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Original Research Article

Native chestnut forests mitigate biodiversity homogenization associated with eucalyptus plantations in Atlantic landscapes

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ABSTRACT

The replacement of native forests by exotic eucalyptus plantations in Atlantic landscapes has raised concerns about biodiversity homogenization, yet multitaxon responses remain poorly quantified. We evaluated bird and bat assemblages across three forest stand types, traditional chestnut orchards (soutos), chestnut coppices, and eucalyptus plantations, using an integrated monitoring framework combining active point counts and passive acoustic recording over two consecutive years (2024–2025). Sampling encompassed 60 stations stratified by stand type and habitat position (edge vs. interior), enabling robust comparisons of richness, diversity, community composition, and habitat associations. Chestnut formations generally supported higher biodiversity than eucalyptus plantations. Bird richness peaked in orchards (up to 21 species under passive monitoring), whereas eucalyptus interiors exhibited the lowest values. Bat communities showed similar trends, with Shannon diversity declining sharply in eucalyptus interiors (≈0.65) compared with orchards (≈1.28). Forest specialist birds, including *Certhia brachydactyla* and *Sitta europaea*, were strongly associated with chestnut habitats, whereas eucalyptus stands were characterized by more generalist assemblages. Exploratory comparisons suggested higher bird richness and bat diversity in managed orchards, particularly at habitat edges. Multivariate ordinations and PERMANOVA revealed differences in bird ($R^2 \approx 0.08$) and bat ($R^2 \approx 0.10$) community composition among stand types, while mixed-effects models showed lower richness and diversity in eucalyptus plantations and stand interiors. Overall, stand type was the main driver of biodiversity patterns. These results highlight native chestnut forests, particularly traditional soutos, as important biodiversity refuges that may help counteract biotic homogenization and support resilient, multifunctional forest ecosystems under environmental change.

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1. Introduction

Monitoring biodiversity across forest ecosystems is necessary for evaluating ecological integrity and guiding conservation efforts. Among vertebrate taxa, birds and bats jointly serve as powerful and complementary bioindicators, offering insights into habitat quality, ecological processes, and responses to environmental change (Jones et al., 2009; Barbaro et al., 2019; Renner et al., 2024). Birds are widely recognized as key indicators of environmental integrity and as model organisms for studying evolutionary processes. Their global diversity, currently comprising more than 11,000 species (Gill et al., 2026), reflects ongoing speciation and extinction dynamics shaped by natural and anthropogenic factors. Understanding how bird species arise, modify, and vanish is necessary for biodiversity conservation and for predicting responses to climate and land-use changes (Tietze, 2018).Beyond their indicator value, birds provide multiple ecosystem services that sustain forest functionality and human well-being (Sekercioglu et al., 2016). These include insect pest control, which reduces herbivory and supports forest health; seed dispersal, facilitating natural regeneration and connectivity among forest fragments; and, in some cases, pollination. Birds also contribute to nutrient cycling through organic matter deposition and offer cultural services such as ecotourism and traditional knowledge linked to emblematic landscapes. Bats similarly offer exceptional bioindicator value, owing to their trophic specialization, sensitivity to contaminants and habitat disturbance, and clear responses to environmental change. As Jones et al. (2009) emphasize, bats integrate multiple ecosystem services, such as pest control, pollination, and seed dispersal, making them effective indicators of ecological health across spatial and temporal scales. Thus, birds and bats, as sensitive bioindicators, respond to variations in forest composition, management intensity, and habitat configuration, making them suitable taxa for assessing ecosystem health (Jones et al., 2009).

In recent decades, shifts in land ownership, rural abandonment, and the expansion of fast-growing tree plantations have transformed traditional forested landscapes. Particularly, in the Iberian Peninsula, the rapid expansion of exotic and intensively cultivated eucalyptus plantations, mainly dominated by *Eucalyptus globulus* Labill., has raised ecological concerns, especially in the western and northern areas such as Portugal, Galicia, Asturias, Cantabria, and the Basque Country, where they have replaced native forests and pine plantations (Goded et al., 2019; Sertutxa et al., 2025a). These plantations typically consist of even-aged, monospecific stands exploited in short rotations for pulp and timber (Tomé et al., 2021). Despite their continuous expansion, eucalyptus plantations coexist with native chestnut forests (*Castanea sativa* Mill.), including traditionally managed orchards (locally known as *soutos*) and coppice stands, creating a heterogeneous mosaic of forest stands and land uses with sharply contrasting structural and ecological characteristics. Chestnut stands are now largely abandoned and lack active management, and they differ in structure and historical use. *Soutos* are long-standing socioecological systems shaped by centuries of agroforestry use, traditional management practices for chestnut fruit production, and local ecological knowledge, which retain a high ecological, cultural, and socio-economic potential (Díaz-Varela et al., 2025, 2026). Coppice stands are high-density systems historically exploited for timber, mining props, and firewood (Roces-Diaz et al., 2018).

Building on these contrasts, traditional chestnut orchards are not only biodiversity reservoirs but also cultural heritage systems that can inspire sustainable forest management. Their long-standing integration of ecological functions and human responsible use shows how restoration and adaptive management can reverse biodiversity loss and strengthen socioecological resilience. In the NW iberian peninsula, these orchards represent emblematic socioecological production landscapes (SEPLS), combining high biodiversity with multifunctional ecosystem services (Díaz-Varela et al., 2025). These systems deliver provisioning services (e.g., chestnuts, mushrooms, honey, timber), regulating services (e.g., fire mitigation, soil conservation), and cultural services (e.g., landscape identity, traditional knowledge, traditional wooden barns called "*horreos*"). Their management blends traditional practices with modern approaches, and their biodiversity spans genetic, species, and ecosystem levels, including umbrella species such as the brown bear (*Ursus arctos* L.) (Pérez-Girón et al., 2022, 2025). Likewise, documentary evidence shows that the restoration of chestnut orchards promotes high bird species richness (Morelli et al., 2019) and fosters sensitive bat communities, including species such as *Nyctalus leisleri* Kuhl (Leisler's bat) and several *Myotis* spp., which rely on hollow trees and structurally open habitats for roosting and foraging (Obrist et al., 2011; Moretti et al., 2021; Zambelli et al., 2021).

Such shifts in land-use and forest management have not only altered the composition and structure of Iberian landscapes but have also generated ecological consequences that are increasingly evident across the region. Recent studies have highlighted the negative impact and ecological limitations of exotic forest plantations, particularly those dominated by eucalyptus. Their simplified vertical structure, reduced canopy heterogeneity, and altered soil conditions promote biotic homogenization and the decline of forest specialists (Calviño-Cancela et al., 2012; Goded et al., 2019). As a result, these plantations tend to support lower species abundance, richness, and functional diversity (García-Fernández et al., 2025; Ortega-Barrueta et al., 2025) and to induce shifts in bat activity driven by changes in habitat structure, foraging conditions, and prey availability (Sertutxa et al., 2025a). In contrast, native and restored forests provide structurally complex habitats that support diverse assemblages of flora and fauna, including saproxylic fungi, shade-tolerant plants, and cavity-nesting birds (Sertutxa et al., 2025b; García-Fernández et al., 2025). Particularly, chestnut orchards harbor rich bat and bird communities, with several threatened species relying on hollow trees and open canopies for roosting and foraging (Moretti et al., 2021; Python et al., 2021). Consequently, their replacement by fast-growing exotic plantations and the simplification of their habitats have contributed to reductions in biodiversity and ecosystem resilience.

Because structurally complex habitats sustain these functions more effectively, while simplified systems such as exotic plantations often erode them (Sekercioglu et al., 2016; Whelan et al., 2008; García-Fernández et al., 2025), evaluating bird and bat communities together provides a robust, multitaxon perspective for assessing forest biodiversity across contrasting forest ecosystems and management contexts, and for understanding the consequences of ongoing land-use transitions. In this context, we assessed biodiversity patterns across contrasting forest stands (chestnut orchards, chestnut coppices, and eucalyptus plantations) and habitat positions (forest edge and interior) using birds and bats as bioindicators.

We formulated three hypotheses. **H1**: Forest stands with greater structural complexity support higher biodiversity than simplified forest systems. **Prediction 1:** Chestnut orchards and coppices will exhibit higher bird and bat richness and diversity than eucalyptus plantations. **H2**: Species-habitat associations reflect differences in forest composition and structure. **Prediction 2**: Indicator species composition will differ among stand types and habitat positions, with forest specialists being more strongly associated with chestnut stands and generalist species with eucalyptus plantations. **H3**: Management of traditional chestnut orchards is associated with changes in community composition and diversity. **Prediction 3:** Managed orchards will show higher richness, diversity, and occurrence of characteristic forest species than unmanaged orchards. To test these hypotheses, the objectives of this study were: (***i***) to quantify bird and bat richness and diversity across forest stand types and habitat positions (edge versus interior); (***ii***) to identify indicator species associated with different stand types and habitat positions and evaluate the relationship between biodiversity patterns and forest structural attributes; and (***iii***) to compare biodiversity patterns between managed and unmanaged chestnut orchards.

2. Materials and methods

2.1. Study area and sampling design

The study was conducted in Asturias (NW Spain) within a temperate Atlantic forest landscape (Fig. 1). We selected 30 forest stands, 10 per stand type (chestnut orchards, chestnut coppices, and eucalyptus plantations), representing contrasting ecological conditions and management histories.

