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Tree-dwelling bats as indicators of forest landscapes

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ABSTRACT

Adopting standalone indicators to characterise landscape composition is vital because it allows for targeted assessments without surveying entire communities. We hypothesised that barbastelle bat (*Barbastella barbastellus*) presence would provide sufficient indication power to characterise forest landscapes in Italy and employed logistic regression to explore this relationship across the Alpine and Apennine regions. We selected three spatial scales (200 m, 1000 m, and 3000 m). We predicted distinct association patterns across biogeographic areas, sensitivity to multiple spatial scales, strong associations with altitude and specific forest types, and avoidance of intensive agricultural areas. Using opportunistically collected data from non-invasive acoustic surveys, we recorded effective responses despite methodological heterogeneity. We revealed significant positive associations in the Alpine region, with deciduous oak forests at the 3000 m scale, while showing negative correlations with mesophilic and mesothermophilic broadleaved mixed forests. In the Apennine region, albeit at different spatial scales, barbastelle bat presence was strongly associated with altitude, beech forests, and natural grasslands with trees and shrubs. It also exhibited negative associations with intensive crops. Furthermore, barbastelle bats exhibited varied relationships with landscape metrics, such as patch density and landscape evenness, indicating a reduced likelihood of presence in fragmented landscapes, particularly at larger scales. This highlights the complexity of their role in indicating forest landscape structure. Our findings support the potential role of barbastelle bats as reliable indicators of forest landscapes. Future work should test the ability to describe different forest management practices, high-resolution structures, and the amount of deadwood.

1. Introduction

Understanding the influence of land use and landscape structure on animal communities is crucial for effective biodiversity conservation and sustainable management of forest ecosystems. Animal indicators, particularly those sensitive to changes in habitat quality and landscape composition, play a pivotal role in this process. By identifying and monitoring these species, we can gain valuable insights into the level of integrity of forest landscapes. Animal species exhibit varied responses to landscape composition and structure, influenced by species traits and the analytical scale. Identifying these responses is crucial for assessing landscape suitability for biodiversity and detecting thresholds of landscape change that elicit measurable responses from animal communities (Dale and Beyeler, 2001; Lindenmayer et al., 2000; Noss, 1999).

Operationally defining forest "landscapes" requires understanding how animals perceive their environments. Consequently, discerning animal responses to forest landscape features is complicated by the need to establish their "landscape," given species-specific perceptions (e.g., Spirito et al., 2020; Tolkachev, 2023; Cardoso et al., 2023). Moreover, the multiscale nature of responses to habitat and landscape features within forest ecosystems further complicates this task (Moll et al., 2020; Hooven et al., 2023). Ecosystem dynamics and management actions

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operate on forest landscapes across various scales, necessitating multiscale analyses to identify organisms that indicate ecological responses to human activities (Rondinini and Boitani, 2002).

Using animal indicators to assess landscape conditions and trends is crucial for optimising forest management practices that balance human activities with biodiversity conservation. Identifying these indicators provides valuable insights into how forest management practices affect biodiversity (Lindenmayer et al., 2000; Shanley et al., 2013; Oettel and Lapin, 2021). In this way, forest managers can make informed decisions that promote sustainable practices, mitigate negative impacts, and enhance the resilience of forest ecosystems. This approach ensures that biodiversity conservation is integrated into forest management strategies, ultimately leading to more sustainable landscape management.

Despite international recognition of the importance of establishing effective indicators in forest landscapes, much remains to be done in this area. For instance, only one of the six indicators of forest restoration identified by the EU's Nature Restoration Law (Hering et al., 2023) relies on animals — the "common bird index" — potentially overlooking the nuanced responses of different animal species to forest structure and management. Conversely, identifying key landscape characteristics conducive to the presence of endangered animal species could significantly inform management and optimise conservation efforts (Collier et al., 2012; Watson et al., 2014; Li et al., 2021). This dual-purpose approach could prove rewarding for ecological indication and species conservation simultaneously.

With 1482 bat species known to science (Simmons and Cirranello, 2024), bats are often considered excellent bioindicators due to their k-selected nature, rapid population changes, clear reactions to anthropogenic pressures, and sensitivity to changes in insect availability (e.g., Jones et al., 2009; Russo et al., 2021). However, few studies have thoroughly examined the potential of bats as bioindicators, necessitating scientific support to ascertain their role in various environmental contexts.

The use of bats as bioindicators presents operational difficulties, including technical challenges in species identification from echolocation and social calls (Russo and Voigt, 2016; Russo et al., 2018), expertise required for capture campaigns, and associated costs (Russo et al., 2021). While bats hold promises for bioindication in certain habitats, at least at the community scale (De Conno et al., 2018; López-Bosch et al., 2024), selecting single surrogate bat species to cover entire species assemblages or guilds presents tantalising possibilities but is fraught with challenges (Russo et al., 2021). Bats are mainly forest-dwelling mammals, with many species selectively roosting in trees or specialised in clutter space foraging: thus, forest management practices greatly affect their foraging habits, and roosting behaviours (e.g., Lacki et al., 2007; Russo et al., 2016). Despite most studies focusing on conserving at-risk bat species, little research explicitly addresses their use as indicators in European forests (but see Cistrone et al., 2015; Rachwald, 2019).

