indicate that the combination of both SAR bands (L and C) plays an important role in estimating vegetation height, which is consistent with other studies (e.g. Li et al. 2020; Morin et al. 2022; Nandy et al. 2021). Regarding the use of texture variables derived from the L-band, this study also demonstrated, similar to what was observed in Huang et al. (2019), that texture metrics calculated from HV, Horizontal-Horizontal (HH), VV, and VH polarizations contribute more to estimating vegetation height than the original backscatter values from both sensors (Sentinel-1 and ALOS2/PALSAR2). This result may suggest that SAR image texture measurements have a greater capacity to discriminate spatial information, as well as to reduce speckle noise in SAR data (e.g. Laurin et al. 2017; Sarker et al. 2012). The Random Forest model estimated values for VCH ranging from 0.58 m to 24.6 m (Figure 4).

#### 3.2. Bat occupancy modelling

Over 177 sampling nights 47,652 bat call records were collected, identifying nine distinct species. Modelled-average occupancy estimates varied (Table S4), with *Rhinolophus ferrumequinum* having the lowest value at 0.19 (Bayesian credible interval [BCI] 0.02–0.84) and *Pipistrellus pipistrellus* the highest at 0.86 (0.52–0.98). Notably, *Pipistrellus pygmaeus* and *Nyctalus leisleri* also