- **Chestnut orchards (soutos)**: Historically managed for fruit production, these stands are characterized by large-diameter trees (often 1–2 m DBH), low tree density, and relatively open canopies. Four orchards were managed during 2025 by Fundación Oso Asturias, Fundación Oso Pardo, and project partners, whereas six remained unmanaged.
- **Chestnut coppices**: Dense stands originating from vegetative regeneration, typically characterized by high stem density, closed canopies, and well-developed understories.
- **Eucalyptus plantations**: Exotic even-aged stands dominated by *Eucalyptus globulus*, managed for pulpwood production and characterized by a relatively homogeneous structure. Mean tree diameter was 11.2 ± 4.3 cm DBH, with most trees falling within the 5–20 cm diameter classes. Although exact stand ages were not available, diameter distributions suggest that the plantations were predominantly young to medium-aged stands, likely within the typical pulpwood rotation period (approximately 5–15 years). No silvicultural operations or understory management activities were observed in any of the plantations during the two years of field surveys (2024–2025).

Selected stands exceeded 2 ha, which was the minimum area required for inclusion in the study, although most sampled stands were substantially larger. Within each stand, two sampling stations were established to represent contrasting habitat positions: an edge station located ≤ 20 m from the stand boundary and, whenever stand size allowed, an interior station located approximately 100 m or more from the nearest edge. Sampling stations within the same stand were separated by approximately 200 m whenever possible to reduce spatial dependence. This design resulted in a total of 60 sampling stations (30 edge and 30 interior stations).

All stations were georeferenced and surveyed during the same seasonal periods (late spring and early summer) in both 2024 and 2025. Thus, the same stations were repeatedly sampled across years, providing temporal replication while maintaining a consistent

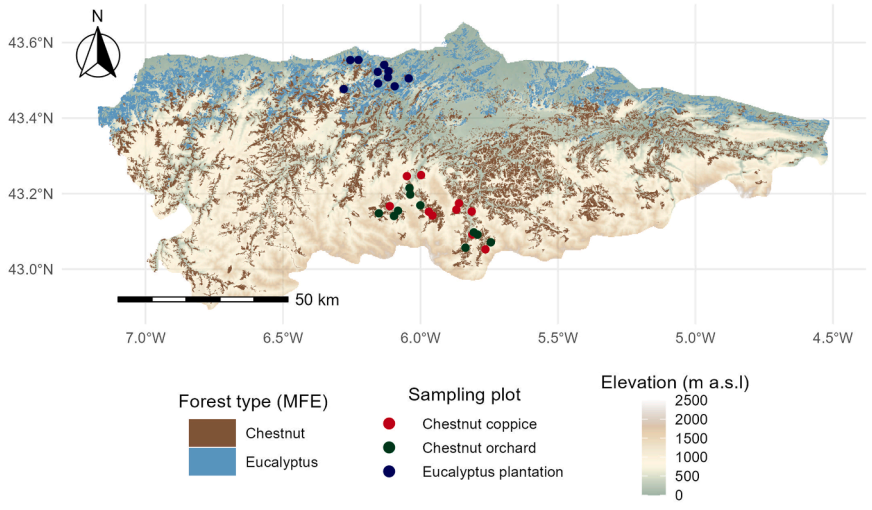

Fig. 1. Location of sampling plots in chestnut and eucalyptus stands. Forest types were extracted from the Forest Map of Spain (MFE) and only the predominant species is represented, although co-occurrence of species is possible.

spatial framework. The design was intended to capture variation among stand types and habitat positions while minimizing spatial autocorrelation.

2.2. Vegetation and habitat characterization

To characterize local habitat structure and relate it to biodiversity patterns, a vegetation inventory was conducted within a 15-m-radius circular plot (706.9 m^2) centered on each sampling station (van Laar and Akça, 2007; West, 2015). Recorded variables included topographic attributes (elevation, slope, and aspect), canopy cover, understory composition, tree density, diameter structure, crown height, and the occurrence of accompanying woody species.

The selected plot size is widely used in forest inventories and ecological studies because it provides an appropriate balance between stand representativeness and field efficiency. Across the three forest formations examined, the plots contained sufficient numbers of dominant trees to adequately characterize canopy structure, stem density, diameter distribution, and understory composition, thereby allowing robust comparisons among habitat types.

Understory vegetation was characterized by visually estimating the percentage cover of the main vegetation groups, including brambles (*Rubus* spp.), ferns (*Pteridium aquilinum*, *Dryopteris* spp., and *Blechnum* spp.), blueberries (*Vaccinium myrtillus*), gorse (*Ulex* spp.), herbaceous vegetation, heathers (*Erica* spp.), ivy (*Hedera helix*), and bare ground. Tree structural attributes included the density of dominant trees, diameter-class distribution, mean diameter at breast height (DBH), and mean crown height. The occurrence and abundance of accompanying woody species were also recorded to assess stand compositional complexity.

The three forest formations differed markedly in habitat structure (Table S1). Eucalyptus plantations occurred at lower elevations and were characterized by the lowest canopy cover (70.5 ± 19.6%), the highest cover of *Pteridium aquilinum* (58.5 ± 37.6%), and the smallest dominant trees (mean DBH = 11.2 ± 4.3 cm), reflecting the relatively homogeneous structure typical of managed even-aged stands. Chestnut coppices exhibited the highest canopy cover (95.5 ± 7.2%), high densities of dominant stems (92.7 ± 55.5 trees per plot), and intermediate tree diameters (16.2 ± 5.6 cm), consistent with their origin through vegetative regeneration and the development of dense multi-stemmed stands. In contrast, chestnut orchards (soutos) displayed the lowest density of dominant trees (38.4 ± 22.2 trees per plot), the largest mean diameter (41.7 ± 17.9 cm DBH), and a substantial proportion of veteran trees, with 18.5% of stems exceeding 100 cm DBH. Despite their lower stem density, canopy cover remained relatively high (82.8 ± 11.3%), reflecting the contribution of large mature trees. Consequently, soutos exhibited the greatest structural heterogeneity among the three forest formations. Understory composition also differed substantially: bramble cover was considerably higher in chestnut formations (46.0–49.0%) than in eucalyptus plantations (11.5%), whereas *P. aquilinum* was strongly associated with eucalyptus stands and occurred only sporadically in chestnut coppices and orchards (3.8 ± 9.9% and 8.8 ± 18.7%, respectively).

Accompanying woody species included both native and non-native taxa commonly found in the study area, such as *Quercus robur*, *Betula* spp., *Frangula alnus*, *Acer* spp., and *Pinus radiata*. Summary statistics describing habitat structure and vegetation characteristics are provided in Table S1.

2.3. Monitoring techniques

Bird communities were surveyed using a dual approach that combined active point counts and passive acoustic monitoring, whereas bats were surveyed exclusively through passive acoustic monitoring.

2.3.1. Birds

Two complementary techniques were applied:

Active census: Visual and auditory point counts were conducted during morning hours, from dawn until 11:00 AM, coinciding with peak bird activity. Each sampling station was surveyed for 10 min. To ensure consistency and minimize observer bias, two expert ornithologists participated in the study, one conducting the surveys during the first year and another during the second. All detected species were recorded. Sampling was conducted only under favourable weather conditions (no rain or fog) to ensure a reliable detection.

Passive acoustic monitoring: Autonomous recording units (AudioMoth v1.2.0; Hill et al., 2018) were installed at each station, mounted on tree trunks at a height of 2 m. Devices were programmed to record during two key periods: dawn (07:20–08:20) and dusk (21:20–22:20). Recorders were configured with a sampling rate of 250 kHz and operated using a recording schedule of 59 min 50 s of continuous recording followed by a 10 s pause, resulting in an effective one-hour monitoring interval. Each station was monitored over a two-day period to capture temporal variation in vocal activity. Bird vocalizations were detected and identified using BirdNET-Analyzer GUI v.1.5.1 (K. Lisa Yang Center for Conservation Bioacoustics, Cornell Lab of Ornithology; Kahl et al., 2021). A list of potentially occurring species was first generated using the Species tool and subsequently used for all sampling stations. Automated classifications were obtained using the Batch Analysis module with the following settings: minimum confidence = 0.1, sensitivity = 1, and overlap = 0 s. To assess classification accuracy, a manual validation procedure was conducted. For each species, up to 100 recordings were randomly selected, comprising up to 10 recordings from each confidence class after grouping confidence scores by their first decimal digit (0.1, 0.2, 0.3, etc.). When fewer than 10 recordings were available within a confidence class, all available recordings were reviewed manually.

Species-specific logistic regression models were then fitted to relate BirdNET confidence scores to the binary outcome (correct/incorrect) obtained during manual validation. Following the approach proposed by Wood and Kahl (2024), these models were applied to all detections to estimate the probability that each BirdNET classification was correct. Only detections with an estimated probability

of correct identification ≥ 0.80 were retained for subsequent analyses.

