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RESEARCH ARTICLE

Habitat heterogeneity from lidar and hyperspectral data: Implications for bird guilds and restoration management of coal mines

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Abstract

1. A global transition of energy production is underway. Coal-based power production is gradually being replaced by renewable energies, leading to the decommissioning of coal-mining sites. In Europe, this presents an opportunity for restoring degraded habitats, in alignment with the goals of the Nature Restoration Law. However, systematic approaches to monitoring restoration of mining sites are lacking as current practices are often labour-intensive and (both spatially and temporally) constrained.
2. In this study, we evaluated the suitability of habitat heterogeneity metrics derived through airborne remote sensing for monitoring the restoration of coal-mining sites. Specifically, we tested the response of guild-specific bird species richness to various metrics of habitat heterogeneity, both at and around a restored coal-mining site. We (i) examined differences in habitat heterogeneity, including terrain characteristics, vegetation structure and senescent vegetation, between restored and surrounding areas; (ii) documented key aspects of habitat heterogeneity that influence bird richness and different bird guilds; and (iii) tested for significant differences among bird responses between restored and surrounding areas.
3. Generalised additive models explained between 19% and 78% of the variability in guild richness. Canopy cover, understory cover, the standard deviation of vegetation height, and senescent vegetation positively affected overall bird richness, while terrain characteristics significantly influenced some guilds (e.g. ground-nesting birds). The effects of evaluated variables on guild diversity were generally similar in both restored and surrounding areas, with the standard deviation of vegetation height being the only exception. Increasing standard deviation of vegetation height positively affected the richness of understory nesters and foragers in the restored area but had no (or slightly negative) effect in the surrounding area.

4. *Synthesis and applications*. This study underscores the need to design a mosaic of habitats with complex vertical structures, emphasising the critical role of senescent vegetation and unaltered terrain features in supporting biodiversity. Finally, it provides evidence that integrating habitat heterogeneity metrics derived from airborne remote sensing data into restoration success assessment can support biodiversity-promoting management measures.

KEYWORDS

birds, habitat structure, hyperspectral, lidar, mining, PSRI, spoil heap, terrain characteristics

1 | INTRODUCTION

Coal mining has long served as the backbone of economic development (Betz et al., 2015; Ericsson & Löf, 2019). However, mining in general, and coal mining in particular, also has direct impacts on nature. This is especially true for open-pit mining, associated with the formation of large pits and the deposition of the excavated material on spoil heaps leading to the destruction of original habitats and biodiversity losses (Aska et al., 2024). As a result, tremendous efforts are then made to restore degraded, damaged or destroyed ecosystems to minimise the environmental impact of mining (Brock, 2023; Martins et al., 2020).

Restoration approaches predetermining the future character of emerging ecosystems are highly debated in relation to biodiversity conservation. Restored sites after coal mining are increasingly recognised for their ecological value to various groups of organisms, including invertebrate and vertebrate species (e.g. Harabiš, 2023; Šálek, 2012). Habitat heterogeneity (i.e. the variability of environmental conditions such as the dominance and composition of plant species, topographic variability, vegetation structure or soil types) is one of the important factors supporting biodiversity. According to the habitat heterogeneity hypothesis, environments with greater variability provide more niches, supporting a higher number of species (see review by Stein et al., 2014). Therefore, habitat heterogeneity is central to ecosystem restoration, and explicit manipulations of habitat heterogeneity—such as targeting specific terrain characteristics and vegetation structure parameters in restored ecosystems—can help achieve restoration goals (Hendrychová et al., 2020; LaRue et al., 2023; Lengyel et al., 2020).

For successful restoration, it is crucial to understand the habitat requirements of the target species (or groups of species); otherwise, even well-intentioned restoration efforts may fail to benefit biodiversity (Poskočilová et al., 2024). Additionally, having detailed and continuous data that accurately represent habitats in the respective area is essential for monitoring restoration progress and optimising resource allocation. Although direct field surveys of habitat attributes can provide valuable insights into habitat heterogeneity and species-habitat associations (e.g. Harabiš et al., 2013; Poláková et al., 2022), they are limited in time and space. Rough subjective estimates of vegetation cover or terrain characteristics, represented by discontinuous, categorical measures acquired during fieldwork (e.g. Bellamy et al., 2022; Vojar et al., 2016), have limited informative value and do not allow continuous measurement at the comprehensive detail that is much needed for restoration management.

In contrast, remote sensing provides an efficient and cost-effective alternative for such surveys; it, however, remains underutilised in mining restoration studies (Karan et al., 2016; McKenna et al., 2020, 2023; Moudrý et al., 2021). Airborne remote sensing surveys are particularly well-suited for developing indicators for decision-making and effective management of restored sites (Cordell et al., 2017; Kissling et al., 2024). Indeed, hyperspectral and light detection and ranging (lidar) data have revolutionised the measurement of habitat heterogeneity and have been widely used to assess species diversity (Cosgrove et al., 2024; LaRue et al., 2023; Moudrý et al., 2023; Sweeney et al., 2025). The integration of hyperspectral and lidar data supports the characterisation of multiple aspects of species' habitats such as vegetation structure, land-use and land-cover, terrain characteristics, as well as vegetation health and composition (e.g. Acebes et al., 2021; Cooper et al., 2020; Prošek et al., 2020). Many previous studies have focused particularly (or exclusively) on birds due to the ease of bird data availability and the strong relationship between birds and the 3D environment structure (see review by Bakx et al., 2019), as well as the fact that birds can serve as a good proxy for overall biodiversity (Anderle et al., 2024). While such studies are well-documented in spatially complex ecosystems such as forests (McNeil et al., 2023; Renner et al., 2024; Tew et al., 2022; Wallis et al., 2016), research is comparatively limited in agricultural landscapes (Anderle et al., 2023; Torresani et al., 2024), urban areas (Choi et al., 2021) and early successional habitats resulting from natural disturbances (Kebrle et al., 2022), human disturbances (Singh et al., 2017) or in restored sites (Moudrý et al., 2021).