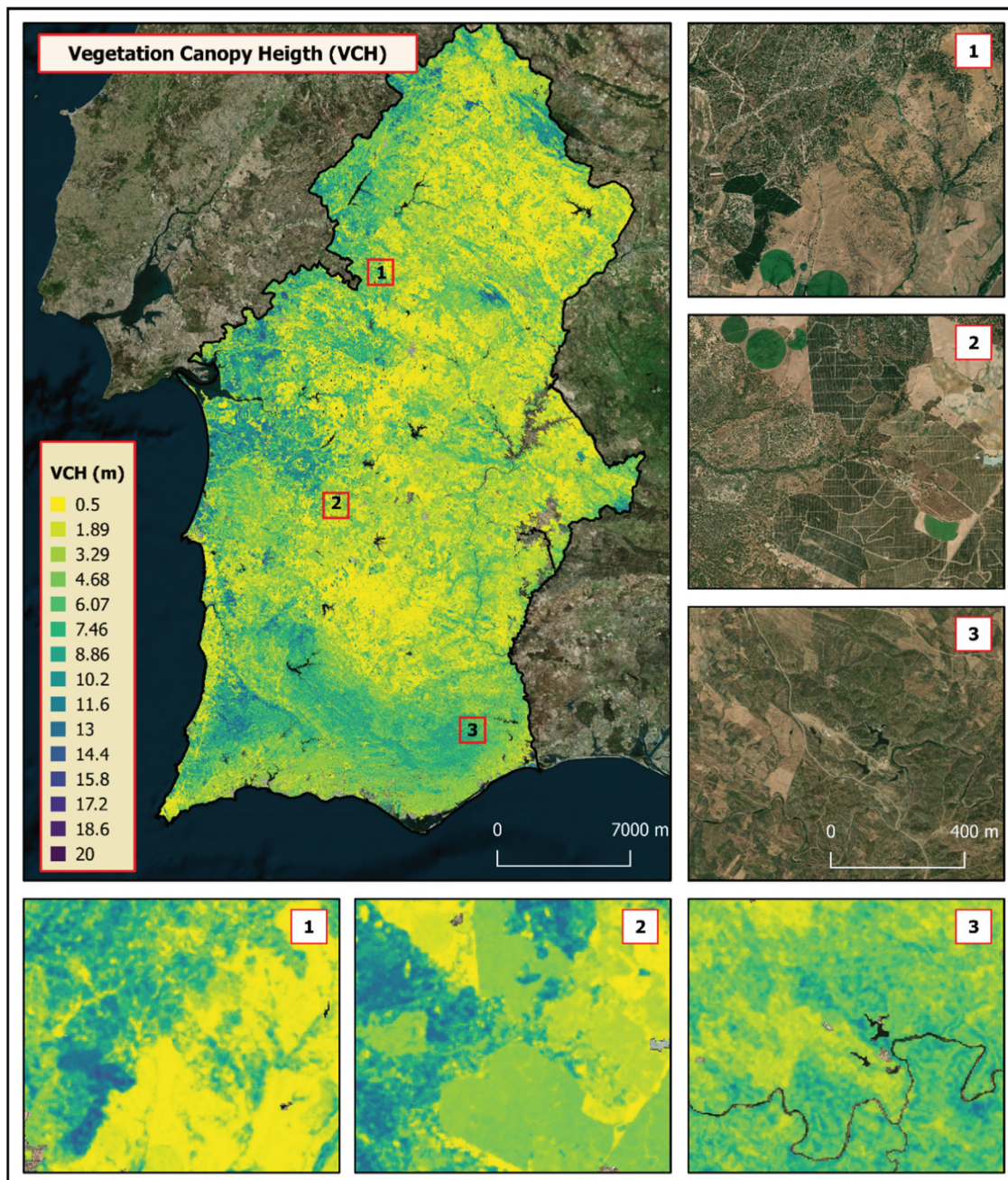




**Figure 3.** Ranking of the relative importance of the 51 independent variables tested in the Random Forest model. Relative importance of each variable was assessed by calculating the percentage increase in mean squared error, where higher values indicate higher importance for vegetation canopy height estimation. Sentinel-1 (S1) variables were derived between January and December 2019. Texture features (Mean, Variance [var], and Homogeneity [hom]) were computed from the Vertical-Vertical (VV), Vertical- Horizontal (VH), Horizontal- Horizontal (HH), and Horizontal-Vertical (HV) polarisations. The vertical red dashed line represents the average Mean Squared Error of the 51 predictors.

presented high mean occupancy estimates of 0.82 (0.32–0.99) and 0.75 (0.47–0.93). *P. pipistrellus* and *Pipistrellus kuhlii*, displayed suboptimal model goodness of fit ( $\sim 0.2$ ) (Hobbs and Hooten, 2015), and their results are only presented in the supplementary materials (Table S4). Four species' models revealed evidence supporting the impact of vegetation

structure, mainly vegetation canopy height (VCH), on bat occupancy (Table 2). Furthermore, occupancy models indicated moderate to strong support for bats' presence in forest and shrubland land cover types. While the occupancy models had a moderate to strong association with climate variables, the responses varied among species (Figures 5, 6).



**Figure 4.** Spatial distribution of vegetation canopy height (VCH) values estimated from the Random Forest model. Snapshots (1, 2 and 3) of aerial pictures and corresponding estimated values of VCH in the study area.

### 3.2.1. Vegetation structure

Regarding vegetation structure, four species responded to VCH (Table 2); notably, *Barbastella barbastellus* was positively associated with the variance of VCH (Figure 5), suggesting a preference for areas exhibiting higher heterogeneity in terms of canopy structure. This heterogeneity is known to contribute to a diversity of microhabitats, providing resources for some bat species (Russo and Jones 2003; Vehviläinen

et al. 2008). The other three species exhibited a significant relation with the minimum VCH values (Table 2). Contrarily and unexpectedly, *Tadarida teniotis* showed a negative relationship with the minimum VCH. Both *Myotis daubentonii* and *Rhinolophus hipposideros* demonstrated a positive relation with the minimum VCH, implying that as the minimum VCH value for an area increases, the likelihood of occupancy for these two bat species also increases

**Table 2.** Top-ranked models for occupancy ( $\Psi$ ) and detection probability ( $p$ ) for seven bat species. Widely Applicable Information Criterion (wAIC), delta Widely Applicable Information Criterion ( $\Delta$ wAIC) and k-fold cross-validation (k-fold).  $\Delta$ wAIC and k-fold were used for model comparison and assessment.