Barbastelle bats (*Barbastella barbastellus*) appear promising as forest indicators due to their preference for roosting in standing dead trees within well-preserved, heterogeneous old-growth forests (Russo et al., 2004; 2005; 2015; 2018; Carr et al., 2018). However, their flexible generalist nature and wide range of foraging habitats (e.g., Hillen et al., 2009; 2011, Zeale et al., 2012) raise questions regarding using their presence alone to characterise the surrounding landscape. While barbastelle bat echolocation calls are generally easy to identify and relatively well-detected (Denzinger et al., 2001), barbastelle bat responses to forest structure and management are not clearcut, further challenging their utility as forest indicators (Russo et al., 2021).

In this study, we employ a multiscale methodology to evaluate the potential of barbastelle bats' presence as a standalone indicator for characterising forest landscape composition and structure. Our focus lies in investigating whether the mere presence of this species, as opposed to more complex data – such as bat activity, which requires additional time for collection – is adequately informative in characterising forest landscape composition and structure. We employ acoustic records, hypothesising that barbastelle bat presence provides sufficient indication power to characterize landscapes. We predict that:

1. Barbastelle bats exhibit distinct habitat selection patterns across Italy's biogeographic regions, leading to varied forest landscape associations that reflect roosting or foraging requirements.
2. Barbastelle bats are sensitive to multiple spatial scales, so association patterns vary according to the selected scale.
3. In the Apennine region, barbastelle bats are strongly associated with altitude and beech forests (Russo et al., 2004; 2010; 2017), while in the Alpine region, other forest types are also associated with the species' presence (Toffoli and Cucco, 2020).
4. Foraging preferences lead to avoidance of intensive agricultural areas and a preference for hygrophilous vegetation, contributing to the observed association patterns.
5. In fragmented forest landscapes, barbastelle bats likely show decreased presence in highly fragmented areas. Greater landscape connectivity and higher interspersion of habitat types may enhance foraging opportunities and overall presence.

2. Materials and methods

2.1. Data collection

We recorded bats in flight between 1998 and 2022 during faunal surveys across 12 regions of continental Italy (Fig. 1; Appendix A). Recordings predominantly used direct ultrasound sampling, employing either manually operated devices (D1000X, Pettersson Elektronik AB, Uppsala, Sweden) or sound-triggered, automated systems (D500X, Pettersson Elektronik AB, Uppsala, Sweden; SM2BAT, SM4BAT FS, and Song Meter Mini Bat, manufactured by Wildlife Acoustics Inc., Maynard, USA). Additionally, manually operated time expansion detectors were employed in certain instances (D980X and D240X, Pettersson Elektronik AB, Uppsala, Sweden). The devices used differed in ultrasound processing and storing, microphone sensitivity, frequency response, and signal-to-noise ratio, inevitably introducing some variability into the dataset. Nonetheless, this diversity provided a realistic representation of data sources, testing the robustness of our approach and facilitating contributions from various stakeholders, including park operators, citizen scientists, and volunteers.

In most instances, recordings started 30 min after sunset and continued for 4 hours. The dataset was divided into sites where barbastelle bats were detected and those where they were not recorded. While we classify the latter as sites where barbastelle bats were "absent," the absence of detection may suggest that the species was not prevalent at the site but could still have been present. Barbastelle bats show movement across wide home ranges including many habitats (Hillen et al., 2009; 2011; Zeale et al., 2012). Therefore, we presume that detection sites correspond to "typical" barbastelle bat habitats, unlike sites where bats remained undetected, which are likely rare or devoid of the species. We manually identified barbastelle bats from recordings using the BatSound software ver. 4.7 (Pettersson Elektronik AB, Uppsala, Sweden), generating 512 sample-point spectrograms. Barbastelle bat echolocation calls are typically distinctive due to their frequency range and the characteristic alternation of call structure, allowing for confident identification and differentiation from other bat species occurring in Italy (Russo and Jones, 2002).

All data were geolocated using WGS84 geographic coordinates (Fig. 1). Our dataset included 176 records (82 presence points and 94 "absence" points; Appendix A).

2.2. Environmental and geographic characterisation of sampling locations

We imported geolocated records into QGIS (version 3.28.12 "Firenze"). We created three circular buffer areas around each sampling point

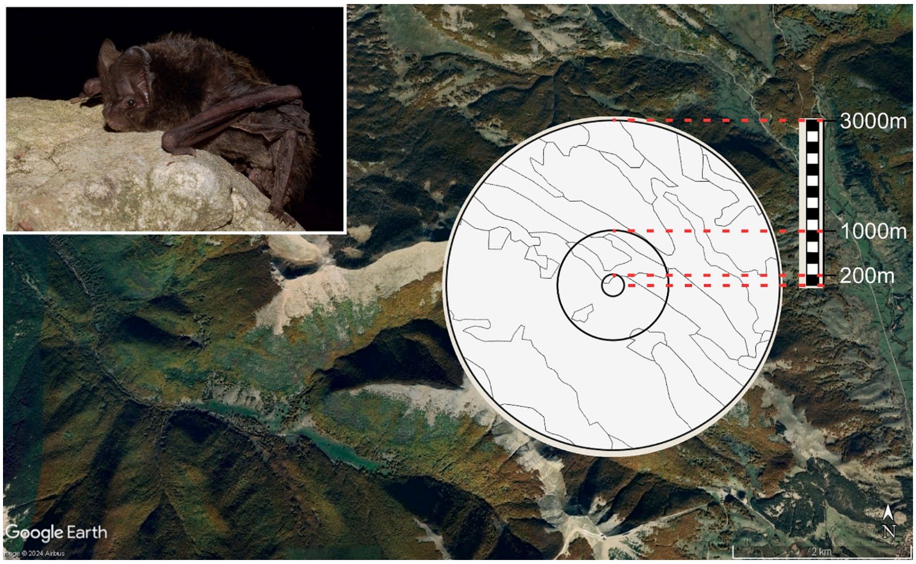

Fig. 1. Example of the 200, 1000, and 3000 m buffer zones used to extract landscape data for each study site. Image © Google Earth, Imagery © Airbus 2024. Accessed on January 7, 2025.

corresponding to three “landscapes” with radii of 200 m, 1000 m, and 3000 m (Fig. 1). To analyse habitat composition associated with *B. barbastellus*, we employed the CORINE Land Cover 2018 (hereafter, CLC18) layer. The CLC18 adopts a four-level hierarchical classification system for the Italian peninsula. A 4-digit code identifies each category; to aid interpretation, acronyms, and explanations for the most representative CLC18 categories are provided in Appendix B.