This study aims to assess the applicability of habitat heterogeneity metrics for understanding habitat-bird relationships within the restored and surrounding areas. By analysing datasets from both early successional habitats (on the restored site) and more typical cultural landscapes, such as managed forests and agricultural areas (surrounding the restored site), this research seeks to provide insights into how bird communities respond to habitat heterogeneity in both early successional and conventional cultural habitats. Specifically, we (i) analysed differences in habitat heterogeneity between the restored and surrounding areas of a recently restored mining site to (ii) identify the key aspects of habitat heterogeneity

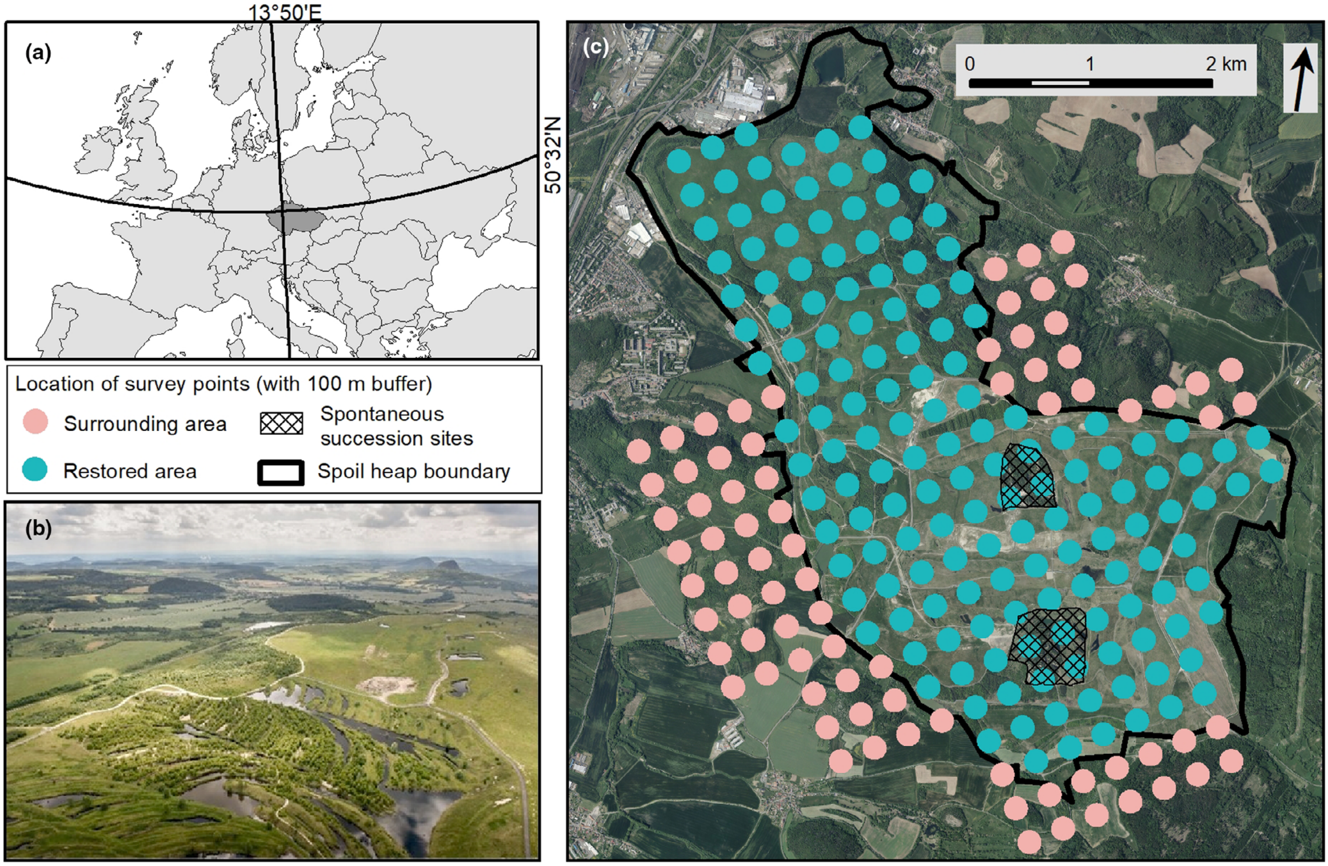

FIGURE 1 Study site location and description. (a) Location of the study area within Czechia; (b) aerial photo of the study area from 2020 (photo by Marketa Hendrychova). Note in the lower part of the image the area left to spontaneous succession; (c) location of survey points on the actual spoil heap (restored area; blue) and in its surroundings (surrounding areas; pink).

most relevant for birds with different guilds (i.e. nesting, foraging and diet preferences). In addition, we (iii) investigated whether the observed associations between habitat heterogeneity and richness of bird guilds differed between the restored and surrounding areas.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was carried out on the Radovesická spoil heap and its surrounding area, located in the Northern Bohemian lignite basin in Czechia (Figure 1). The region is one of the largest active brown coal-mining districts in Europe. From 1964 to 2003, the site served as a deposition of overburden soils from a nearby surface mine. Since 1989, the spoil heap (15.5 km^2; hereafter referred to as 'restored area') has undergone technical reclamation, including terrain modifications and agricultural as well as forestry restoration. In addition, 19% of the spoil heap was left to spontaneous succession. These areas are characterised by specific rugged terrain resulting from the heaping of the overburden material, early successional stages of vegetation (Figure 1b), and old dead aquatic vegetation such as *Phragmites australis* and *Typha latifolia* from the previous vegetation season. The surroundings of the restored area (hereafter referred to as 'surrounding area') consist of agricultural fields and mixed forests.

2.2 | Bird surveys and diversity indices

Bird data were collected in May 2012 by five experienced ornithologists, co-authors of this study, using the point count method (Bibby et al., 1992). Survey points (n = 231) were drawn from a grid with 300 m spacing (Figure 1), including 153 points in the restored area and 78 in the surrounding area. Each survey point was visited twice during the season (5–6 May and 28–29 May) to maximise the detection of both early and late breeders. At each survey point, a 5-min bird survey was conducted during peak bird activity between 06:00 and 10:00 UTC. All individuals detected by sight or sound within a 100 m radius were recorded, except for all birds flying over the points. No specific ethical or fieldwork permits were required for this study. Following Šálek et al. (2010), we distinguished functional life-history guilds (i.e. groups of species that exploit similar environmental resources in comparable ways; Root, 1967) according to birds' nesting (i.e. ground, understorey, and canopy nesters), foraging (i.e. ground, understorey, and canopy