Species	Model	wAIC	$\Delta$ wAIC	k-fold
<i>B. barbastellus</i>	$\Psi$ (VCH variance + evapotransp.); $p$ (moon phase <sup>2</sup> + VCH25m <sup>2</sup> )	154.62	0	156.4
	$\Psi$ (VCH variance); $p$ (moon phase <sup>2</sup> + VCH25m <sup>2</sup> )	154.58	0.04	158.6
	$\Psi$ (VCH variance + forest proportion); $p$ (moon phase <sup>2</sup> + VCH25m <sup>2</sup> )	156.16	1.55	163.9
<i>M. daubentonii</i>	$\Psi$ (forest proportion + humidity); $p$ (water distance + land surface temp. <sup>2</sup> )	180.43	0	187.2
	$\Psi$ (VCH minimum + forest proportion + humidity); $p$ (water distance + land surface temp. <sup>2</sup> )	180.75	0.32	190.8
<i>N. leisleri</i>	$\Psi$ (shrubland proportion <sup>2</sup> + evapotransp. <sup>2</sup> ); $p$ (water distance + land surface temp. <sup>2</sup> )	207.23	0	214.5
	$\Psi$ (shrubland proportion <sup>2</sup> + temp. mean + evapotransp. <sup>2</sup> ); $p$ (water distance + land surface temp. <sup>2</sup> )	207.55	0.33	216.8
<i>P. pygmaeus</i>	$\Psi$ (agriculture edge <sup>2</sup> + built up edge + temp. wettest quarter <sup>2</sup> + water edge <sup>2</sup> + evapotransp. <sup>2</sup> ); $p$ (moon phase <sup>2</sup> )	188.24	0	190.
	$\Psi$ (agriculture edge <sup>2</sup> + built up edge + temp. wettest quarter <sup>2</sup> + water edge <sup>2</sup> ); $p$ (moon phase <sup>2</sup> )	188.24	0.01	190.7
	$\Psi$ (agriculture edge <sup>2</sup> + temp. wettest quarter <sup>2</sup> ); $p$ (moon phase <sup>2</sup> )	189.07	0.84	190.9
	$\Psi$ (temp. wettest quarter <sup>2</sup> + evapotransp. <sup>2</sup> ); $p$ (moon phase <sup>2</sup> )	189.78	1.54	192.7
<i>R. ferrumequinum</i>	$\Psi$ (temp. driest quarter <sup>2</sup> + water distance + primary productivity <sup>2</sup> ); $p$ (julian day <sup>2</sup> )	53.27	0	59.6
	$\Psi$ (rainfall + temp. driest quarter <sup>2</sup> + water distance); $p$ (julian day <sup>2</sup> )	53.05	0.69	72.6
	$\Psi$ (temp. avg <sup>2</sup> + temp. driest quarter <sup>2</sup> + water distance); $p$ (julian day <sup>2</sup> )	53.97	1.02	73.4
	$\Psi$ (temp. avg <sup>2</sup> + rainfall + temp. driest quarter <sup>2</sup> + water distance + primary productivity <sup>2</sup> ); $p$ (julian day <sup>2</sup> )	54.30	1.14	75.2
	$\Psi$ (temp. avg <sup>2</sup> + temp. driest quarter <sup>2</sup> + primary productivity <sup>2</sup> ); $p$ (julian day <sup>2</sup> )	54.42	1.14	75.2
<i>R. hipposideros</i>	$\Psi$ (VCH minimum + EVI minimum + temp. wettest quarter <sup>2</sup> ); $p$ (water distance + land surface temperature <sup>2</sup> + VCH25m <sup>2</sup> )	93.34	0	93.6
	$\Psi$ (EVI minimum + temp. wettest quarter <sup>2</sup> ); $p$ water distance + (land surface temp. <sup>2</sup> + VCH25m <sup>2</sup> )	93.58	0.24	93.9
	$\Psi$ (VCH minimum + water distance <sup>2</sup> + temp. wettest quarter <sup>2</sup> ); $p$ (water distance + land surface temp. <sup>2</sup> + VCH25m <sup>2</sup> )	94.96	1.61	97.0
	$\Psi$ (VCH minimum + EVI minimum water distance <sup>2</sup> + temp. wettest quarter <sup>2</sup> ); $p$ (water distance + land surface temp. <sup>2</sup> + VCH25m <sup>2</sup> )	95.18	1.84	97.1
<i>T. teniotis</i>	$\Psi$ (temperature + rainfall seasonality); $p$ (julian day + water distance <sup>2</sup> )	128.25	0	123.3
	$\Psi$ (VCH minimum + temperature + rainfall seasonality); $p$ (julian day + water distance <sup>2</sup> )	128.51	0.26	123.7
	$\Psi$ (VCH minimum + temperature + rainfall seasonality + shrubland proportion <sup>2</sup> ); $p$ (julian day + water distance <sup>2</sup> )	129.27	1.03	124.6