2.3.2. Bats

Bat monitoring was conducted exclusively through passive acoustic monitoring, using the same AudioMoth devices deployed for bird surveys. Recordings were scheduled to coincide with nocturnal activity peaks: pre-dawn (05:30–06:45) and night (22:20–02:20). Devices operated at a sampling rate of 250 kHz and followed a near-continuous recording schedule (59 min 50 s recording, 10 s pause) during the nocturnal monitoring periods. Each station was monitored over two consecutive nights. Audio files were processed using the AutoID tool in Kaleidoscope Pro. All identifications made automatically have been validated by an expert, with species or genus-level.

Bat activity was quantified as the total number of validated acoustic detections recorded at each sampling station during the monitoring period. Therefore, activity represents an acoustic detection metric rather than a direct estimate of abundance, since multiple detections may originate from the same individual

2.4. Community composition analysis

To evaluate differences in the composition of bird and bat communities across forest stands, habitat types (interior vs. edge), study years (2024 and 2025), and sampling methods (active and passive, in the case of birds), we applied multivariate analytical techniques.

We first used Non-metric Multidimensional Scaling (NMDS) to provide a graphical representation of compositional similarities among sampling units, reducing data complexity to two dimensions. We then applied Permutational Multivariate Analysis of Variance (PERMANOVA) to test the effects of stand type, habitat position and elevation on community composition, based on Bray-Curtis dissimilarities. Unlike traditional ANOVA, PERMANOVA does not assume multivariate normality and relies on permutations to test hypotheses, making it particularly appropriate for ecological data. PERMANOVAs were run separately for each combination of year and sampling method, and each term was tested conditional on the others (marginal tests). To respect the nested structure of the design (stations nested within plots), terms varying among plots (stand type and elevation) were tested by permuting whole plots, whereas habitat position was tested with permutations restricted within plots, so that stations were only exchanged within their shared stand (999 permutations in both cases). To ensure that any compositional differences were not confounded by differences in within-group multivariate dispersion, we complemented each PERMANOVA with a test of homogeneity of multivariate dispersions (PERMDISP; Anderson, 2006), applied to stand type and habitat position. All analyses were conducted in R version 4.5.0 (R Core Team, 2025) using the vegan package (Oksanen et al., 2025), with permutation schemes defined through the permute package.

2.5. Diversity metrics

Species richness, defined as the number of species present in a community at a given time, is one of the most direct and widely used measures of biological diversity, although it is sensitive to sampling effort and sample size (Magurran, 2004). In this study, species richness was estimated for birds and bats using data obtained from active point counts (birds) and passive acoustic monitoring. In addition to richness, we computed the Shannon (H) and Simpson (D) diversity indices to capture both the species abundance distribution and dominance patterns, providing complementary perspectives on community structure.

To assess differences in richness and diversity among forest stand types (chestnut orchards, chestnut coppices, and eucalyptus plantations) and between habitat positions (edge vs. interior), we fitted generalized linear mixed models (GLMMs) and linear mixed models (LMMs), using the glmmTMB package (Brooks et al., 2017). Because the sampling design comprised 60 stations nested within 30 plots (two stations per plot) and surveyed over two consecutive years, we included plot as a random intercept to account for the non-independence of edge and interior stations sharing the same stand, and year as a fixed factor to accommodate interannual variation. Fixed effects were stand type, habitat position, elevation and year. As the only continuous predictor in these models, elevation was centered and scaled to unit variance prior to model fitting, so that its coefficient represents the change in the response per standard deviation. Categorical predictors were coded as treatment contrasts relative to their reference levels. Species richness, being a count variable, was modelled with a Poisson error distribution; overdispersion was assessed with performance package (Lüdecke et al., 2021), and, as no overdispersion was detected (dispersion ratios < 0.7 in all cases), the Poisson distribution was retained. Shannon and Simpson diversity, being continuous indices, were modelled with a Gaussian error distribution. Separate models were fitted for each taxon and, for birds, for each sampling method (active and passive).

We also evaluated a more complex random-effects structure with station nested within plot, to account for the repeated measurement of each station across years; however, this nested structure was consistently singular or not favoured by AIC, reflecting that two temporal replicates per station are insufficient to estimate a separate station-level variance. We therefore retained plot as the sole random effect. In the few cases where the plot-level variance was itself estimated at zero (singular fit), the corresponding model was reduced to its fixed-effects form. The significance of fixed effects was evaluated at $\alpha = 0.1$, and model fit was summarized using marginal and conditional R^2.

Finally, we performed an indicator species analysis using the Indicator Value (*IndVal*) approach proposed by Dufrêne and Legendre (1997), which quantifies the strength of association between a species and a predefined group of sites by combining measures of specificity and fidelity. This method was particularly relevant to our study because it identifies species that are not only frequent within a forest type but also highly characteristic of it, providing robust ecological signals of habitat quality and structural complexity. Such indicators are essential for understanding how biodiversity responds to differences in forest composition and management, and for guiding conservation strategies. The Indicator Value was applied separately to birds and bats across stand types and habitats using

multilevel pattern analysis with permutation tests to ensure reliability. To account for complex habitat configurations, we applied the multipatt function, which extends the *IndVal* approach to detect indicators for both individual and combined site groups (De Cáceres et al., 2010). Analyses were conducted in R version 4.5.0 (R Core Team, 2025) using the *indicspecies* package (De Cáceres and Legendre, 2009). This approach was critical for distinguishing species that serve as bioindicators of soutos, coppices, and eucalyptus plantations, thereby supporting our objective of linking biodiversity patterns to forest structure and management practices.

2.6. Relationship between diversity and forest structure

As a complementary, exploratory analysis, we examined whether fine-scale forest structure was associated with bird and bat richness and diversity. For each combination of taxon, sampling method, year, and diversity metric (richness, Shannon, and Simpson), we fitted separate linear models using richness or diversity as the response variable and the local structural variables as predictors: tree cover, shrub cover, mean crown height, mean diameter of the dominant species, tree density, tree species richness, and patch area. Stand type and habitat position were not included in these models, as their effects were addressed by the mixed models described in Section 2.5; this analysis was instead intended to explore the association of within-stand structural attributes with diversity. Because the structural variables differ widely in their units and ranges, all predictors were standardized (centered and scaled to unit variance) prior to model fitting, so that the resulting coefficients are directly comparable in magnitude across variables. Multicollinearity among predictors was checked using variance inflation factors (VIF); as all values were below 4, no variable was removed. Given the limited number of observations relative to the number of predictors, and the low and often negligible variance explained by these models, we treat this analysis as exploratory rather than inferential, and interpret it alongside the main mixed models.

3. Results

3.1. Species detections and community composition

Across the two sampling years, bird detections varied substantially between sampling methods and forest stands. Passive acoustic monitoring produced far higher detection numbers than active point counts, increasing from 92,731 detections in 2024 to 154,843 in 2025, whereas active surveys rose from 881 observations in 2024 to 1939 in 2025.

When analysing forest stands, patterns differed between years. In 2024, active surveys recorded higher bird activity, measured as the number of detections, in chestnut orchards (310) than in eucalyptus plantations (293), while chestnut coppices (278) showed slightly lower activity. In 2025, both chestnut coppices (660) and orchards (716) exceeded eucalyptus plantations (563). Passive monitoring revealed similar variation among forest stands, with eucalyptus plantations registering the highest numbers of bird detections in both years, although chestnut coppices and orchards also supported high levels of activity. Detailed detection data by forest type and year are provided in Tables S2 and S3 of the Supplementary material.

For bats, whose nocturnal activity was monitored exclusively through passive acoustic sampling, total detections increased from 18,148 in 2024–21,094 in 2025. Bat activity, quantified as the number of validated acoustic detections, varied among forest stands and between years. In 2024, activity was highest in chestnut orchards (7715 detections), followed by eucalyptus plantations (5449 detections) and chestnut coppices (4984 detections). In 2025, activity increased in both orchards (8750 detections) and eucalyptus plantations (8421 detections), whereas chestnut coppices showed a slight decrease (3923 detections). Detailed bat activity data across forest stands and years are provided in Table S4 of the Supplementary material. Regarding community composition, NMDS ordinations showed multivariate differences among sampling units for both birds and bats (Fig. S1 in the Supplementary material). To statistically test these patterns while respecting the nested structure of the design, PERMANOVAs were run separately for each year and sampling method, including stand type, habitat position and elevation as explanatory terms and testing each term conditional on the others. Terms varying among plots (stand type and elevation) were tested by permuting whole plots, whereas habitat position was tested with permutations restricted within plots (i.e., edge and interior stations were only exchanged within their shared stand) (Table S5). For birds, stand type explained the largest proportion of variation in community composition ($R^2 = 0.048–0.083$), although its effect was significant only under active sampling in 2025 ($R^2 = 0.081$, $p = 0.005$) and passive monitoring in 2024 ($R^2 = 0.083$, $p = 0.009$). Habitat position (edge vs. interior) contributed significantly in all combinations of year and sampling method, albeit with smaller effect sizes ($R^2 = 0.028–0.037$, $p \leq 0.032$), whereas elevation explained a small fraction of the variation ($R^2 = 0.019–0.047$) and was significant only under passive monitoring in 2025 ($R^2 = 0.047$, $p = 0.023$). For bats, stand type significantly affected community composition in 2024 ($R^2 = 0.099$, $p = 0.010$) but not in 2025 ($R^2 = 0.047$, $p = 0.434$). Elevation was significant in 2024 ($R^2 = 0.055$, $p = 0.010$) and marginally so in 2025 ($R^2 = 0.044$, $p = 0.086$), whereas habitat position had no significant effect in either year ($R^2 = 0.014$, $p = 0.226–0.307$). Homogeneity of multivariate dispersions (PERMDISP) was non-significant in all cases ($p \geq 0.051$), confirming that the differences detected reflected shifts in community composition rather than differences in within-group dispersion (Table S6). The lowest value corresponded to habitat position for birds under passive monitoring in 2024 ($p = 0.051$), where this borderline dispersion effect suggests the corresponding edge-interior contrast should be interpreted with some caution.