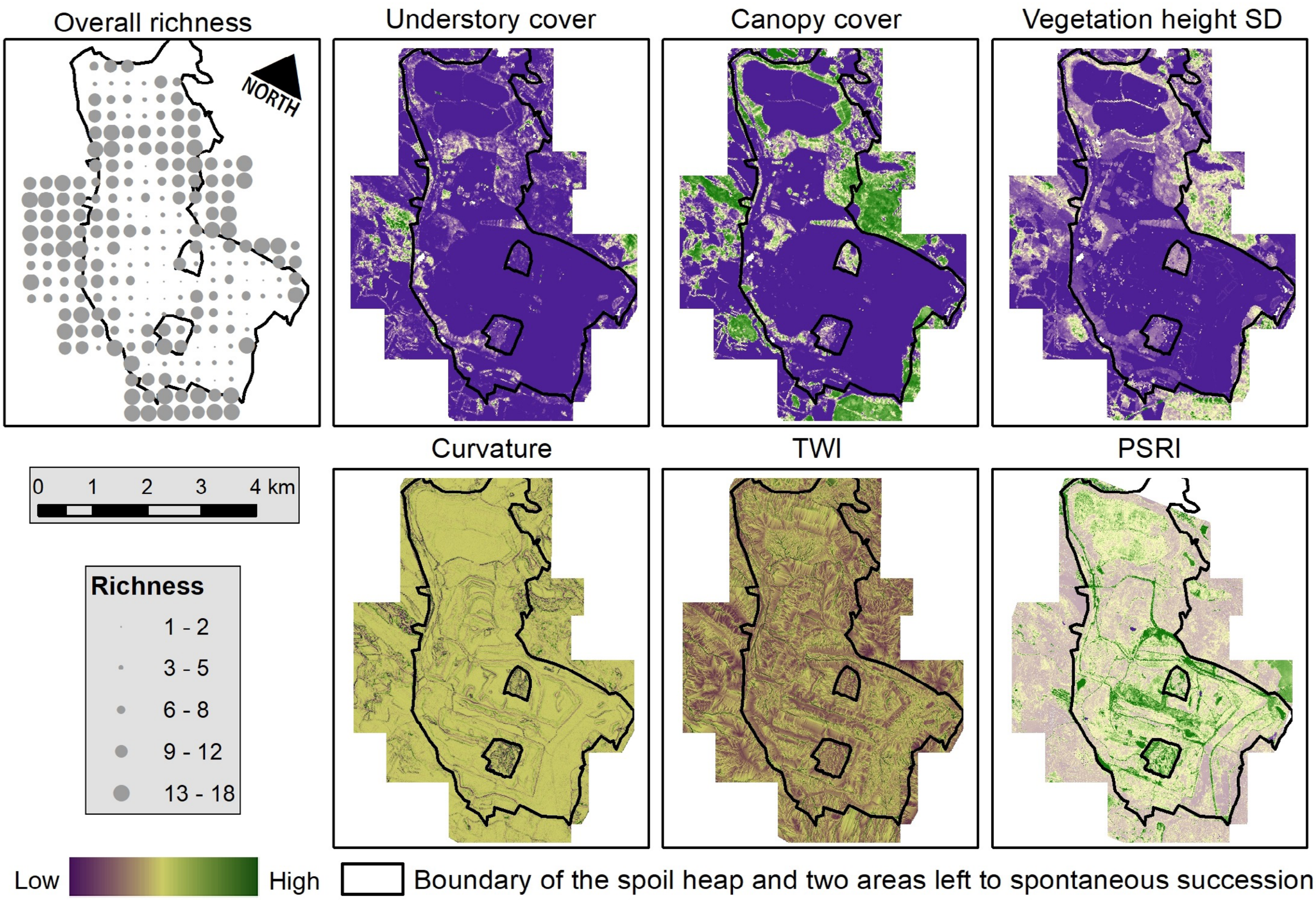

FIGURE 2 Bird species richness and explanatory variables. Depiction of the overall bird species richness and six explanatory variables derived from lidar and hyperspectral data that were used for modelling. PSRI, Plant Senescence Reflectance Index; TWI, topographic wetness index; SD, standard deviation.

foragers), and diet (carnivores, granivores, omnivores) preferences. Note that species may fall into more than one group (e.g. species can forage on the ground and understorey). The point counts from both visits were summed. See Appendix S1 for a list of observed species and their attribution to individual guilds. The overall and guild-specific species richness was calculated for each survey point as the number of distinct bird species detected (Figure 2). We checked for the completeness of the survey by computing and visualising the species accumulation curve (see Figure S1).

2.3 | Airborne data collection and preprocessing

The airborne hyperspectral (sensor CASI-1500) and lidar (sensor Riegl LMS Q-780) data were acquired using a remote sensing platform FLIS (The Flying Laboratory of Imaging Spectroscopy; Hanuš et al., 2016). Flights were conducted on the 18th of May 2017 at an altitude of 1030 m above-ground and a velocity of 110 knots (ground speed).

The hyperspectral imagery contained 48 spectral bands. These covered the visible near-infrared range, from 380 to 1050 nm, with a bandwidth of 7.2 nm. Pre-processing of the hyperspectral images, including radiometric correction, georeferencing and atmospheric corrections, was carried out by the data provider (CzechGlobe). The average point density of the lidar point cloud data was 8 points per m^2. The data were processed following Moudrý et al. (2021) and georeferenced to the local Datum of Uniform Trigonometric Cadastral Network (EPSG: 5514) and Baltic Vertical Datum—After Adjustment (EPSG: 5705). Following preprocessing, the point cloud was classified into 'ground' and 'vegetation' classes using LAStools, and ground points were used to derive a digital terrain model (DTM) with a 1 m resolution. In addition, prior to the calculation of vegetation metrics (see Section 2.4), the point cloud was height-normalised (i.e. the returns' height above DTM was calculated).

2.4 | Habitat heterogeneity variables

We used six variables describing habitat heterogeneity with potential relevance to bird richness; four were related to vegetation characteristics and two to terrain characteristics (Table 1; Figure 2). For characterising the local vegetation structure, we focused on variables distinguishing individual vegetation layers (i.e. strata). Authors typically recognise two or three layers of vegetation

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TABLE 1 Overview of explanatory variables. Variables derived using lidar and hyperspectral data. Note that the variables were derived within a 100-m buffer of the survey points.