(Table 2, Figure 6). As small forest-dwelling bats, these two species are best adapted to maneuverable flight in vegetated areas (Bader et al. 2015; Motte and Libois 2002). In addition, *R. hipposideros* was positively related to enhanced vegetation index within the buffer of 500 m (Figure 6).

### 3.2.2. Land cover

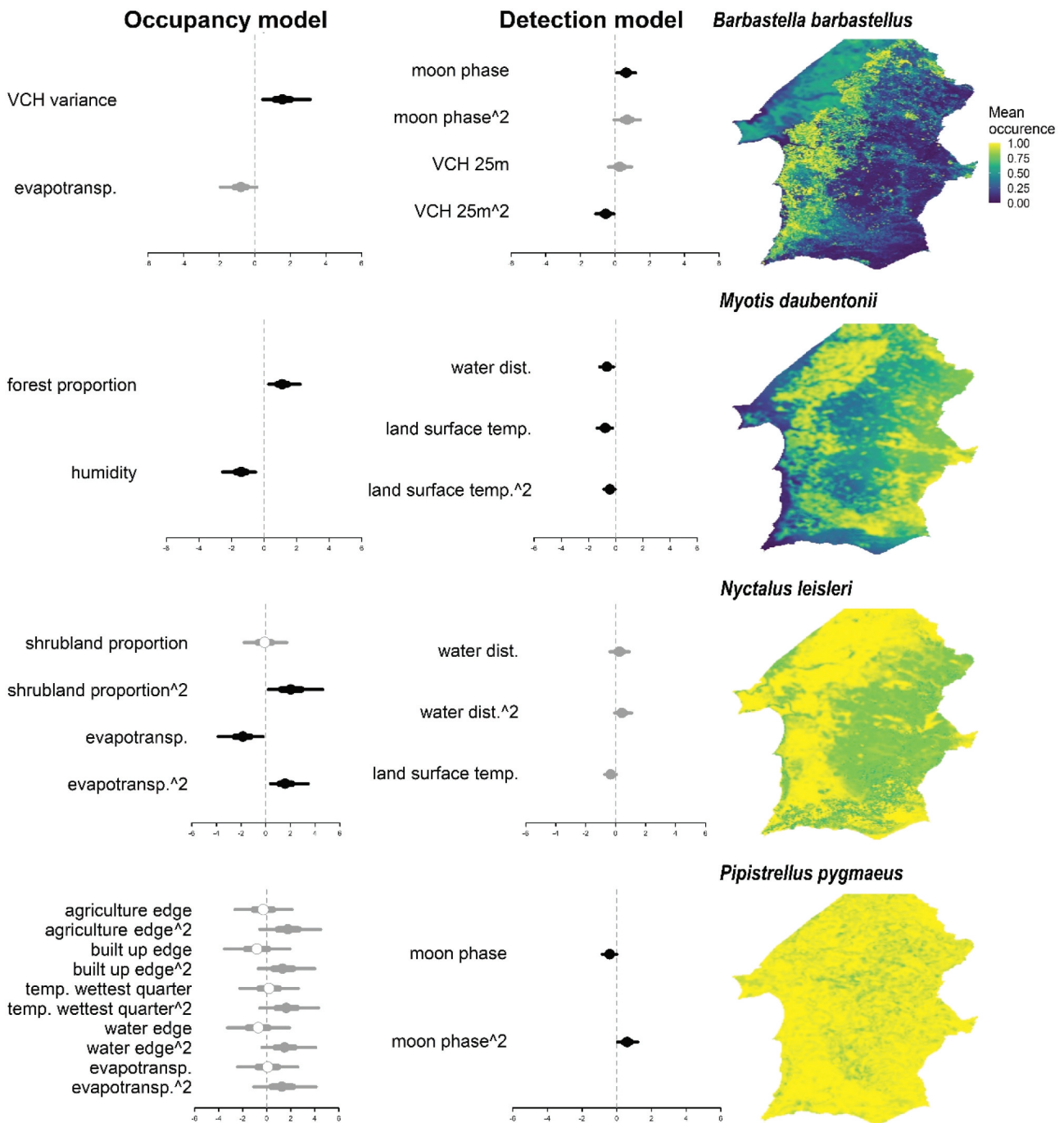
Occupancy for both *B. barbastellus* and *M. daubentonii* demonstrated a pronounced positive relation with the proportion of forest patches (Table 2, Figure 5). Occupancy for *N. leisleri* displayed a positive quadratic relationship with the shrubland proportion (Figure 5). This species can be found in various habitats, favoring forested habitats with lower levels of vegetation clutter, especially for foraging (Ferreira et al. 2022; Shapiro et al. 2020). *P. pygmaeus* stood out as the sole species with a positive occupancy association concerning other land cover types, precisely edge density of built-up areas, agriculture, and water bodies (Figure 5). This species has been previously identified as positively associated with urban environments, possibly exploiting these areas as supplementary feeding grounds due to high prey availability (Avila-Flores and Fenton 2005; Mendes et al. 2014).