3.2. Patterns of species richness and diversity

Overall, 59 bird species (50 detected by active sampling and 58 by passive acoustic monitoring) and 15 bat taxa (13 species and two genus-level groups: Myotis spp. and Plecotus spp.) were recorded over the study period. Across sampling sites, bird and bat communities showed broadly comparable patterns of richness and diversity across forest stands, habitat types, and sampling methods

(Fig. 2 and Figs. S2–S4 in Supplementary material). For birds, passive sampling detected substantially higher richness (17.5–21.0 species) than active sampling (9.0–11.5 species), with similar patterns across chestnut coppices, orchards, and eucalyptus stands. Richness tended to be slightly higher at edges than interiors in both chestnut ecosystems, while eucalyptus plantations showed comparable richness to chestnut stands at edges but lower values in interior plots. Shannon and Simpson diversity were generally higher under active sampling (Shannon ≈ 2.1–2.3; Simpson ≈ 0.9), whereas passive sampling produced lower diversity values (Shannon ≈ 1.6–1.9; Simpson ≈ 0.7–0.8), reflecting differences in detection processes between methods. Despite these methodological contrasts, richness patterns were broadly consistent among forest types, with modest edge-interior declines.

Bat communities exhibited relatively limited variation in richness among forest stand types, with values ranging from 6.5 to 9 species. Richness was generally slightly higher at edges than in interiors across forest types. Chestnut orchards showed a distinct pattern, with higher diversity in interior habitats (Shannon = 1.28; Simpson = 0.62) than at edges (Shannon = 0.93; Simpson = 0.47). Richness in chestnut orchards was similar between habitats, varying around 8–9 species. In eucalyptus plantations and chestnut coppices, diversity patterns were more homogeneous, with moderate Shannon and Simpson values across habitats (Shannon ≈ 0.65–1.08; Simpson ≈ 0.32–0.52). Overall, bats showed relatively small differences in richness and diversity among forest stand types, with limited edge-interior contrasts except in chestnut orchards.

To formally test these patterns while accounting for the nested sampling design, we fitted mixed models with stand type, habitat position, elevation and year as fixed effects and plot as a random intercept (see Methods). For birds, richness was significantly higher in 2025 than in 2024 under both sampling methods (active: $\beta = 0.43$, $p < 0.001$; passive: $\beta = 0.18$, $p < 0.001$), and was generally lower in interior than in edge stations (active: $\beta = -0.11$, $p = 0.053$; passive: $\beta = -0.08$, $p = 0.048$) (Fig. 3). Stand type also affected bird richness: eucalyptus plantations supported fewer species than chestnut coppices (the reference level) under passive monitoring ($\beta = -0.21$, $p = 0.018$), with a similar trend under active sampling ($\beta = -0.22$, $p = 0.052$), whereas chestnut orchards did not differ from coppices (all $p > 0.59$). Similar patterns emerged for Shannon and Simpson diversity: the interior position was associated with lower diversity (Shannon, active: $\beta = -0.08$, $p = 0.034$; passive: $\beta = -0.10$, $p = 0.052$; Simpson, passive: $\beta = -0.04$, $p = 0.031$), and eucalyptus plantations showed significantly lower diversity than chestnut coppices under both methods (Shannon, active: $\beta = -0.26$, $p = 0.006$; passive: $\beta = -0.36$, $p = 0.025$; Simpson, active: $\beta = -0.04$, $p = 0.009$; passive: $\beta = -0.11$, $p = 0.033$). Year effects on diversity differed between methods, being positive under active sampling (e.g. Simpson: $\beta = 0.05$, $p < 0.001$) and slightly negative under passive monitoring (e.g. Simpson: $\beta = -0.04$, $p = 0.016$). Elevation had a consistently negative effect on richness and diversity, which was significant for bird richness under passive monitoring ($\beta = -0.09$, $p = 0.015$), bird Shannon and Simpson diversity under

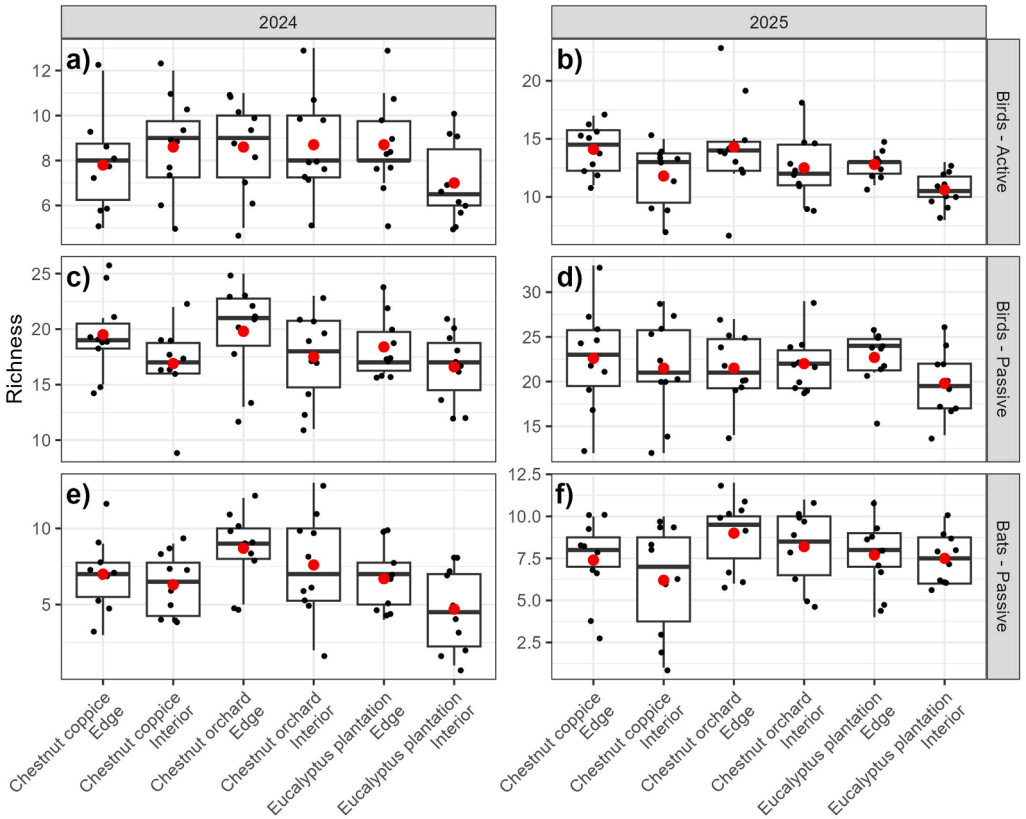

Fig. 2. Boxplots showing bird and bat species richness across stand types, habitat, and years. Red dots indicate mean values. These plots are descriptive; statistical differences among stand types and between habitat positions were assessed with the mixed models (see Fig. 3 and Table S7).

active sampling ($\beta = -0.10$, $p = 0.012$ and $\beta = -0.02$, $p = 0.011$, respectively) and bat richness ($\beta = -0.22$, $p < 0.001$).

For bats, stand type also influenced richness. Eucalyptus plantations supported fewer species than chestnut coppices ($\beta = -0.42$, $p = 0.003$), whereas chestnut orchards showed a non-significant tendency towards higher richness ($\beta = 0.14$, $p = 0.100$). Bat richness tended to be lower in interior than in edge stations ($\beta = -0.13$, $p = 0.064$). Shannon diversity showed a marginal tendency to be higher in chestnut orchards ($\beta = 0.16$, $p = 0.091$), while eucalyptus plantations did not differ from coppices ($\beta = -0.17$, $p = 0.267$), and neither habitat position nor year had significant effects on bat Shannon or Simpson diversity (all $p > 0.20$). Overall, these models indicate a consistent, if modest, edge-to-interior decline in richness and diversity across both taxa, a negative effect of elevation, and lower richness and diversity in eucalyptus plantations than in chestnut stands for both birds and bats, with no significant differences between chestnut coppices and orchards Fig. 3.

3.3. Indicator species analysis

The indicator species analysis identified multiple significant associations between bird species and specific combinations of stand types, habitats, sampling method, and year (Fig. 4). In active sampling, *Troglodytes troglodytes* L. (Eurasian wren) showed consistent and highly significant associations with eucalyptus plantations at both edges and interiors in 2024 and 2025. Several species were associated with chestnut stands, particularly interiors, including *Certhia brachydactyla* Brehm (Short-toed treecreeper) in both years and *Sitta europaea* L. (Eurasian nuthatch). In 2025, strong associations were detected for *Turdus merula* L. (Common blackbird) and *Turdus philomelos* Brehm (Song Thrush) across all chestnut stand types and habitat positions. Other species associated with chestnut coppice or orchard edges included *Cyanistes caeruleus* L. (Eurasian blue tit) in 2024, *Erithacus rubecula* L. (European robin) in 2025, and *Anthus trivialis* L. (Tree pipit). Eucalyptus plantations also displayed indicator species in 2025 under active sampling, including *Periparus ater* L. (Coal tit), *Carduelis carduelis* L. (European goldfinch), *Pyrrhula pyrrhula* L. (Eurasian bullfinch), and *Lophophanes cristatus* L. (Crested tit).