Variable	Description
Vegetation height SD	Standard deviation of vegetation returns from heights >1 m
Understorey cover	Number of points between 1 m and 3 m divided by the total number of all points
Canopy cover	Number of points >3 m divided by the total number of all points
Plant senescence reflectance index (PSRI)	$(R_{678} - R_{500})/R_{750}$ where R_x denotes the reflectance at the wavelength of x nm. Water bodies were excluded from its calculation. The value of this index ranges from −1 to 1. An increase in this index indicates the onset of canopy senescence. The common range for green vegetation is −0.1 to 0.2
Curvature	Curvature values for a moderate relief typically vary from −0.5 to 0.5. Positive values indicate ridges, while negative values indicate depressions. Near-zero values indicate relatively flat areas or slopes
Topographic wetness index (TWI)	$\mathrm{TWI} = \ln(\alpha/\tan\beta)$, where α is the specific catchment area and β is the local slope in radians. TWI is a surrogate for soil moisture, with low values (<5) on steep slopes where water drains quickly and high values (>10) indicating high moisture in flatter areas or valleys with large contributing areas

(Jones et al., 2013; Lesak et al., 2011; Vogeler et al., 2014). Here, we distinguished between the understorey cover (1–3 m) and the canopy cover (>3 m). The height intervals of vegetation layers are based on our field experience. The same vegetation layers are typically recognised during field surveys on postmining sites (e.g. Šálek, 2012). We calculated the understory and canopy cover by counting the number of returns in each layer and dividing it by the total number of vegetation returns (Moudrý et al., 2023). In addition, we calculated the standard deviation of point returns to capture the vertical variability in vegetation structure (e.g. Goetz et al., 2010; Vogeler et al., 2014). We also considered other common vegetation structure variables (i.e. maximum and mean canopy height), but they highly correlated with the canopy cover (Pearson's $|r| \geq 0.70$).

Previous research has highlighted the usability of the foliage water content or vegetation senescence as a metric of the habitat suitability for birds (Jones et al., 2013; Moudrý et al., 2021; Soto et al., 2017). Therefore, we calculated the Plant Senescence Reflectance Index (PSRI; $(R_{678} - R_{500})/R_{750}$), which is sensitive to the carotenoid/chlorophyll ratio and, therefore, can serve as an estimate of the amount of old, dead vegetation (i.e. a measure of the vegetation senescence; Merzlyak et al., 1999). The old, dead vegetation from the previous season is mainly present in aquatic vegetation (e.g. *Phragmites australis* and *Typha latifolia*) and, to a lesser extent, in low-steppe vegetation (e.g. *Calamagrostis epigejos* and *Arrhenatherum elatius*).

In addition, variables characterising the complexity of the terrain have been shown to be particularly important for ground and understorey species (Toivonen et al., 2023; Vogeler et al., 2014). Therefore, to characterise terrain heterogeneity, we calculated the following terrain characteristics from the DTM: curvature (rate of slope change over the surface), topographic wetness index (TWI), and slope (rate of elevational change over the horizontal surface), which have been previously used to predict bird occurrences (Anderle et al., 2023; Hoefs et al., 2021; Reif et al., 2018). However, the slope was highly negatively correlated with TWI (Pearson's $|r| \geq 0.70$) and it was, therefore, removed from the subsequent analysis.

The terrain characteristics were aggregated using the mean value within a 100 m buffer (Moudrý, Lecours, et al., 2019). We used LAStools (version 200112), ENVI (version 5.5), and ArcGIS (version 10.3) to calculate vegetation structure, senescence and terrain characteristics, respectively. All metrics were calculated in a 100 m buffer of grid survey points.

2.5 | Statistical analyses

We assessed the effect of vegetation and terrain characteristics on bird species richness in restored and surrounding areas using generalised additive models (GAMs), which allowed for non-linear relationships. We used the Poisson distribution family with a log link function, which was justified by the fact that no over-dispersion was identified in model diagnostics (the maximum dispersion parameter was 0.99). We used thin plate regression spline smoothers with the basis dimension set to 10. The smoothing parameters were estimated by the generalised cross-validation criterion (Wood, 2017).

We fitted 10 separate models, each sharing the same predictors (Table 1) but differing in the response variable, represented by the species richness of one of the following groups of species (guilds): all species, three nesting guilds (i.e. canopy, understorey and ground nesters), three foraging guilds (i.e. canopy, understorey and ground foragers), and three diet guilds (i.e. granivores, carnivores

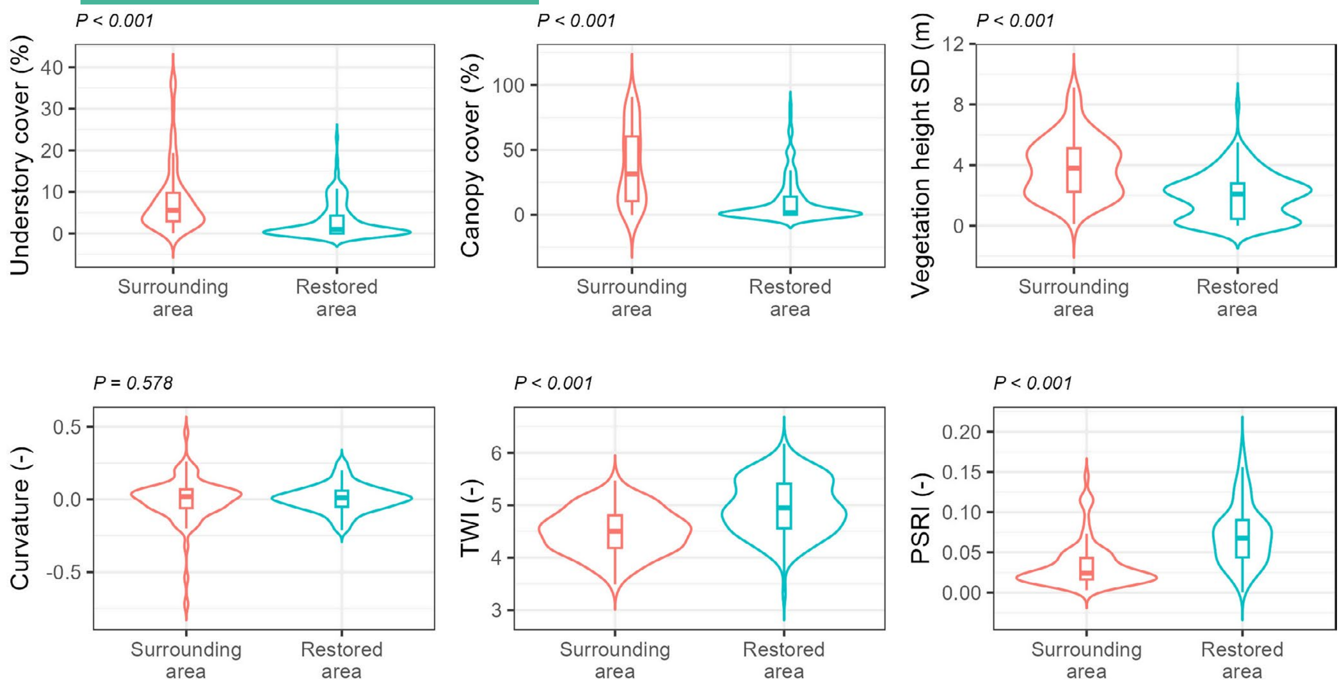

FIGURE 3 Habitat heterogeneity. Violin plots showing the differences in habitat heterogeneity variables between restored and surrounding areas. PSRI, Plant Senescence Reflectance Index; TWI, topographic wetness index; SD, standard deviation. The *p* values refer to Welch two-sample *t* tests comparing the given variable in the restored versus surrounding areas.

and omnivores). Additionally, a two-level factor indicating whether a survey point was in the restored or surrounding area (hereafter restoration status) was used, both as a main-effect predictor and as interacting with all other predictors.