### 3.2.3. Climate

Best-fitting models for *B. barbastellus*, *N. leisleri*, and *P. pygmaeus* included mean evapotranspiration within a two-kilometer radius, displaying different responses (Table 2, Figure 5); *B. barbastellus* exhibited a negative relation with evapotranspiration, while both *N. leisleri* and *P. pygmaeus* showed a positive quadratic response, indicating that occupancy rates are lowest at intermediate levels of evapotranspiration (Figure 5). Moreover, occupancy estimates for *N. leisleri*, *R. ferrumequinum*, and *T. teniotis* were related to mean annual air temperature (Table 2). *N. leisleri* and *R. ferrumequinum*'s occupancy exhibited a positive quadratic relationship with temperature, characterized by lower occupancy at median temperature values, whereas the occupancy of *T. teniotis* was inversely related to temperature (Figures 5, 6).

### 3.3. Bat detection modelling

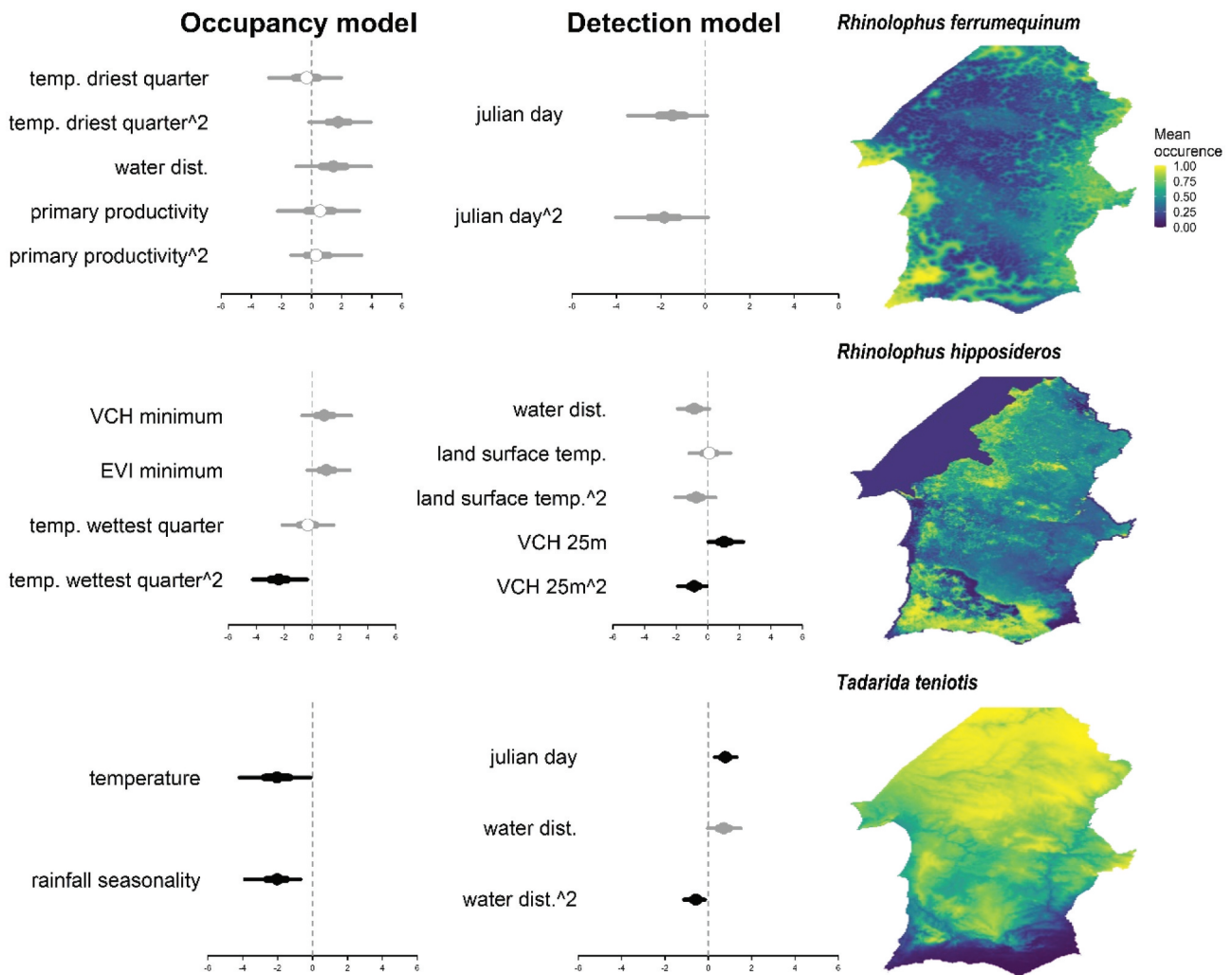
Detection probabilities for all bat species studied were significantly lower than one, ranging from 0.19 (0.02–0.84) for *R. ferrumequinum* to 0.94 (0.19–0.96) for *P. kuhlii*. Detection rates for all species were influenced by at least one nightly environmental covariate, land surface



**Figure 5.** Mean beta coefficients for four (*B. barbastellus*, *M. daubentonii*, *N. leisleri*, *P. pygmaeus*) bat species occupancy (left) and detection (middle). Points represent standardised estimates from the covariates on the best-fitting model. Black error bars show relationships in which 95% Bayesian credible interval (BCI) does not overlap zero, grey error bars indicate overlap between 95% and 50% BCI and white points indicate the overlap within 50% BCI. Resulting map of occupancy probability estimates for the study area (right).