Under passive sampling, significant indicators for eucalyptus plantations included *Troglodytes troglodytes* L. (Eurasian Wren),

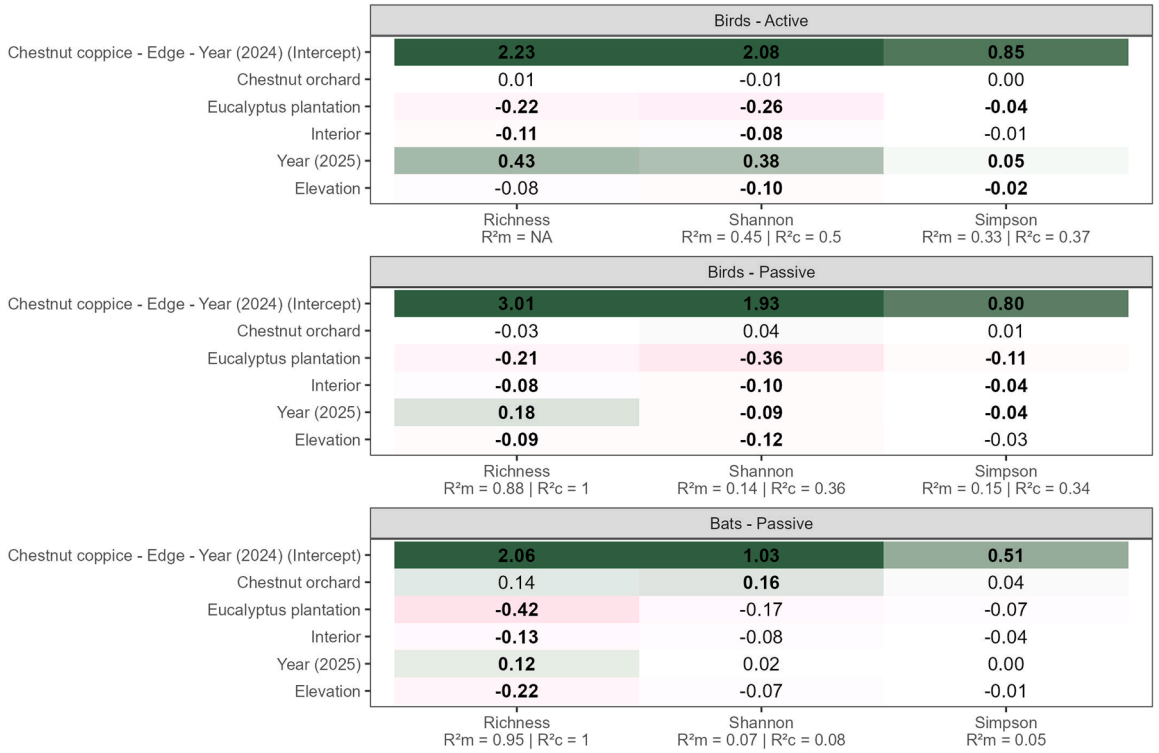

Fig. 3. Coefficient estimates from the mixed models relating species richness and diversity (Shannon and Simpson indices) to stand type, habitat position, year and elevation, for birds (active and passive sampling) and bats (passive sampling only). Each panel corresponds to a taxon-sampling method combination, and each column to a diversity metric. Cell values are the model coefficients for each fixed effect, relative to the reference level (chestnut coppice, edge, 2024). Coefficients are shown on the model scale: the log scale for richness (Poisson models) and the index scale for Shannon and Simpson diversity (Gaussian models); positive values (green) indicate higher richness or diversity than the reference level and negative values (pink) indicate lower values. Bold values denote coefficients significant at $p < 0.1$. Plot was included as a random intercept in all models; where the random-effect variance was estimated at zero (singular fit), the corresponding model was reduced to its fixed-effects form. R^2m and R^2c below each metric denote the marginal and conditional R^2 (variance explained by fixed effects alone, and by fixed plus random effects, respectively); R^2c is not reported when the model lacks a random effect. See Table S7 for complete coefficient estimates from the mixed models.

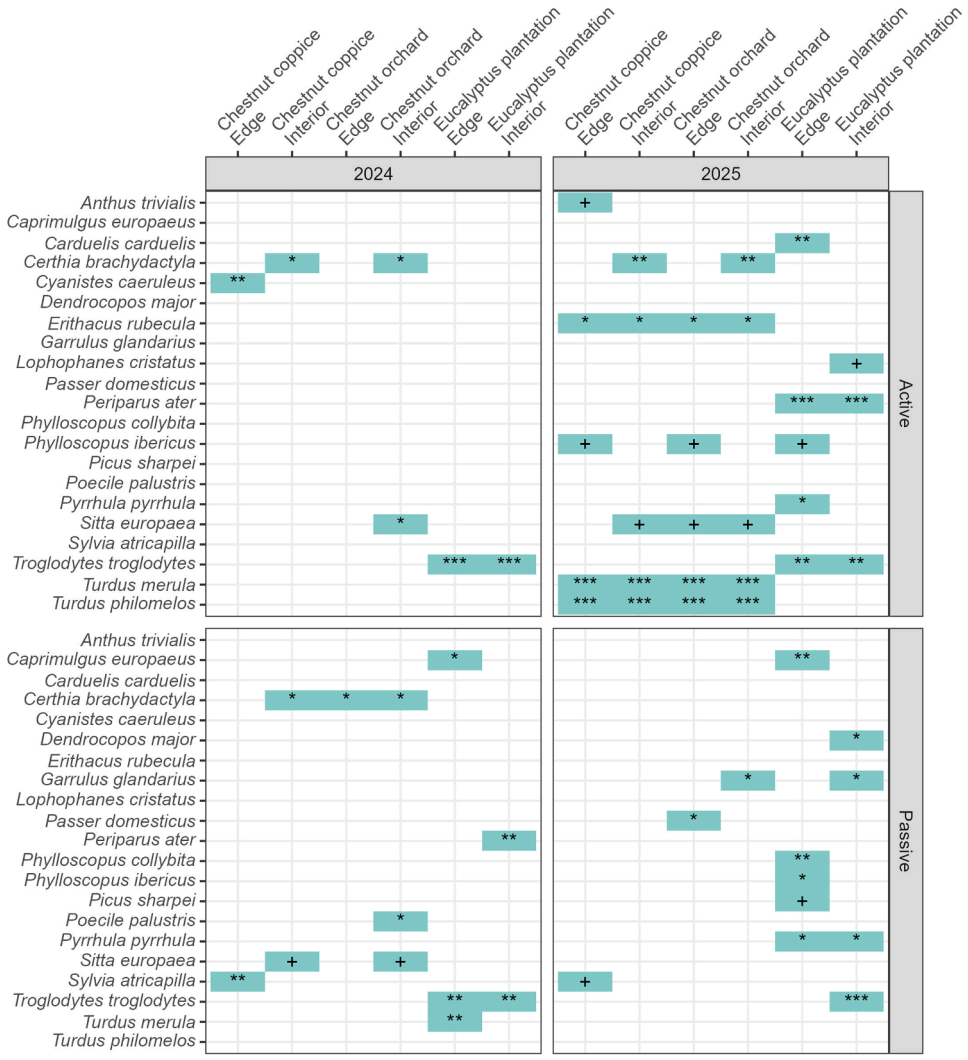

Fig. 4. Indicator species analysis for birds showing significant associations across stand types and habitats. Colored grids represent species-habitat associations identified through permutation tests with asterisks denoting significance. Significance levels are: *** for $p \leq 0.001$, ** for $p \leq 0.01$, * for $p \leq 0.05$, and + for $p \leq 0.10$. Associations that did not reach significance are left blank.

Turdus merula L. (Common Blackbird), and *Periparus ater* L. (Coal Tit) in 2024. Additional significant associations with eucalyptus in 2025 included *Picus sharpei* Nordsieck (Iberian green woodpecker), *Caprimulgus europaeus* L. (European nightjar), *Dendrocopos major* L. (Great spotted woodpecker), *Pyrrhula pyrrhula* L. (Eurasian bullfinch), and *Phylloscopus collybita* Vieillot (Common chiffchaff). Chestnut stands also showed indicator species, including *Sylvia atricapilla* L. (Eurasian blackcap) in 2024, *Certhia brachydactyla* Brehm (Short-toed treecreeper) across multiple habitats that same year, *Poecile palustris* L. (Marsh tit) in 2024, and *Garrulus glandarius* L. (Eurasian jay) in 2025. Several species exhibited marginal associations with specific stand-habitat combinations, such as *Sitta europaea* L. (Eurasian nuthatch), *Phylloscopus ibericus* Ticehurst (Iberian chiffchaff), and *Sylvia atricapilla* L. (Eurasian blackcap).