With each model, we performed a stepwise backward model selection based on AIC. We then recorded the residual autocorrelation (i.e. by computing Moran's correlograms) and overdispersion of the final model. Although we found a significant residual autocorrelation in some models, its actual magnitude was negligible (the maximum of the residual Moran's *I* for the first distance class of ~500 m was 0.1; the correlograms are shown in Figure S2). We evaluated the goodness of fit of each model based on the proportion of the null deviance explained by the model. The effect of each significant predictor ($p < 0.05$) was assessed by plotting a model prediction across the range of the observed predictor values, together with the associated confidence bands.

To compare the relative importance of vegetation characteristics, terrain characteristics and restoration on the bird species richness, we performed variation (deviance) partitioning (Ozdemir, 2015). This technique consists of comparing the deviance explained by the models with and without the given group of predictors and includes an estimate of parts of deviance that cannot be solely attributed to a single predictor group due to its collinearity with another group(s). The resulting fractions of the deviance explained by the individual groups, as well as that shared by multiple groups (due to the collinearity among them), were then visualised using Venn diagrams.

All statistical analyses were performed in R 4.3.1 (R Core Team, 2023). We used the *mgcv* package for GAM modelling (Wood, 2017), the *pgirmess* package for computing correlograms (Giraudoux, 2023), and the *tidyverse* meta-package to process data and to produce graphics (Wickham et al., 2019).

3 | RESULTS

3.1 | Habitat heterogeneity in restored and surrounding areas

A comparison of the habitat heterogeneity of the 231 survey points, with 153 in the restored area and 78 in the surrounding area, showed the following differences. The restored area was characterised by low canopy and understory cover, and a relatively low standard deviation of vegetation height. In contrast, the surrounding area had higher understory and canopy cover, as well as a higher standard deviation of vegetation height. In terms of terrain characteristics, curvature was similar in both areas, while the TWI was higher in the restored area. Similarly, the PSRI was considerably higher in the restored area (Figure 3).

3.2 | Overall richness

We observed 83 bird species from a total of 1340 individual bird records. The overall bird species richness in restored and surrounding areas ranged from 1 to 17 and 1 to 18 species per survey point, respectively. The bird community was diverse, with dominant species typical of farmland, including *Alauda*

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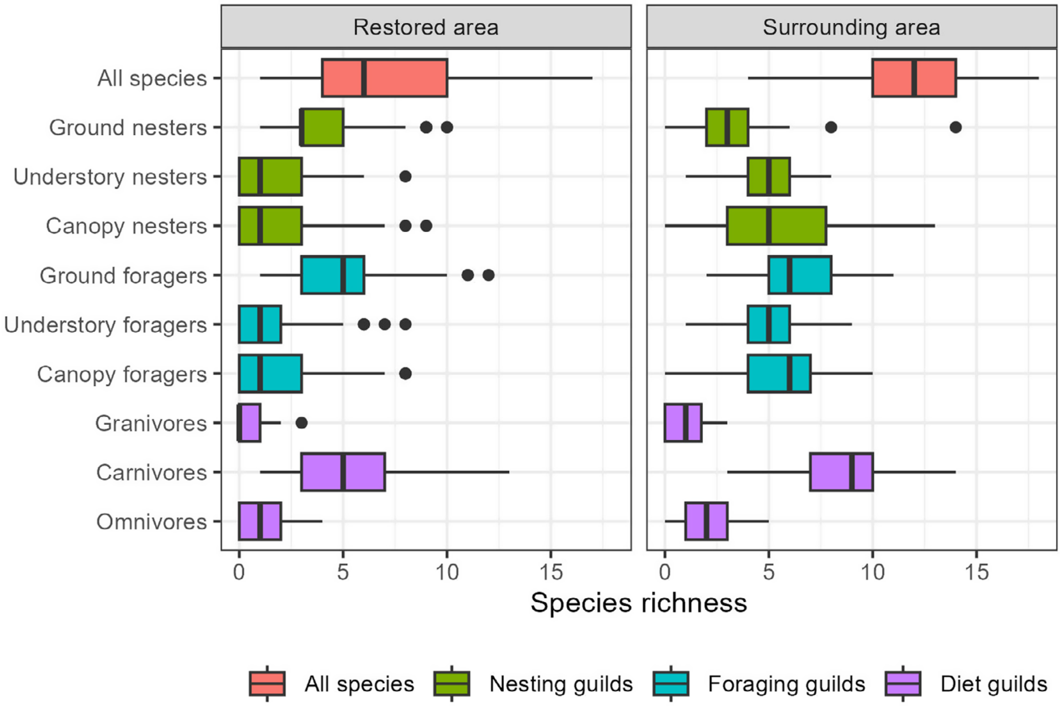

FIGURE 4 Species richness. Differences in species richness of nine guilds between restored and surrounding areas.

arvensis, *Emberiza citrinella* and *Sylvia communis*, which were the three most abundant species. Additionally, species associated with wetter open habitats, such as *Anthus trivialis* and *Locustella naevia*, were also well represented. Birds characteristic of forest edges and field-woodland mosaics were commonly observed, including *Sylvia atricapilla*, *Phylloscopus trochilus*, *Phylloscopus collybita*, *Luscinia megarhynchos* and *Cuculus canorus*. Among rarer species, we recorded a few that reflect less intensively managed open landscapes with rich insect communities, such as *Miliaria calandra*, *Lanius collurio*, *Saxicola rubetra* and *Jynx torquilla*, as well as species associated with moist to wet habitats, including *Luscinia svecica cyanecula*, *Tachybaptus ruficollis* and *Charadrius dubius*. The median species richness in the restored area was 6, and it was dominated by carnivorous ground-foraging and ground-nesting birds (Figure 4). The median species richness in the surrounding area was 12, and it was dominated by carnivorous understory- and canopy-nesters (Figure 4).