We imported the different “landscapes” into FRAGSTATS ver 4.2 for analysis (McGarigal, 1995). From this analysis, we extracted six main metrics related to landscape structure (diversity, and fragmentation). These are, respectively: Patch Richness Density (PRD); Simpson’s Diversity Index (SIDI); Simpson’s Evenness Index (SIEI); Edge Density (ED); Interspersion and Juxtaposition Index (IJI); and the Connectance Index (CONNECT) (McGarigal *et al.*,1995). PRD expresses the number of different patch types occurring within the landscape divided by the total landscape’s area converted to 100 ha. SIDI is calculated as the difference of 1 and the total, across all types of patches, of the square of the proportionate abundance of each patch type. SIDI equals zero in scenarios where the landscape comprises only one patch, indicating the absence of diversity. As the number of distinct patch types increases and the distribution of the areas among patch types becomes more balanced, SIDI approaches unity. SIEI is calculated as 1 minus the sum, across all patch types, of the proportionate abundance of each patch type squared, divided by 1 minus 1 divided by the total number of patch types. Therefore, it represents the observed Simpson’s Diversity Index divided by the maximum Simpson’s Diversity Index attainable for that specific number of patch types. SIEI is 0 in a landscape made of one patch, indicating no diversity, and approaches 0 as the area distribution among different patch types becomes more skewed, with dominance by one type. Conversely, the index equals 1 when the area distribution among patch types is perfectly even, i.e., proportional abundances are identical. These landscape metrics were then integrated as variables in the dataset.

Edge Density (ED) measures the edge length within the landscape, standardised by the total area. It is expressed as meters of edge per hectare. ED equals 0 when the landscape has no edges, i.e., the entire landscape, including any boundary, includes a single patch. Higher values of ED indicate more fragmentation, with a greater proportion of edge habitat relative to the total landscape area.

The Interspersion and Juxtaposition Index (IJI) quantifies the degree to which patch types are interspersed or mutually adjacent. An IJI value of 0 indicates a highly uneven distribution of patch type adjacencies, and a value of 100 represents maximum evenness, where all patch types are equally adjacent to all other types.

The Connectance Index (CONNECT) measures the degree to which patches of the same class are spatially connected. It is calculated as the proportion of connected patches, relative to a specified threshold distance. CONNECT equals 0 when the landscape consists of a single patch or no patches are connected within the specified distance and 100 when all landscape patches are connected.

Since each bat detector site displayed distinct CLC categories across diverse regions throughout the Italian peninsula, it was determined that the study area should be divided into two regions: Northern Italy and Central-Southern Italy, denoted as the ’Alpine’ and ’Apennine’ regions, respectively, considering the predominant mountain chains where most sampling points were located. However, instead of subjectively attributing data points to either region, a Principal Component Analysis (PCA) was conducted on data for the 3000 m buffer radius, encompassing the highest number of CLC categories. Subsequently, the data points were attributed to the two regions based on the data partitioning generated by the PCA.

2.3. *Statistical analysis*

We applied Z-score standardisation ($((x_i\text{-}x)/s)$) to land use variables and landscape index values before any statistical analysis and log transformations when needed to conform to statistical tests’ assumptions.

After an initial examination of the data, we excluded variables with insufficient records to ensure consistent variance calculation from the model. Specifically, we omitted CLC categories occurring in ≤ 5 records. We used the extension of CLC categories as independent or explanatory variables to understand the distribution of *B. barbastellus*. Furthermore, we included only CLC categories at the fourth level to avoid spatial overlaps with higher-level categories. Based on the results of PCA, we independently analysed the occurrence data for Italian regions (Alpine and Apennine regions) in response to land use and landscape structure variables using a logistic regression (logit) model. We used the likelihood function to estimate the probability of independent variables predicting the barbastelle bat’s observed presence. The likelihood ratio test compares the full model to a reduced model and was chosen for its great reliability and power. We incorporated a topography variable indicating the altitude above sea level at each sampling point.

The analyses were conducted for each buffer radius (200 m, 1000 m, and 3000 m), resulting in six models for land use composition and six for landscape structure (diversity and fragmentation).

The Z-score standardisation was done using RStudio version 4.3.1 ({base} package), while the correlation analyses and PCA were done in STATISTICA rel. 10, the logit models were developed using RStudio version 4.3.1 ({stats} package) and STATISTICA 10. For all tests, significance was set at $P < 0.05$.