The indicator species analysis for bats identified a limited number of significant associations between species detections and specific combinations of stand type and habitat position (Fig. 5). Most significant indicator values were recorded in chestnut orchard habitats, with additional associations detected at eucalyptus plantation edges. In 2024, *Hypsugo savii* Bonaparte (Savi's pipistrelle) showed significant indicator values in both edge and interior chestnut orchard habitats. Significant indicator values were also obtained for *Tadarida teniotis* Rafinesque (European free-tailed bat) and *Barbastella barbastellus* Schreber (Barbastelle bat) in orchard interiors. At eucalyptus plantation edges, significant associations were observed for *Eptesicus serotinus* Schreber (Serotine bat) and *Pipistrellus kuhlii* Kuhl (Kuhl's pipistrelle). In 2025, orchard edges were associated with *Nyctalus leisleri* Kuhl (Leisler's bat), while *H. savii* again showed a strong and significant indicator value in this habitat.

Several bat indicator-species associations were not consistently detected across years, suggesting that these patterns should be interpreted with caution. Given the high mobility of most bat species, indicator values may reflect interannual variation in activity, detectability, prey availability, or local environmental conditions rather than stable habitat preferences. Consequently, significant

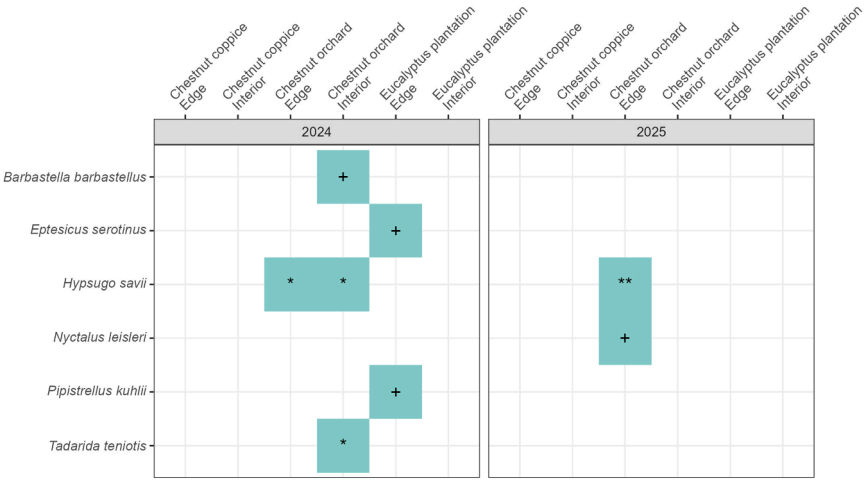

Fig. 5. Indicator species analysis for bats showing significant associations across stand types and habitats. Colored grids represent species-habitat associations identified through permutation tests with asterisks denoting significance. Significance levels are: *** for $p \leq 0.001$, ** for $p \leq 0.01$, * for $p \leq 0.05$, and + for $p \leq 0.10$. Associations that did not reach significance are left blank.

associations identified for a particular stand type or habitat position should be viewed as statistical relationships within the sampling framework rather than evidence of ecological specialization. This consideration is particularly relevant for species such as *Tadarida teniotis*, a highly aerial open-space forager, whose significant indicator value in chestnut orchard interiors in 2024 is more likely to reflect the spatial distribution of detections during the study period than a specific affinity for orchard interiors. The absence of a similar association in 2025 further suggests that this result may be driven by transient ecological conditions, such as interannual variation in aerial insect biomass (e.g. nocturnal Lepidoptera populations), rather than by a stable habitat relationship.

3.4. Relationship between diversity and forest structure

The explanatory power of the fine-scale structural variables measured around sampling stations was generally low for both birds and bats (Fig. S5). Adjusted R^2 values were modest across models, rarely exceeding 0.25 and often approaching zero, indicating that local structural attributes measured within a 15-m radius around survey points accounted for only a limited portion of the observed variation in richness and diversity. This weak explanatory power likely reflects a scale mismatch between the structural measurements and the spatial scales at which birds and especially bats perceive and use habitat. Consequently, the results should be interpreted as exploratory assessments of local habitat conditions rather than comprehensive evaluations of habitat selection.

Despite the overall weak relationships, a small number of structural variables showed recurrent associations with biodiversity. For birds, shrub cover was consistently associated with lower richness and diversity, whereas tree-species richness tended to show positive effects and was among the strongest predictors in several models, particularly under active sampling in 2025. For bats, shrub cover was likewise negatively associated with richness and Shannon diversity, while mean tree diameter showed a positive relationship with richness in both years. Although these relationships were not always statistically consistent across years and diversity metrics, they suggest that structurally heterogeneous stands containing larger trees and a more diverse woody component may provide more favourable conditions than sites characterised by dense shrub layers.

Overall, the results indicate that local structural variables measured at the plot scale were weaker correlates of bird and bat diversity than stand type and habitat position. Nevertheless, the recurring positive effects of tree-species richness and tree diameter, together with the negative effect of shrub cover, suggest that habitat heterogeneity and the presence of mature trees may be more relevant for these taxa than other fine-scale structural attributes considered here.

3.5. Exploratory comparison of orchards differing in management status

We conducted an exploratory comparison between chestnut orchards classified as managed ($n = 4$) and unmanaged ($n = 6$). Results are presented descriptively and should be interpreted as differences between orchard groups rather than as evidence of management effects.

Bird richness and diversity tended to be higher in orchards classified as managed than in those classified as unmanaged, although differences were generally not statistically significant (Fig. S6). Passive monitoring detected approximately 25–26 bird species in managed orchards compared with 20–21 species in unmanaged orchards, with slightly higher Shannon ($\approx$ 2.5 vs. 2.3) and Simpson ($\approx$ 0.90 vs. 0.87) diversity values. Active point counts showed similar patterns, with managed orchards supporting approximately 14–15 species compared with 12–13 species in unmanaged orchards, and somewhat higher diversity values (Shannon $\approx$ 2.1 vs. 1.8; Simpson $\approx$ 0.88 vs. 0.76).

Bat assemblages showed a similar pattern (Fig. S7). Richness and diversity tended to be greater in orchards classified as managed, particularly at habitat edges, where managed orchards averaged approximately 11 species compared with 8 species in unmanaged orchards. Interior habitats showed smaller differences (approximately 10 vs. 7 species). Shannon and Simpson indices varied among habitats and orchard groups without a consistent pattern.

Overall, orchards classified as managed tended to support higher bird and bat richness and diversity than orchards classified as unmanaged. Differences were particularly evident for bats at habitat edges, whereas patterns for birds were generally weaker and mostly non-significant.

The indicator-species analysis identified several significant associations with the two orchard groups (Fig. 6). In 2024, orchards classified as unmanaged showed significant associations with *Certhia brachydactyla* Brehm (Short-toed Treecreeper) in interior habitats under active sampling. Under passive sampling, additional associations were detected for *Turdus philomelos* Brehm (Song Thrush) and *Poecile palustris* L. (Marsh Tit) in orchard interiors. In 2025, unmanaged orchards showed associations with *Sylvia borin* Boddaert (Garden Warbler) at orchard edges and *Garrulus glandarius* L. (Eurasian Jay) in interior habitats.

For orchards classified as managed, significant associations were detected in 2025 for *Certhia brachydactyla* in interior habitats under active sampling, while passive sampling identified an additional association with *Parus major* L. (Great Tit). These associations should be interpreted as statistical relationships within the sampled orchard groups rather than as evidence of species responses to management interventions. Notably, indicator species were detected in both orchard groups and across both years, suggesting that differences between groups may not be exclusively attributable to management actions implemented during the study period.

For bats, the *IndVal* analysis did not identify any significant indicator species in either orchard group, suggesting that no bat species showed a consistent association with either management category during the study period.

4. Discussion

The forest stands examined in this study represent a gradient of structural complexity and management intensity, encompassing traditional chestnut orchards (soutos), chestnut coppice stands, and exotic eucalyptus plantations. This typology is characteristic of Atlantic landscapes in northwestern Spain, where native and traditional formations coexist with simplified monocultures, creating contrasting ecological conditions. Soutos retain open canopies and large-diameter trees, coppices exhibit dense stems and closed canopies, while eucalyptus plantations are even-aged monocultures with low vertical heterogeneity and reduced native flora (Goded et al., 2019; Wohlgemuth et al., 2022; Sertutxa et al., 2025a). These structural differences strongly influence biodiversity patterns, as revealed by multitaxon monitoring of birds and bats.