temperature, julian day, or moon phase (Table 2 and Figure 5). *M. daubentonii*, *N. leisleri*, and *R. hipposideros* demonstrated a negative quadratic response to land surface temperature, showing maximum detectability at moderate nightly temperatures. In contrast, detection of *R. ferrumequinum* and *T. teniotis* was related to the

julian day, while detection of *B. barbastellus* and *P. pygmaeus* was associated with the moon phase. Detection covariates related to the spatial heterogeneity of replicates also played a critical role in the top-ranking model, with proximity to rivers or water bodies exhibiting a negative or negative quadratic relationship with



**Figure 6.** Mean beta coefficients for three (*R. ferrumequinum*, *R. hipposideros*, *T. teniotis*) bat species occupancy (left) and detection (middle). Points represent standardised estimates from the covariates on the best-fitting model. Black error bars show relationships in which 95% Bayesian credible interval (BCI) does not overlap zero, grey error bars indicate overlap between 95% and 50% BCI and white points indicate the overlap within 50% BCI. Resulting map of occupancy probability estimates for the study area (right).

detection for *M. daubentonii*, *N. leisleri*, *R. hipposideros*, and *T. teniotis* (Table 2). Furthermore, the mean VCH within a 25 m buffer notably influenced the detection of *B. barbastellus* and *R. hipposideros*, displaying a negative quadratic relationship.