3. Results

3.1. Characterisation of environmental and geographic sampling locations

The PCA of the distribution of CLC categories among sampling points revealed distinct clusters in the loading plot (Fig. 2). Certain CLC categories, such as *Larix* and *Pinus cembra* forests, natural grasslands without trees and shrubs, and forests dominated by *Abies alba* and *Picea abies*, were grouped in the left quadrant, along with mountain pine and Mediterranean pine forests, coniferous forests, and broadleaved forests. There were variations in the representation of these categories along the second main component (PC2), highlighting differences despite the PC1 grouping. Furthermore, the upper left quadrant of the loading plot displayed associations among Mediterranean pine forests, intensive crops, hygrophilous species forests, *Quercus ilex* and *Quercus suber* forests, and high-altitude sclerophyllous vegetation. Conversely, the lower left quadrant demonstrated segregation, including wood and plantations primarily featuring non-native broadleaf trees, extensive crops, *Castanea* woods, deciduous oaks forests, mesophilic and meso-thermophilic broadleaved mixed forests, and *Fagus* forests. Besides, the score plot (Fig. 2) indicated segregation based on geographic origin. Sites from the Alpine region were predominantly located in the left quadrant, while those from the Apennine region were more prevalent in the right quadrant.

3.2. The predictive power of barbastelle bat presence on landscape composition

Based on the outcome of PCA of sampling points, which supported the classification into Alpine and Apennine regions, we conducted separate logistic regression models for the two areas to analyse the presence and absence of *B. barbastellus* in Italy, using altitude and CLC18 land use categories as predictor variables (Table 1).

For the Alpine region, we found no association between barbastelle bat presence and altitude or land use variables for the 200 m and 1000 m radius buffers, while for the 3000 m buffer, points in the Alpine region displayed a significant positive association with deciduous oak forests and a negative association with mesophilic and mesothermophilic broadleaved mixed forests.

At all scales in the Apennine region, we observed a highly significant positive association with altitude and *Fagus* forests. Natural grasslands with trees and shrubs were positively associated with barbastelle bat presence at 200 m. Hygrophilous forests were positively associated with the species' presence at 3000 m, while Mediterranean pine forests and intensive agriculture were negatively associated at 3000 m and 1000 m, respectively.

The 1000 m- and 3000 m- buffer analyses revealed a strong, positive association with altitude in the same region, with barbastelle bat presence associated with higher elevations. Barbastelle bat's presence was also positively associated with *Fagus* forests at the same spatial scales and hygrophilous forests at 3000 m. Additionally, we observed significant negative associations with intensive crops for 1000 and 3000 m buffers, and Mediterranean pine forests at 3000 m.

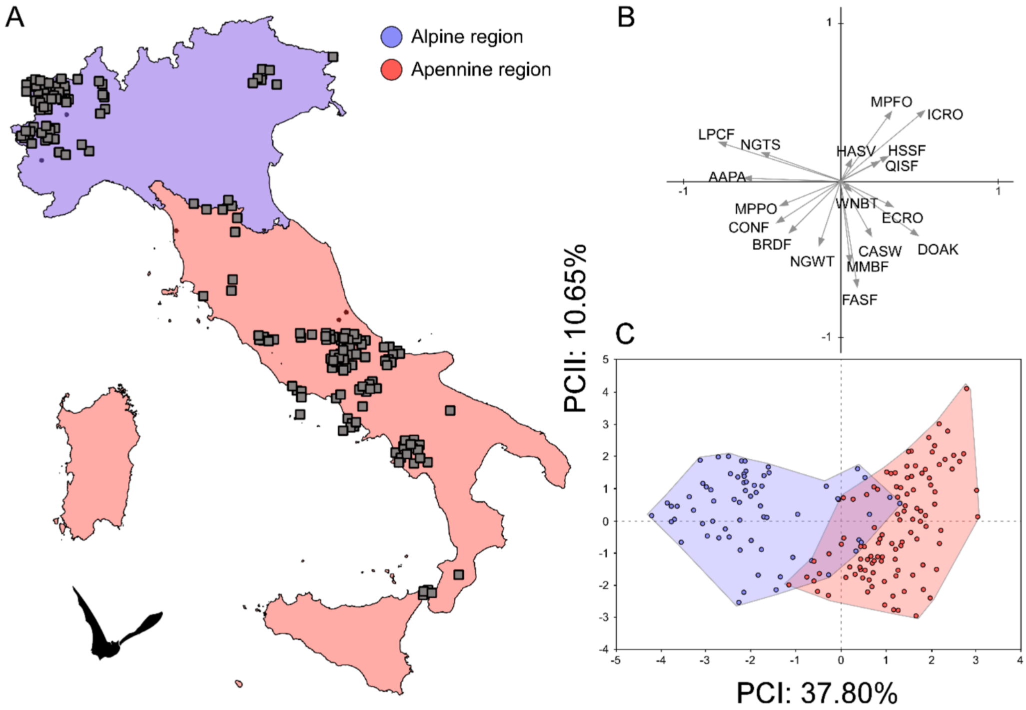

Fig. 2. A) Locations of bat detector sampling sites in the Apennine and the Alpine regions. B) Loading plots with the projections of the eigenvectors in the multivariate space, representing the associations of the individual CLC categories. C) Score plot showing the ordering of sample sites, according to differences in the extent and presence of CLC categories. Extended definitions of categories (clockwise order) are LPCF = *Larix* and *Pinus cembra* forests; NGTS = Natural grassland with trees and shrubs; AAPA = *Abies alba* and *Picea abies* forests; HASV = High altitude sclerophyllous vegetation; MPFO = Mediterranean pine forests; ICRO = Intensive crops; HSSF = Hygrophilous species forests; QISF = *Quercus ilex* and/or *Quercus suber* forests; WNTB = Woods and plantations with a predominance of non-native broadleaf trees; ECRO = Extensive crops; DOAK = Deciduous oaks forest; CASW = *Castanea* woods; MMBF = Mesophilic and mesothermophilic broadleaves mixed forests; FASF = *Fagus* forests.; NGWT = Natural grassland prevailingly without trees and shrubs; BRDF = Broadleaves forests; CONF = Coniferous forests; MPPO = Mountain pine and Oromediterranean pine forests.