The GAM model of overall species richness explained 70.6% of deviance (coefficients of all models are reported in Tables S1 and S2). Overall species richness was strongly affected by vegetation characteristics (i.e. vegetation senescence and structure), while the restoration status (i.e. restored vs. surrounding area) showed a moderate effect and terrain characteristics a weak effect (Figure 5a). Notably, 23.6% of the variability explained by vegetation characteristics overlapped with the variability explained by the restoration status (Figure 5a), indicating that these factors are interrelated. The shapes of observed response curves were similar for both the restored and the surrounding area, except for understorey cover (Figure 5b). Standard deviation of height and presence of senescent vegetation (PSRI) had a strong positive effect and resulted in a gradual increase in overall species richness (Figure 5b). Species richness increased considerably at relatively low values of canopy cover and understorey cover (only in the restored area), with minimal change as these variables continued to increase. The values where the changes took place for the canopy density and understorey density were 0%–25% and 0%–5%, respectively (Figure 5b).

3.3 | Nesting guilds

GAM models explained 71% and 70% of the variability in the richness of canopy and understorey nesters, respectively. The richness of canopy nesters increased with increasing canopy density. Increasing the standard deviation of vegetation height positively affected canopy nesters in the restored area but showed a more complex relationship in the surrounding area. Richness decreased for the standard deviation of vegetation height between 0 and 2.5, then increased for higher values (Figure 6). The richness of understorey nesters increased with increasing understorey density and the standard deviation of height returns (in the restored area only) and decreased with increasing canopy cover. Increasing terrain curvature negatively affected both canopy and understory nesters. For the ground nesting guild, GAM models explained 36% of the variability in its richness. The richness of ground nesters was positively affected especially by PSRI and TWI (only in the surrounding area), and, to some degree, by canopy cover (Figure 6).

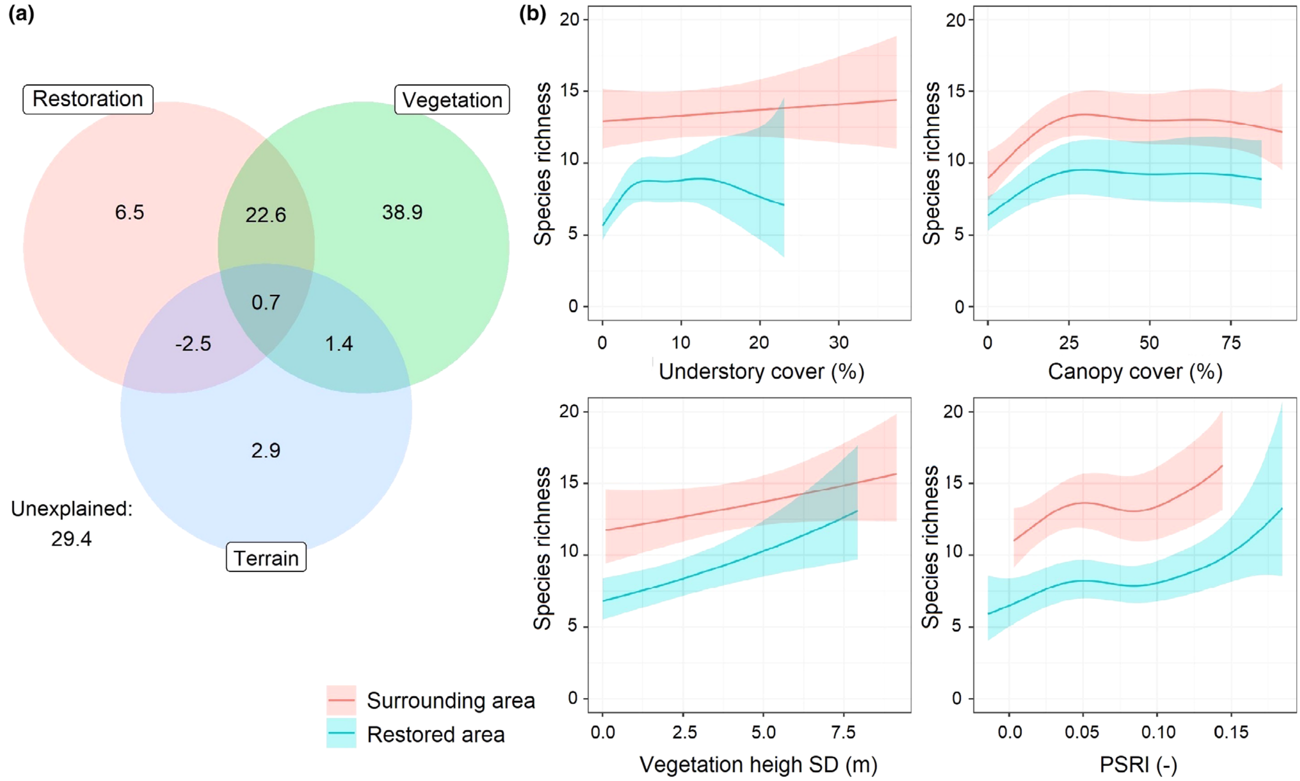

FIGURE 5 (a) Venn diagram showing the percentage of explained (and unexplained) deviance in bird species richness explained by the three groups of predictors: Vegetation characteristics (understorey cover, canopy cover, standard deviation of vegetation height, Plant Senescence Reflectance Index [PSRI]), restoration status (restored vs. surrounding area) and terrain characteristics (curvature, topographic wetness index). The overlap of the circles indicates fractions of the variation that cannot be unequivocally attributed to just one of the overlapping predictors. For example, when vegetation characteristics differ between restored and surrounding areas, a fraction of the explained deviance will be shared between them. Negative numbers can arise due to the spline optimisation algorithm during model fitting; these are, however, usually small and can be interpreted as zeroes. (b) Response curves derived from generalised additive models, showing the relationships between the overall bird species richness and the evaluated habitat heterogeneity variables (only significant variables presented) and the differences between restored and surrounding areas. The shaded areas represent the 95% confidence bands.

3.4 | Foraging guilds

GAM models explained 77%, 74% and 35% of the variability in the richness of canopy foragers, understory foragers, and ground foragers, respectively. The richness of canopy foragers increased with increasing canopy cover and the standard deviation of height returns. The richness of ground and understory foragers increased with canopy cover up to 20%–25% and then gradually decreased. Increasing the standard deviation of vegetation height and, to some degree, the understory cover positively affected understory foragers in the restored area but showed no effect in the surrounding area (Figure 7). Their richness also tended to decrease with terrain curvature but only in the restored area.