## 4. Discussion

### 4.1. Landscape metrics

Our study's occupancy models have disentangled the relationship between bat occurrence and the spatial dynamics of land cover types and vegetation structure across a regional scale. Our analysis revealed a robust relation between bat occupancy and vegetation metrics, notably vegetation canopy

height (VCH). Critically, the minimum VCH metric present in the models highlights the necessary level of tree growth for the occurrence of certain bat species. This finding concurs with the understanding that taller vegetation and trees promote biodiversity (Ausprey et al. 2023; Begehold et al. 2015) and likely offer better roosting opportunities for forest-dwelling bat species (Bader et al. 2015). Several studies have corroborated the importance of vegetation characteristics in bat distribution and other taxonomic groups (Drapeau et al. 2000; McGarigal and McComb 1995), including studies carried out in the Mediterranean region (Novella-Fernandez et al. 2022). These authors identified that the distribution patterns of bats are predominantly influenced by forest variables, with roosting ecology

being a critical factor. These findings collectively underline the significance of vegetation structure and composition in determining species occupancy and distribution.

As expected, land cover was shown to influence bat occupancy estimates, but contrary to initial predictions, built-up areas and agriculture land cover types were not key determinants in occupancy modeling. Previous research has often linked urban growth and agricultural intensification with adverse effects on bat populations (Li and Kalcounis-Rueppell 2018; Jung and Threlfall 2018; Mtsetfwa et al. 2018). Nevertheless, our results indicate a clear preference among four bat species for forests and shrublands, reflecting their reliance on these habitats. This is particularly evident for *B. barbastellus* and *M. daubentonii*, and in fact, both species frequently roost in forested habitats (Russo and Jones 2003; Ngamprasertwong et al. 2014). Consequently, the conservation and, where possible, restoration of mixed-type forests should be encouraged to sustain roosting and foraging opportunities for these and other animal species (Dietz and Kiefer, 2016; Popa-Lisseanu et al. 2009).

Climatic variables, namely temperature-related metrics, were identified as crucial in determining the distribution of five bat species. Typically, temperate bat species tend to avoid excessively warm areas, as such environments can induce ecological stress, often associated with high drought frequency, adversely affecting bats and other mammal species (Santos et al. 2014; Valerio et al. 2023). In our research, we observed a pattern of spatial heterogeneity in detection probabilities related to the proximity of the sampling location to water sources. Our findings align with existing knowledge that, in dry environments, bats frequently exploit areas near water bodies. This habitat preference is reflected in bat activity (Russo and Jones 2003), leading to greater detectability of bat echolocations. Biogeographical patterns have provided evidence on the climatic response of bat populations, suggesting that Mediterranean species may exhibit higher tolerance to temperature increases (Rebelo and Jones 2010). However, it remains imperative to recognize that bat species are susceptible to the effects of climate change, and even in the presence of suitable habitats, such as riparian areas, adverse climatic conditions like drought that are expected to increase in frequency and

severity, can exert temporal constraining effects on species occurrence (Amorim et al. 2018; Milly et al. 2005).