Table 1
The logit models' results for the presence and absence of *Barbastella barbastellus* in the Alpine and Apennine regions across three buffer radii. Landscapes were categorised according to the land use category subdivisions of CORINE Land Cover 2018. Significant results, denoted by bold font, indicate χ values (log-likelihood estimates) with corresponding p-values (p) below the significance threshold ($\alpha < 0.05$). The χ-value signs indicate the effect's direction.

Alpine region	**200 *m***		**1000 *m***		**3000 *m***	
Variable	χ	p	χ	p	χ	p
Intensive Crops	–	–	−0.556	0.456	0.048	0.827
Deciduous Oaks Forests	1.731	0.188	0.759	0.384	6.311	**0.012**
Mesophilic and Mesotermophilic Broadleaved Mixed Forests	0.043	0.837	0.162	0.688	−6.856	**0.009**
Castanea Woods	–	–	–	–	−0.246	0.620
Fagus Forests	–	–	0.045	0.833	−0.094	0.760
Wood and Plantations with a predominance of non-native broadleaf trees	–	–	–	–	0.424	0.515
Mountain Pine and Oromediterranean Pine Forests	0.036	0.850	0.053	0.818	0.047	0.828
Abies alba and *Picea abies* Forests	0.183	0.669	0.200	0.655	1.527	0.217
Larix sp. and *Pinus cembra* Forests	0.151	0.698	2.234	0.135	0.227	0.634
Broadleaves Forests	–	–	0.845	0.358	0.492	0.483
Coniferous Forests	–	–	0.004	0.948	0.000	0.985
Natural Grasslands with Trees and Shrubs	0.217	0.642	0.011	0.916	0.001	0.975
Natural Grasslands without Trees and Shrubs	0.975	0.323	1.744	0.187	0.052	0.819
Altitude (m a.s.l.)	1.57	0.118	1.57	0.118	1.56	0.118
Apennine region	**200 *m***		**1000 *m***		**3000 *m***	
Variable	χ	p	χ	p	χ	p
Intensive Crops	–	–	−9.038	**0.003**	−6.028	**0.014**
Extensive Crops	–	–	0.216	0.642	1.433	0.231
Quercus ilex and/or *Quercus suber* Forests	0.108	0.743	0.003	0.960	0.081	0.776
Deciduous Oaks Forests	0.003	0.959	−0.313	0.576	1.186	0.276
Mesophilic and Mesotermophilic Broadleaved Mixed Forests	0.032	0.857	−1.646	0.200	−3.692	0.055
Castanea Woods	0.856	0.355	0.006	0.940	0.806	0.369
Fagus Forests	10.421	**<0.001**	10.820	**<0.001**	16.840	**<0.001**
Hygrophilous Species Forests	–	–	–	–	7.577	**0.006**
Mediterranean Pine Forests	–	–	−1.775	0.183	−5.370	**0.020**
Mountain Pine and Oromediterranean Pine Forests	–	–	0.027	0.870	0.064	0.801
Broadleaves Forests	–	–	–	–	2.558	0.110
Coniferous Forests	0.503	0.478	0.271	0.602	0.905	0.341
Natural Grasslands with Trees and Shrubs	7.210	**0.007**	1.782	0.182	0.054	0.816
Natural Grasslands without Trees and Shrubs	0.651	0.420	0.868	0.352	0.108	0.743
High Altitude Sclerophyllous Vegetation	–	–	–	–	−2.430	0.119
Low Altitude Sclerophyllous Vegetation	–	–	–	–	−3.625	0.057
Altitude m a.s.l.	4.14	**<0.001**	4.15	**<0.001**	4.15	**<0.001**

3.3. The predictive power of bat presence on landscape structure

In the Alpine Region, barbastelle bat presence was positively associated with patch density (PRD) at the 200 m scale and landscape evenness (SIEI) at the 1000 m scale (Table 2). However, at 3000 m, barbastelle bats were negatively associated with edge density (ED) and the interspersion and juxtaposition index (IJI). A borderline positive association with species diversity (SIDI) was detected in the Apennine Region at 1000 m. At 200 m, barbastelle bats were positively associated with landscape evenness (SIEI), but this association turned negative at the 1000 m scale. At 3000 m, negative associations with ED and IJI were observed, while at 200 m, barbastelle bats showed a positive association with landscape connectivity (CONNECT) (Table 2).

4. Discussion

4.1. Regional Variation in barbastelle bat landscape associations and metrics

Using presence data and comparing it with an absence dataset, we identified associations between bat presence and forest landscape composition in the Alpine and Apennine regions. While it is important to remark that the two areas are not confined to the homonymous mountain chains, this distinction does not reflect an arbitrary classification. It is legitimated by the PCA outcome as a natural, ecologically meaningful grouping. In general, the presence of barbastelle bats was associated with landscape composition, whereas the performance regarding landscape structure varied across regions.

Table 2
Results of logit model based on presence-absence and region using FRAGSTATS landscape diversity and fragmentation metrics. Significant results, denoted by bold font, indicate χ values (log-likelihood estimates) with corresponding p-values (p) below the significance threshold ($\alpha < 0.05$). The χ-value signs indicate the effect's direction.