4.1. Methodological limitations and ecoacoustic insights

Our methodological framework combined expert-led active point counts (visual and auditory) conducted under standardized morning conditions with passive acoustic monitoring (PAM) deployed during both dawn and dusk periods. This dual approach

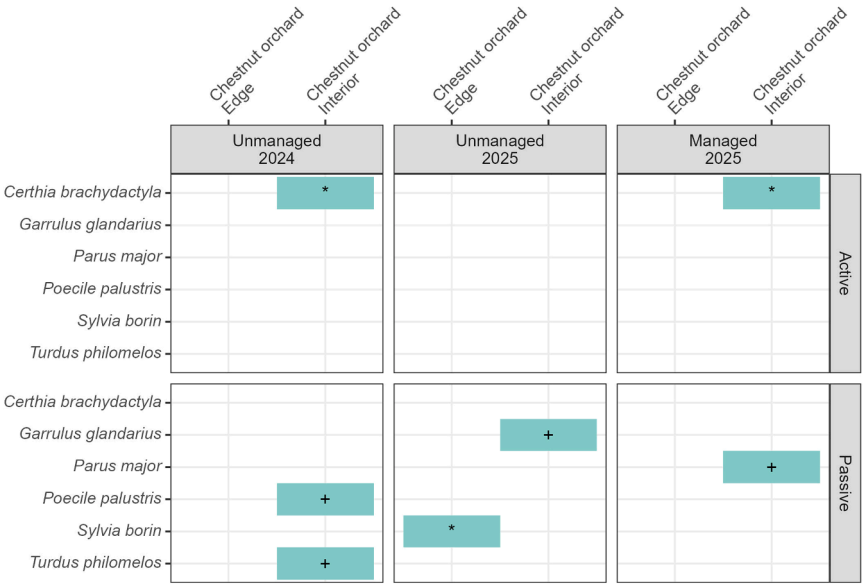

Fig. 6. Indicator species analysis for birds showing associations with managed and unmanaged chestnut orchards (soutos) across edge and interior habitats for 2024 and 2025 using active and passive monitoring methods. Colored grids represent significant associations with asterisks denoting significance. Significance levels are: *** for $p \leq 0.001$, ** for $p \leq 0.01$, * for $p \leq 0.05$, and + for $p \leq 0.10$. Associations that did not reach significance are left blank.

capitalizes on the relative strengths of each technique: active census provides immediate field identification and behavioral context, whereas PAM significantly enhances the detection probability of nocturnal, cryptic, or otherwise inconspicuous taxa, particularly bats and vocal specialist birds, through continuous and minimally invasive recordings. This integration reflects current advances in ecoacoustics, where automated recorders are increasingly recognized as essential tools for long-term biodiversity monitoring due to their capacity to reduce observer bias and standardize sampling efforts (Jones et al., 2009; Buxton et al., 2018; Kahl et al., 2021).

Passive acoustic monitoring substantially increased detection rates and improved the characterization of both bird and bat communities. However, automated species-identification tools also present limitations that should be considered when interpreting the results. Classification accuracy may decrease in acoustically complex environments, potentially increasing the likelihood of false-positive and false-negative classifications (Buxton et al., 2018; Assarzadeh et al., 2025). To minimize these biases, we combined automated identification with an extensive validation procedure. For birds, species-specific logistic regression models were used to calibrate BirdNET confidence scores, and only detections with an estimated probability of correct identification ≥ 0.80 were retained. For bats, all automated classifications generated by Kaleidoscope Pro were manually reviewed and validated by an experienced expert. These validation procedures reduce the influence of misclassifications and increase the reliability of the biodiversity patterns reported in this study, although some degree of classification uncertainty is unavoidable in large acoustic datasets (Wood and Kahl, 2024; Assarzadeh et al., 2025). Accordingly, the metrics derived from passive acoustic monitoring in this study should be interpreted as measures of acoustic activity (i.e., number of detections) rather than direct estimates of abundance (Gasc et al., 2015), since a single individual may generate multiple acoustic records during a sampling period.

By combining PAM with active surveys, our study mitigated these constraints and yields a more reliable characterization of community structure, supporting multi-method approaches in ecoacoustic research. This integration is particularly relevant because BirdNET confidence scores, commonly used in PAM workflows, are not probabilities and vary across species and recording contexts (Wood and Kahl, 2024). Therefore, applying species-specific thresholds and probabilistic calibration (e.g., logistic regression) is essential to minimize false positives and ensure comparability. Future protocols should standardize hardware, sampling schedules, and validation datasets to strengthen inference reliability.

4.2. *Biodiversity patterns*

Stand type and habitat position emerged as the main correlates of biodiversity, although they acted on different facets of the communities. For birds, stand type contributed to differences in community composition, as indicated by the PERMANOVA analyses, although this effect was significant only in some combinations of sampling method and year. Stand type also affected local species richness and diversity: eucalyptus plantations supported fewer species and lower diversity than chestnut stands (both traditional orchards and coppices), whereas the two chestnut stand types did not differ from each other. The models also detected a negative interior effect, with richness and diversity being generally lower in interior than in edge stations, although some of these effects were only marginally significant. Descriptively, active point counts detected between 9 and 11.5 species, whereas passive acoustic monitoring nearly doubled detection rates, recording 17.5–21 species. Orchards reached 10.5–11 species under active counts and 20–21 species under passive monitoring; coppices ranged from 9.5 to 11.5 (active) and 19–20 (passive). Eucalyptus plantations showed similar active counts but lower passive values in interiors ($\approx$17.5 species) compared to edges ($\approx$21 species). These descriptive patterns align with evidence from northwestern Spain, where eucalyptus plantations reduce bird richness and abundance and promote biotic homogenization (García-Fernández et al., 2025; Goded et al., 2019).

Diversity indices mirrored these trends. Under active counts, Shannon values ranged from 2.10 to 2.30 and Simpson from 0.86 to 0.89, with eucalyptus edges unexpectedly highest (Shannon $\approx$2.296, Simpson $\approx$0.888), likely reflecting dominance by generalist species. Passive monitoring yielded lower Shannon (1.57–1.92) and Simpson (0.68–0.81). These values suggest greater evenness in chestnut stands, and the lower diversity of eucalyptus plantations was statistically significant for birds in the mixed models, confirming previous findings for exotic plantations versus chestnut forests in NW Iberia (García-Fernández et al., 2025; Goded et al., 2019).

Patterns for bats were even more pronounced. Chestnut orchards reached up to 9 species at edges and 8 in interiors (Shannon $\approx$1.28, Simpson $\approx$0.62), while coppices recorded 7 and 6.5 species (Shannon $\approx$1.02–0.93). Eucalyptus plantations exhibited similar richness (7 and 6.5 species) but sharp declines in diversity inside stands (Shannon $\approx$0.65, Simpson $\approx$0.31). The mixed models showed significantly lower bat richness in eucalyptus plantations than in chestnut stands, whereas differences in Shannon and Simpson diversity were not statistically significant. These results underscore the role of vertical heterogeneity and roost availability as key determinants of bat diversity (Puelles-Escobar & Muñoz-Sáez, 2024).

Edge effects were modest overall: bird differences rarely exceeded two species in active counts and were negligible in passive surveys, except in eucalyptus edges (+3.5 species). For bats, coppices and eucalyptus showed slight edge gains, whereas orchards favored interiors, contrary to expectations; this pattern may reflect differences in bat activity and habitat use within these interior habitats. This result has relevant implications for management in mature chestnut stands, suggesting that thinning dense chestnut masses may be less critical than previously assumed for promoting bat activity. Thus, stand type outweighed edge influence, which became more evident in simplified systems (García-Fernández et al., 2025; Matlack, 1993; Rodríguez-San Pedro and Simonetti, 2013; Aragón et al., 2015; Vallejos et al., 2024).

Functionally, reduced diversity in eucalyptus plantations implies diminished ecosystem services, such as insect pest control by bats (Kunz et al., 2011; Wanger et al., 2014). In contrast, chestnut formations act as biodiversity reservoirs, sustaining richer and more balanced assemblages. Together with evidence from previous studies, our findings confirm that eucalyptus plantations cannot substitute traditional landscape forests, as they harbor only subsets of bird species and distinct herb communities driven by turnover. Conservation strategies should therefore prioritize native forest remnants and structurally diverse landscapes to mitigate biodiversity

loss and maintain ecosystem functionality.

4.3. Indicator species and forest structure

Indicator species analysis revealed clear differences in habitat associations between birds and bats, reflecting how stand structure and management shape species occurrence. Among birds, interior habitats of chestnut stands, both coppices and orchards, supported several forest-associated species, including *Certhia brachydactyla*, *Sitta europaea*, *Turdus merula*, *Turdus philomelos*, and *Erithacus rubecula*. These patterns align with the high structural complexity typically found in chestnut orchards, where mature trees, branching depth, and microhabitats provide favourable conditions for cavity-nesters and canopy-foraging species (Carrascal & Tellería, 1985). Recent studies further emphasize that structural complexity, rather than single habitat attributes, is a key predictor of bird abundance and diversity (Catfolis et al., 2023; Concha et al., 2023). Chestnut coppices also hosted characteristic species detected through passive sampling, such as *Poecile palustris* and *Sylvia atricapilla*, confirming the role of dense canopies and understory layers in supporting small woodland specialists, which exploit high stem density and complex understory for foraging and nesting.

In contrast, eucalyptus plantations were consistently associated with a different group of species, including *Troglodytes troglodytes*, *Periparus ater*, *Carduelis carduelis*, *Pyrrhula pyrrhula*, and woodpeckers such as *Picus sharpei* and *Dendrocopos major*. The recurrence of these species as indicators reflects the simplified structure of eucalyptus stands, characterized by reduced cavity availability, limited horizontal layering, and homogeneous canopy conditions (García-Fernández et al., 2025). Beyond local structure, evidence from Australian plantation landscapes shows that landscape-scale factors, such as the amount and connectivity of remnant vegetation, strongly shape bird communities (Thompson et al., 2025).