3.5 | Diet guilds

GAM models explained 15%, 63% and 46% of the variability in the richness of granivores, carnivores and omnivores, respectively. The observed patterns were relatively similar for both the restored and the surrounding area, except for a few exceptions mentioned below. The richness of carnivores increased with canopy cover, peaking at 25% in the restored areas and 50% in surrounding areas, respectively. PSRI also positively affected the richness. Decreasing curvature and increasing standard deviation of height returns positively affected the richness of carnivores in the restored area but showed no effect in the surrounding area (Figure 8). TWI was the only variable that significantly affected granivores, but its effect on their richness was negligible. The richness of omnivores increased with the increasing standard deviation of height returns, understory and canopy cover.

4 | DISCUSSION

In this study, we evaluated the effect of habitat heterogeneity derived from airborne lidar and hyperspectral data on the overall and guild-specific bird species richness, both within the area of a restored spoil heap and in its surrounding areas. Models of the overall and guild-specific bird species richness demonstrated a relatively good performance. The explained variability ranged from 15% to 77%, depending on the guild, and is slightly higher than that

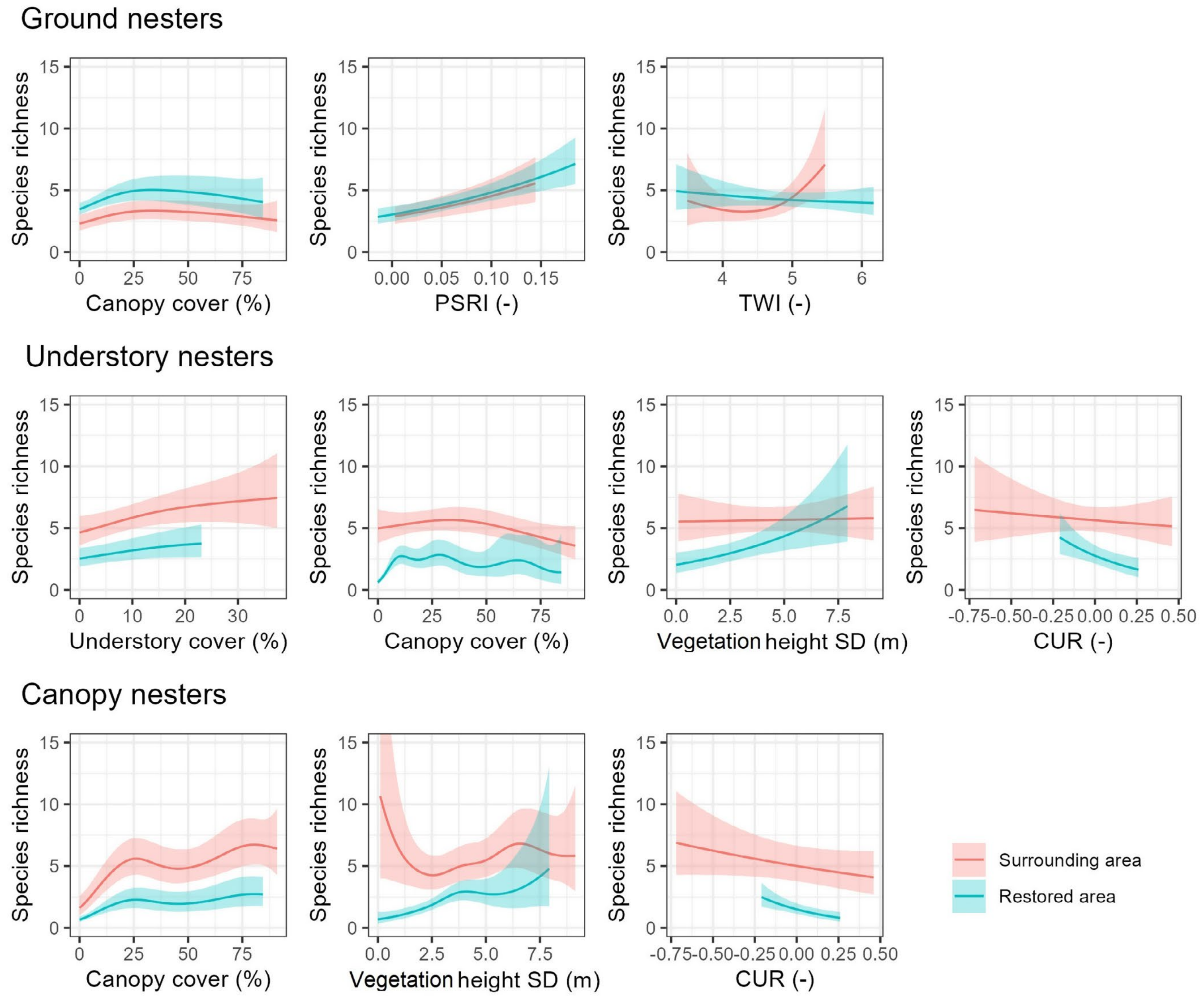

FIGURE 6 Response curves derived from generalised additive models, showing the relationship between the nesting guilds richness (ground, understory and canopy nesters) and the evaluated habitat heterogeneity variables (only the significant variables are shown) and the differences between restored and surrounding areas. CUR, curvature; PSRI, Plant Senescence Reflectance Index; SD, standard deviation; TWI, topographic wetness index.

reported by prior studies exploring the relationship between habitat heterogeneity (derived from lidar and passive remote sensing data) and various guild-specific bird species richness. For example, Goetz et al. (2007) and Jones et al. (2013) distinguished avian guilds according to habitat preferences, with their models explaining 30%–48% and 20%–65% of variability, respectively. Vogeler et al. (2014) focused on nesting guilds, and their models explained 5%–42% of the variability. Similarly, Lesak et al. (2011) categorised guilds based on nesting and foraging behaviours, with their models accounting for 15%–20% of the variation in guild richness. The higher explained variability in our study could be attributed to the inclusion of a wide range of environments, from early successional stages in restored areas to the mature forest in the surrounding areas, which led to greater variability in habitat characteristics and allowed the models to explain a greater portion of the variability in bird species richness. When considering the variability of vegetation structure solely within forest ecosystems, the explained variability is naturally lower (e.g. Lesak et al., 2011; Vogeler et al., 2014).