	200 *m*				1000 *m*				3000 *m*			
Landscape structure metric	Alpine		Apennine		Alpine		Apennine		Alpine		Apennine	
	χ	p	χ	P	χ	p	χ	p	χ	p	χ	p
PRD	**9.584**	**0.002**	−2.053	0.152	0.046	0.829	−1.488	0.223	0.383	0.536	−1.888	0.169
SIDI	0.474	0.491	−0.024	0.878	−2.640	0.104	**4.172**	**0.041**	−0.261	0.609	0.148	0.701
SIEI	n.c	n.c	**7.041**	**0.008**	**12.347**	**0.000**	**−4.548**	**0.033**	0.389	0.533	−0.672	0.412
ED	−0.114	0.735	−4.417	1.000	−2.232	0.135	2.051	0.152	**−7.423**	**0.006**	**9.290**	**0.002**
IJI	2.078	0.149	0.245	0.621	−2.162	0.141	0.850	0.357	**−4.348**	**0.037**	**−4.273**	**0.039**
CONNECT	0.869	0.351	**5.414**	**0.020**	−0.681	0.409	−0.180	0.671	−3.779	0.052	−0.464	0.496

4.2. Barbastelle bats indicate landscape characteristics but are sensitive to geography and spatial scales

This study supports several of our predictions, revealing important regional and spatial differences in how land use composition influences barbastelle bat presence in Italy. First, we verified Prediction 1, with distinct habitat selection patterns emerging between the Alpine and Apennine regions, reflecting likely differences in roosting and foraging needs. Prediction 2 was also confirmed, as barbastelle bats displayed sensitivity to multiple spatial scales. Additionally, Prediction 3 was substantiated, with the species showing strong associations with altitude and beech forests in the Apennines, and deciduous oak forests in the Alpine Region. Lastly, Prediction 4 was consistent with our findings, as barbastelle bat occurrence was negatively associated with intensive agriculture and favoured by hygrophilous forests.

Our study reveals important regional and spatial differences in how land use composition influences barbastelle bat presence in Italy. In the Alpine region, barbastelle bats showed no significant associations at finer scales (200 m and 1000 m). However, at a broader landscape scale (3000 m), there was a clear preference for deciduous oak forests and avoidance of mesophilic and mesothermophilic broadleaved mixed forests. This finding is likely linked to barbastelle bat's roosting ecology, as deciduous oaks provide more suitable roosting options than coniferous or mixed forests. Oak trees, particularly in unmanaged stands, tend to develop cavities as they age, making them ideal roosting sites (Gottfried et al., 2015; Carr et al., 2018). In alpine environments, richly structured forests with large oak trees are important barbastelle bat foraging sites (Sierro, 1999).

In contrast, coniferous forests, which dominate higher elevations in the Alps, typically lack such roosting features unless the trees are dead, such as in bark beetle (*Ips typographus*) outbreaks in the Białowieża Forest (Poland), where roost availability for barbastelle bats has increased due to the flaking bark on Norway spruce trees killed by the beetle (Rachwald et al., 2022a; b). Apart from these exceptional cases, managed coniferous stands often lack deadwood, limiting roost availability. Similarly, mixed forests in the region are frequently managed as coppice, preventing trees from reaching the size necessary to support cavities, thus reducing habitat quality for forest bats (Ancillotto et al., 2022a). This is likely the reason for the observed negative association with these forests.

In the Apennine region, barbastelle bats displayed strong and consistent associations with altitude and *Fagus* forests across all spatial scales. In this region, barbastelle bats primarily roost in beech trees, particularly under the flaking bark of standing dead trees (e.g., Russo et al., 2004; 2015; 2017). The positive association with altitude likely reflects the conditions where beech forests grow in the country: on the Apennine mountains, beech generally thrives above 900–1000 m a.s.l. (Nocentini, 2009). The significant positive association with natural grasslands at smaller scales (200 m) suggests that these open habitats, interspersed with trees and shrubs, offer foraging opportunities close to roosts (Hillen et al., 2011).

At broader scales (3000 m), the strong association with hygrophilous forests, often found along rivers, likely reflects barbastelle bats' preference for moths, their primary prey, which are abundant in these wet environments. Blossoming willows (*Salix* spp.) have been found to support moth populations – a staple food source for the species (Apoznański et al., 2023). These linear habitats also function as commuting corridors for bats, facilitating movement across the landscape (Cortes and Gillam, 2020). Conversely, Mediterranean pine forests and intensive agricultural areas were negatively associated with barbastelle bat presence. Managed pine forests are often plantations with low structural complexity, offering little in terms of insect prey or roosting cavities for bats (Ancillotto et al., 2022a). More broadly, conifer plantations are suboptimal habitats for bats, although management practices can enhance roosting and foraging opportunities (Kirkpatrick et al., 2017a, 2017b; Cook et al., 2023). The negative association with intensive agriculture likely stems from the heavy use of pesticides in these areas, drastically reducing moth populations and thus depleting the food supply for barbastelle bats (Ancillotto et al., 2022b). Additionally, intensive agricultural landscapes offer limited cover for commuting or foraging, making them less suitable for several bat species (Russo et al., 2024).

4.3. Can the presence of the barbastelle bat indicate forest landscape structure?

As predicted (Predictions 1, 2, and 5), the likelihood of bat presence exhibited contrasting patterns across scales and regions and was reduced in fragmented landscapes, particularly at larger scales. This likely reflects how barbastelle bats exploit landscapes differently for foraging and roosting depending on local habitat and landscape structure. In the Alpine Region, positive associations at smaller scales (200 m, PRD; 1000 m, SIEI) suggest that barbastelle bats benefit from patchier, more heterogeneous forest environments that provide diverse foraging opportunities within confined areas, as known from previous studies set in the same biogeographic context (Sierro and Arlettaz, 1997; Sierro, 1999). However, at broader scales (3000 m), negative associations with edge density (ED) and interspersion and juxtaposition (IJI) indicate that extensive fragmentation and excessive edge creation reduce habitat quality, potentially disrupting movement corridors between patches.