#### **4.2. Considerations of data integration and methodology**

Our vegetation canopy height model results (VCH) exhibit some limitations (Figure S1), but we believe that these have a limited impact on our key findings. The VCH model shows a pattern of overestimation and underestimation of vegetation height in the intervals between 0–2 and > 20 meters, respectively, which has been reported in other studies (Dorado-Roda et al. 2021; Huettermann et al. 2022; Guerra-Hernández and Pascual 2021; Potapov et al. 2021). In areas covered by sparser canopies or lower vegetation (e.g. vineyards, herbaceous), spaceborne LiDAR systems, like GEDI and ICESat-2, are less able to measure vegetation height accurately, as photons reflected by the canopies can be incorrectly identified as ground or noise (e.g. Atmani et al. 2022). However, GEDI's ability to estimate the height of shrub and herbaceous vegetation has not been extensively studied, making it necessary to develop more studies focused on comparing field data with measurements from this sensor (e.g. Leite et al. 2022; Li et al. 2023). On the other hand, the underestimation of vegetation height values for taller vegetation (>20 m) may be associated with denser canopy coverage, which can result in insufficient recording of ground-related photons, hindering the sensor's ability to accurately determine canopy height (Dorado-Roda et al. 2021; Dubayah et al. 2020b, 2020c; Hancock et al. 2019; Neuenschwander et al. 2020). The uncertainty associated with the 0–2 meters vegetation height is unlikely to strongly affect the occupancy estimates as there is evidence that small insectivorous bats have stereotyped flight paths when foraging near vegetation and avoid flying very close to the ground (Hermans et al. 2023). On the other hand, areas covered by trees taller than 20 m are scarce in the study area and trees with such heights are only present in old pine and eucalyptus plantations.

#### **4.3. Remote sensing in species distribution**

Spaceborne LiDAR data is becoming more readily available, with an improved spatial and temporal resolution (Aguilar et al. 2024; Hancock et al. 2019). The comprehensive three-dimensional data provided by LiDAR

offers the means to generate distribution maps at increased spatial and temporal resolutions which, is particularly important in the current scenario where climate change can drive changes in forest structure and, therefore, impact specialized forest species at a regional scale (Novella-Fernandez et al. 2022). This predictive capacity is pivotal in the field of biodiversity monitoring and conservation, where such detailed and regular mappings are currently inadequately obtained (Schulte To Bühne et al. 2018). When implemented, predictions of future distribution and range shifts are often exclusively based on climatic scenarios under alternative socio-economic settings (Amorim et al. 2014; Rebelo et al. 2010) and, in a few cases, integrated with land cover (Mantyka-Pringle et al. 2015). Insectivorous bats and forest specialist species are predicted to be particularly vulnerable to the interaction between climate and land cover change (Tuan et al. 2023). Therefore, applying modeling techniques incorporating forest structure will likely significantly improve the precision and timeliness of biodiversity assessments, addressing a knowledge gap in current conservation practices. Consequently, management strategies focused on expansion of mixed-type and heterogeneous forest patches that support high-quality habitats for diverse species will enhance the forest's resilience to climate change (Jandl et al. 2019). Implementing these strategies could be instrumental in advancing the conservation of Mediterranean forests and their native wildlife on a broader scale.

## 5. Conclusion

Our research contributed to validating a method primarily based on remote sensing data, emphasizing the role of vertical vegetation structure in determining bat occupancy. Specifically, using bat species as an example, this study highlighted how GEDI LiDAR measurements can play a critical role in enhancing our ability to capture the spatial patterns of species occupancy across the landscape. The approach of modeling species occurrence using GEDI-derived VCH can yield valuable insights into biodiversity distribution on a broad landscape scale and has the potential to reveal changes such as predicting shifts in species range in different forest management scenarios. On the other hand, future studies using other vegetation metrics can be useful in investigating species' fine-scale response to forest management. Our work paves the way for the application of our methodology

to a wider range of elusive species with imperfect detection, for which it can be harder to produce sustainable land management guidelines and assure the resilience of wild species.

## Disclosure statement

No potential conflict of interest was reported by the author(s).

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Review & Editing. Pedro Segurado: Conceptualisation, Writing – Review & Editing, Supervision. João Tiago Marques: Conceptualization, Writing – Review & Editing, Supervision, Project administration.

## Data availability statement

The data set for bat species' occurrence is available from the data paper Grilo et al. 2022. The data supporting analysis and the study's findings are available from the corresponding author, FCM, upon reasonable request.

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