Bat indicator species showed a different yet complementary pattern. Chestnut orchards, particularly their interior habitats, concentrated most indicator detections, including *Hypsugo savii*, *Tadarida teniotis* Rafinesque, and *Barbastella barbastellus*. Although *H. savii* and *T. teniotis* typically forage above the canopy and are therefore less constrained by fine-scale habitat structure, the higher prey availability expected around traditional chestnut orchards may help explain their association with these interiors. Thus, these associations suggest that orchard interiors offer favourable roosting or foraging conditions linked to heterogeneous internal structure. Eucalyptus edges, by contrast, were associated with edge-adapted or flexible aerial foragers such as *Eptesicus serotinus* and *Pipistrellus kuhlii* reflecting their tolerance of structurally simplified or disturbed habitats. Contrasting preferences between edges and interiors, combined with tolerance to disturbed habitats, highlight the role of spatial heterogeneity and connectivity in maintaining functional diversity (Rodríguez-San Pedro and Simonetti, 2013; SECEM, 2022; Hutson et al., 2023).

Overall, the combined IndVal patterns across taxa reinforce the importance of structural complexity as a driver of forest biodiversity (Miret-Minard et al., 2026). Forest-specialist birds (e.g., *C. brachydactyla*, *S. europaea*) associated with large trees, diverse canopies, and multilayered vegetation were consistently linked to chestnut stands, whereas generalist or edge-tolerant species (e.g., *T. troglodytes*) predominated in eucalyptus plantations. Bat indicators further emphasize this gradient, with traditional chestnut orchards supporting a suite of species typically associated with heterogeneous forest interiors. This reinforces the need for biodiversity indicators based on species sensitive to structural complexity, rather than aggregated indices that obscure these patterns. It is worth noting, however, that in our exploratory models the fine-scale structural variables measured at each station were, by themselves, weak and inconsistent predictors of richness and diversity; the influence of structural complexity was thus expressed mainly through differences among stand types and through species-level indicator associations, rather than through continuous within-stand structural attributes. Moreover, the consistency of these results across Atlantic and Mediterranean regions suggests common principles for adaptive management: promoting vertical and horizontal heterogeneity through restoration and conservation of traditional formations, while integrating multitaxon approaches and ecoacoustic monitoring to enhance large-scale biodiversity assessments.

It is worth noting, however, that the weak relationships observed between biodiversity metrics and local structural variables should be interpreted with caution. Birds and, particularly, bats respond to habitat conditions over spatial extents that often exceed the 15-m radius used for vegetation measurements in this study. Consequently, the limited explanatory power of the structural models may partly reflect a mismatch between the scale of habitat characterization and the scale at which these highly mobile taxa select foraging, commuting, and breeding habitats. Future studies would benefit from incorporating stand- and landscape-scale structural metrics derived from larger field plots, remote-sensing approaches (e.g., LiDAR), or measures of landscape connectivity. Under this perspective, the recurring positive associations with tree-species richness and large-diameter trees, and the negative associations with dense shrub cover, should be regarded as indicative trends rather than definitive drivers of bird and bat diversity.

Thus, the stronger biodiversity patterns observed among stand types likely capture broader differences in habitat composition and structural complexity operating at spatial scales more relevant to these taxa than the local vegetation measurements considered here.

4.4. Biodiversity patterns in managed and unmanaged chestnut orchards

Managed orchards exhibited higher avian richness than unmanaged plots and greater diversity. For bats, managed edges supported more species and higher diversity. These patterns suggest that management practices such as pruning and maintaining open-canopy conditions may be associated with increased habitat heterogeneity and the occurrence of forest specialists. Similar patterns have been reported in Swiss chestnut orchards, where managed stands showed greater cavity availability and supported indicator species such as *C. brachydactyla* and *Sitta europaea* (Moretti et al., 2021).

Evidence from NW Iberia reinforces this pattern: vascular plant richness peaks under moderate management intensity, while both abandonment and intensive use reduce diversity. This suggests that biodiversity is often maximized at intermediate levels of disturbance, where competitive and disturbance-tolerant species coexist (Guitián et al., 2012). Moreover, patch shape interacts with

management, with irregular fragments supporting higher richness under moderate use, emphasizing the importance of structural heterogeneity at multiple scales.

Managed orchards tended to exhibit higher richness and diversity than unmanaged orchards. Although these patterns are consistent with a beneficial effect of management, the observational design of the study did not follow a Before-After Control-Impact (BACI) framework. Consequently, the observed differences cannot be unequivocally attributed to management actions, as pre-existing differences among sites may also have contributed to the observed patterns. Future studies based on replicated BACI designs would be necessary to establish causal relationships between management interventions and biodiversity responses.

4.5. Broader implications and management strategies

The ecological implications of these findings are profound. While abandonment of chestnut systems may increase carbon storage and woody biomass, it reduces structural diversity and the availability of microhabitats such as cavities and sunlit foraging areas, leading to functional homogenization (Obrist et al., 2011; Goded et al., 2019). Mature forests remain irreplaceable for specialist taxa, yet their conservation alone cannot sustain landscape-level diversity. Integrating restored traditional chestnut orchards (soutos) into forest mosaics offers a synergistic approach, combining cultural heritage and land use for rural communities with biodiversity conservation. This strategy aligns with international principles, such as those promoted by the Satoyama Initiative, which advocate for socioecological production landscapes that balance provisioning, regulating, and cultural services (Díaz-Varela et al., 2025).

Analogous evidence from urban Nature-based Solutions (NbS) demonstrates that interventions combining structural heterogeneity, native species planting, and invasive species removal can rapidly enhance multi-taxon biodiversity and ecosystem resilience (Pinto et al., 2025). These parallels reinforce the need for integrated management strategies in rural landscapes, prioritizing structural complexity, edge diversity, and connectivity to sustain ecological functions under climate and land-use change.

From a management perspective, our results highlight the need to maintain structural complexity through selective pruning and retention of veteran trees, which provide cavities and foraging substrate for forest specialists. In contrast, our exploratory analyses suggest that a dense shrub layer was, if anything, negatively associated with bird and bat richness, so management should aim to preserve structural heterogeneity and mature-tree features rather than to maximize understory cover per se. These measures not only safeguard species of conservation concern but also sustain ecological functions critical for resilient socio-ecological systems. Supporting chestnut-related businesses and restoration programs can further enhance biodiversity while revitalizing rural economies, as demonstrated in some areas of Galicia and southern Switzerland (Díaz-Varela et al., 2025; Moretti et al., 2021).

5. Conclusions

Native chestnut formations, particularly traditional orchards (soutos), constitute important biodiversity reservoirs within Atlantic forest landscapes. Across two years of multitaxon monitoring, chestnut stands generally supported higher bird and bat richness and diversity than eucalyptus plantations. Stand type also contributed to differences in community composition, although these differences were not consistent across years and sampling methods.

Indicator-species analyses further highlighted the ecological value of these systems. For birds, *Certhia brachydactyla* (Short-toed Treecreeper) and *Sitta europaea* (Eurasian Nuthatch) were strongly associated with chestnut interiors, whereas *Troglodytes troglodytes* (Eurasian Wren) was consistently associated with eucalyptus stands. For bats, *Hypsugo savii* (Savi's Pipistrelle) was associated with chestnut orchards in both years, whereas *Pipistrellus kuhlii was* more frequently associated with eucalyptus plantations. Together, these patterns highlight the importance of structurally diverse forest habitats for maintaining characteristic bird and bat assemblages.

Methodologically, the study confirms the complementarity of active point counts and passive acoustic monitoring. Active surveys provide behavioral context and improve the detection of diurnal species, whereas passive methods increase the detection of cryptic and nocturnal taxa, substantially increasing bird detections and enabling the assessment of bat communities. The combined use of both approaches strengthens biodiversity assessments and improves the identification of potential indicator species.

The ecological importance of chestnut systems extends beyond species richness alone. Their structural heterogeneity, mature trees, large-diameter stems, open-canopy conditions, and diverse microhabitats support a wide range of species and ecosystem functions. Although orchards classified as managed tended to support higher bird and bat diversity than those classified as unmanaged, the observational nature of this comparison precludes attribution of these differences to management actions alone. Nevertheless, the overall results indicate that traditional chestnut landscapes provide valuable habitat for forest biodiversity. Conserving, restoring, and promoting the sustainable management of soutos within heterogeneous forest mosaics may help counteract biotic homogenization associated with exotic plantations and land abandonment, while contributing to more resilient and multifunctional landscapes under ongoing environmental change.

CRediT authorship contribution statement

Pedro Álvarez-Álvarez: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **José Carlos Pérez-Girón:** Writing – review & editing, Visualization, Validation, Supervision, Software, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Bárbara Reguera Alonso:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Methodology, Investigation, Data curation. **Roberto J. Hermida Lorenzo:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Methodology, Investigation, Data curation. **Nicolás López-Jiménez:** Writing – review &

editing, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Funding acquisition, Data curation, Conceptualization.

Declaration of Generative AI and AI-assisted technologies in the writing process

The author(s) declare that no Generative AI was used in the creation of this manuscript.

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2026.e04497.

Data availability

Data will be made available on request.

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