In the Apennine Region, bats require a specific balance in landscape structure. At 200 m, positive associations with SIEI and CONNECT suggest that connectivity and evenness are important for roosting, foraging, and commuting. In this region, barbastelle bats often roost in beech forests, and higher connectivity may facilitate earlier emergence from roosts, minimising predation risks in patchy landscapes (Russo et al., 2007). Continuous beech forests typically have fewer gaps, which limits light availability on the ground and adversely affects undergrowth development. This is important because dense understory cover likely reduces prey accessibility for barbastelle bats (Froidevaux et al., 2021).

However, the negative association with SIEI at 1000 m implies that increasing evenness may limit the variety of suitable patches for effective foraging. Additionally, negative associations with edge density (ED) and interspersion and juxtaposition index (IJI) at 3000 m, also observed in the Alpine Region, indicate that, as predicted, excessive fragmentation and habitat mixing at larger scales could hinder movement and access to essential roosting and foraging habitats. These results support previous modelling analysis that highlighted the importance of connectivity at a large scale to preserve barbastelle bats in northern Italy (Toffoli and Cucco, 2020).

Our findings highlight that barbastelle bats are sensitive to spatial scale, emphasising the need for forest landscapes that maintain small-scale diversity and larger-scale continuity to support their habitat requirements. Overall, our results verify the prediction that at least at large spatial scales, in fragmented forest landscapes, barbastelle bats likely show decreased presence in areas with high fragmentation, while greater landscape connectivity and higher interspersion of habitat types may enhance foraging opportunities and overall presence. The analysis also highlights the existence of region- and scale-specific responses.

4.4. Can the barbastelle bat be adopted as a forest landscape indicator?

Identifying bioindicators whose presence alone highlights landscape conditions is essential for effective nature conservation and sustainable forest landscape management. This necessity is echoed across various taxa and ecosystems in the ecological literature. For instance, certain macro-benthic organisms have been identified as reliable indicators of water habitat quality and ecosystem health due to their specific habitat requirements and sensitivity to environmental changes (e.g., Chessman, 1995; Lenat, 1988; Barbour, 1999; Ollis et al., 2006; Cortelezzi et al., 2020; Leigh et al., 2013).

We underscore the potential effectiveness of integrating bat activity data with presence data for bioindication, as suggested by previous research (e.g., Cistrone et al., 2015; De Conno et al., 2018). Nevertheless, we recognise the difficulty of establishing clear boundaries for transitioning from detectable responses to bioindication, highlighting the complexity of incorporating activity data into bioindicator frameworks. For infrequent bat species like the barbastelle bat, achieving statistically supported activity levels can be particularly challenging, limiting the feasibility of using quantitative data on bat activity. From this perspective, our study demonstrates that the mere presence of this species can provide valuable information about forest landscape composition and structure, paving the way for the implementation of bioindication using the barbastelle bat.

Integrating barbastelle bats with other ecological indicators, such as saproxylic beetles (Mazzei et al., 2018), cavity-nesting birds (Drever et al., 2008), or other forest-dependent species (Vierikko et al., 2010), could further strengthen landscape planning and biodiversity management. However, our findings highlight that barbastelle bats alone already provide valuable insight into landscape characteristics, making them a strong standalone indicator. While multiple indicators can enhance environmental assessments, barbastelle bats are an efficient and scalable tool for detecting habitat quality and guiding conservation actions. Future work could assess how their indicator role compares to or complements that of other species across different ecological contexts.

Our study highlights the strong geographic disparities in barbastelle bat responses observed between the Alpine and Apennine regions, despite these regions being characterised as mountainous areas within the same country. This variability accentuates the limitations of relying solely on species presence for bioindication, as local variations in species ecology and behaviour can significantly influence their suitability as indicators. This also underscores the importance of caution when extrapolating bioindicator findings across diverse geographic regions and highlights the value of regionally tailored approaches. For instance, populations of barbastelle bats along the Adriatic coast of Italy or on islands (Ancillotto et al., 2014; 2015), where woodland is scarce or absent, exhibit habitat preferences diverging from the typical patterns observed in most European regions.

We recognise the constraints linked to how we selected “absence” data, acknowledging the possibility of misclassification wherein areas designated as lacking barbastelle bats may still occasionally host them. Our absences should therefore be interpreted more accurately as a combination of locations where the species is genuinely absent and areas where it is rare enough to go undetected during a single night of observation. Even where bats were not recorded, their possible sporadic presence would not likely establish a consistent association between species presence and landscape features. Therefore, for our modelling, these sites serve as valid “absence” data, as their occasional use by the species is unlikely to significantly affect the overall conclusions drawn from the landscape-scale habitat associations.

Furthermore, we highlight the non-systematic nature of the data collection method employed in this study, which used various detector types and lacked consistency in sampling methodology. We emphasise the critical importance of standardised data collection protocols for bioindication purposes. While our use of opportunistic recordings from varied situations and devices proved successful in testing the robustness of our indicator, we appreciate that a well-designed data collection strategy tailored to our research questions could yield more informative results. Nevertheless, we stress the necessity for robustness in data collection methods within a bioindication framework, as this would enable the use of data gathered for other purposes, such as faunal surveys or citizen science initiatives.

Selecting appropriate buffer zones as boundaries for “forest landscapes” in wildlife studies, including those on bats, is inherently challenging. Despite examples in the literature (e.g., Ancillotto et al., 2019; Lintott et al., 2015), establishing sound criteria for choosing a specific radius remains difficult. One potential approach could involve considering species mobility data from radiotracking; however, home range size can locally vary strikingly based on resource availability (for barbastelle bats, see e.g., Sierro, 1999; Hillen et al., 2009; Zeale et al., 2012; Ancillotto et al., 2015), making a universal solution elusive even for a certain species. In this study, we chose buffer zones of 200, 1000, and 3000 m, considering the species’ varied roost selection preferences at the local scale and long-range mobility during foraging. However, we acknowledge that our classification may not have been optimal for all points considered, which might have occasionally reduced the performances of our tests.

While our study was limited to acoustic data, the predictive power of barbastelle bat presence could be enhanced by incorporating additional biological information, such as sex. Barbastelle bats exhibit sex-specific differences in habitat selection (Hillen et al., 2009; 2011) and roosting area preferences (Russo et al., 2010), which could be reflected in landscape-level analyses that account for the bat’s sex. However, this would require capture rather than acoustic data, necessitating the involvement of authorised personnel and causing some disturbance to wild barbastelle bats. In contrast, acoustic data are non-invasively collected. They can be gathered by non-specialists, including citizen scientists, who can place passive detectors in the field to gather data over multiple nights.

5. Conclusions

We highlight the potential of opportunistically collected acoustic data to characterise landscape variables influencing barbastelle bat occurrence at large spatial scales. Its ease of collection and cost-effectiveness make it a valuable tool for broad-scale ecological studies, particularly for elusive or wide-ranging species. However, like any method, it has limitations. Opportunistic surveys involve varying recording conditions, including differences in detector models, microphone sensitivities, and deployment protocols, which may influence detection probabilities and introduce potential biases. Environmental factors such as background noise, weather conditions, and habitat structure can further affect detection rates. While these factors do not invalidate our findings, they underscore the need to consider potential confounding effects when interpreting acoustic data. However, a key strength of our approach is its ability to integrate data from diverse sources, reflecting the realities of large-scale acoustic monitoring. Rather than a drawback, this diversity enhances the generalisability of our findings and highlights the feasibility of leveraging broad-scale opportunistic datasets. Despite potential limitations, maximising the use of existing acoustic data at minimal cost remains a crucial advantage, enabling assessments at spatial scales that would be logistically challenging with standardised surveys alone.

Involving citizen science may significantly increase the geographic coverage of bat monitoring and provide robust data on species’ presence and habitat use (Lundberg et al., 2021). The only significant expertise required is in the identification of bat calls, which should be carried out by specialists, either manually or by manually verifying automatically identified barbastelle bat sequences.

Future studies could compare opportunistic and systematic survey approaches to assess potential differences in detection probabilities and habitat associations. Understanding whether and to what extent results differ will help refine best practices for using opportunistic datasets in ecological research. Systematic data collection could be fostered through national or European programs, building upon previous successful large-scale initiatives such as, e.g. the National Barbastelle and Bechstein’s Survey in the UK and the “Protection and Promotion of the Barbastelle Bat in Germany”, with standardized protocols for detector types, sampling frequency, and locations to ensure consistency and reduce regional variability in future acoustic monitoring efforts. The barbastelle bat is a species protected under Annex II of the 92/43/EEC Habitats Directive. Therefore, all EU member states must monitor barbastelle bat populations according to the law. Employing barbastelle bats as indicators of forest landscape structure presents a dual benefit by serving conservation goals and monitoring requirements.

The primary objective of our study was to determine whether the presence of a forest bat species could identify specific landscape features, including composition, diversity, and structure. Our findings demonstrate that this approach is effective. Since the barbastelle bat is a species of conservation concern, our results have broader implications for conservation planning. For example, such results can be applied to enhance landscapes for barbastelles within protected areas or for mitigation purposes within Environmental Impact Assessments.

Despite the significance of our findings, it is essential to acknowledge that detailed data on Italian forests – such as management types, forest structure, and the amount of deadwood – are often unavailable, especially at the large analysis scale we considered. This lack of information is unfortunate, as these factors are likely crucial to understanding barbastelle bat ecology. In scenarios where such data are available, barbastelle bats could show especially high performances as indicators of forest structure and management. Moving forward, researchers should design studies that identify gradients of forest structure, management intensity, and deadwood presence, rigorously testing these variables against the presence of barbastelle bats. This would be essential to open a new research avenue, enhancing our understanding of bat-landscape associations and informing effective forest management practices. Finally, while our modelling approach effectively identifies landscape associations of barbastelle bats using presence-absence comparisons, future studies incorporating independent validation datasets or ground validation could further enhance the reliability of such predictive frameworks.

CRediT authorship contribution statement

Danilo Russo: Writing – review & editing, Writing – original draft, Visualization, Supervision, Methodology, Investigation, Formal analysis, Conceptualization. **Maurizio Zotti:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Formal analysis. **Sabrina Maria Marsala:** Writing – review & editing, Formal analysis. **Enrica Pinelli:** Writing – review & editing, Formal analysis. **Antonello Migliozzi:** Writing – review & editing, Formal analysis. **Elena Patriarca:** Writing – review & editing, Investigation. **Paolo Agnelli:** Writing – review & editing, Investigation. **Donatella Valente:** Writing – review & editing, Visualization, Investigation, Formal analysis. **Luca Cistrone:** Writing – review & editing, Visualization, Investigation, Formal analysis, Conceptualization.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2025.113260.

Data availability

Data will be made available on request.

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