4.1 | Importance of individual variables

Our results show a significant effect of vegetation and terrain characteristics on the richness of individual guilds. Canopy and understory guilds were primarily influenced by vegetation structure, whereas ground nesters and diet guilds were also influenced by senescence and terrain characteristics. This is consistent with previous studies, which have shown that scrub and forest species are relatively easy to model using lidar-derived vegetation structure (e.g. Goetz et al., 2007). In contrast, ground-nesting and foraging species

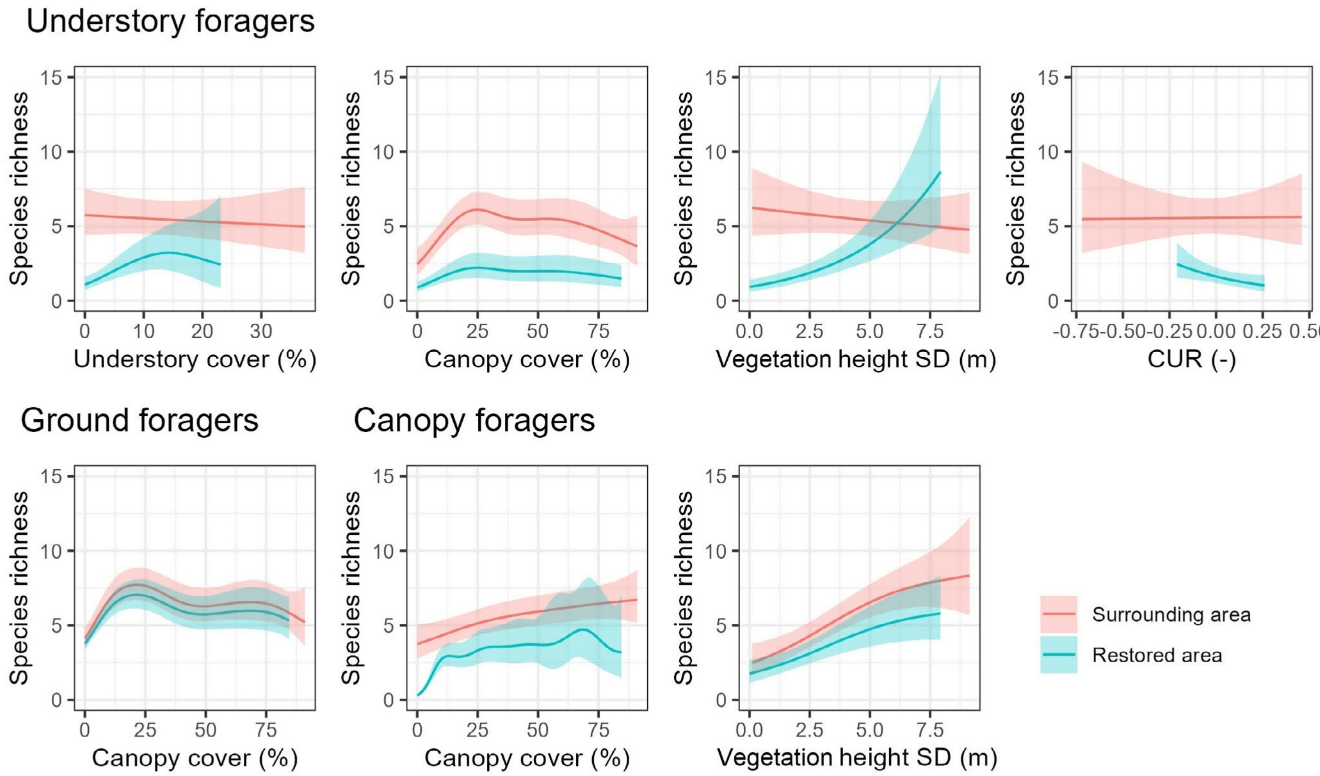

FIGURE 7 Response curves derived from generalised additive models, showing the relationship between the foraging guilds richness (ground, understory and canopy foragers) and the evaluated habitat heterogeneity variables (only significant variables presented) and the distinction between restored and surrounding areas. CUR, curvature; PSRI, Plant Senescence Reflectance Index; SD, standard deviation; TWI, topographic wetness index.

are typically less accurately predicted by vegetation structure alone (e.g. Lesak et al., 2011; Weisberg et al., 2014), with water content in surface vegetation (i.e. senescence) often serving as a more important explanatory factor for their richness (e.g. Cooper et al., 2020; Jones et al., 2013).

Indeed, PSRI (i.e. senescent vegetation) was a significant predictor of the richness of ground nesters and carnivores. Similarly, the TWI was important for granivores and ground nesters, particularly in the surrounding areas, where their richness increased with higher TWI. The importance of both TWI and PSRI might be explained by similar reasons. Areas with higher moisture and a greater density of senescent vegetation offer more food resources and nesting sites. Additionally, reduced predation risk could be another potential factor, although this was not confirmed (Novák & Hendrychová, 2021). Such conditions are typical of areas left to spontaneous succession (Figure 1c; see Figure 2 for high PSRI values on these sites), which are known to positively impact the diversity of multiple taxa (Řehounková et al., 2018; Šálek, 2012). See Figure S3 for the richness of ground nesters and carnivores in these areas.

4.2 | Restored versus surrounding area

The comparison between the restored and surrounding areas showed considerable differences in habitat heterogeneity (Figure 3). This explains why the variability explained by vegetation characteristics often overlaps with the variability explained by the predictor distinguishing restored areas from the surrounding ones (Figure 5a; Figure S4), indicating that these factors are interrelated. We visually assessed the response curves, and their shapes were relatively similar for individual guilds in both the restored and surrounding areas (Figures 6–8). This suggests that the adopted variables can be used as universal metrics suitable for habitat assessment in restored as well as surrounding landscapes. The standard deviation of vegetation height was the most striking exception, showing some differences in effects between the restored and surrounding areas. It is, therefore, important to use such habitat heterogeneity metrics with caution. Understory nesters and foragers were positively associated with the increasing standard deviation of vegetation height in the restored area, but no or only slightly negative effect was observed in the surrounding area. For example, Heidrich et al. (2023) also used the standard deviation of vegetation height as a measure of vertical heterogeneity and found an increase in bird diversity with increasing vertical heterogeneity. The contrasting results in our study are caused by the fact that relatively high values of the standard deviation of vegetation height can be associated with both low vegetation in the restored area and tall vegetation in the surrounding area (Figure 2). In surrounding areas, the combination of a high standard deviation in vegetation height and canopy cover creates conditions that are less suitable for understory foragers and nesters.

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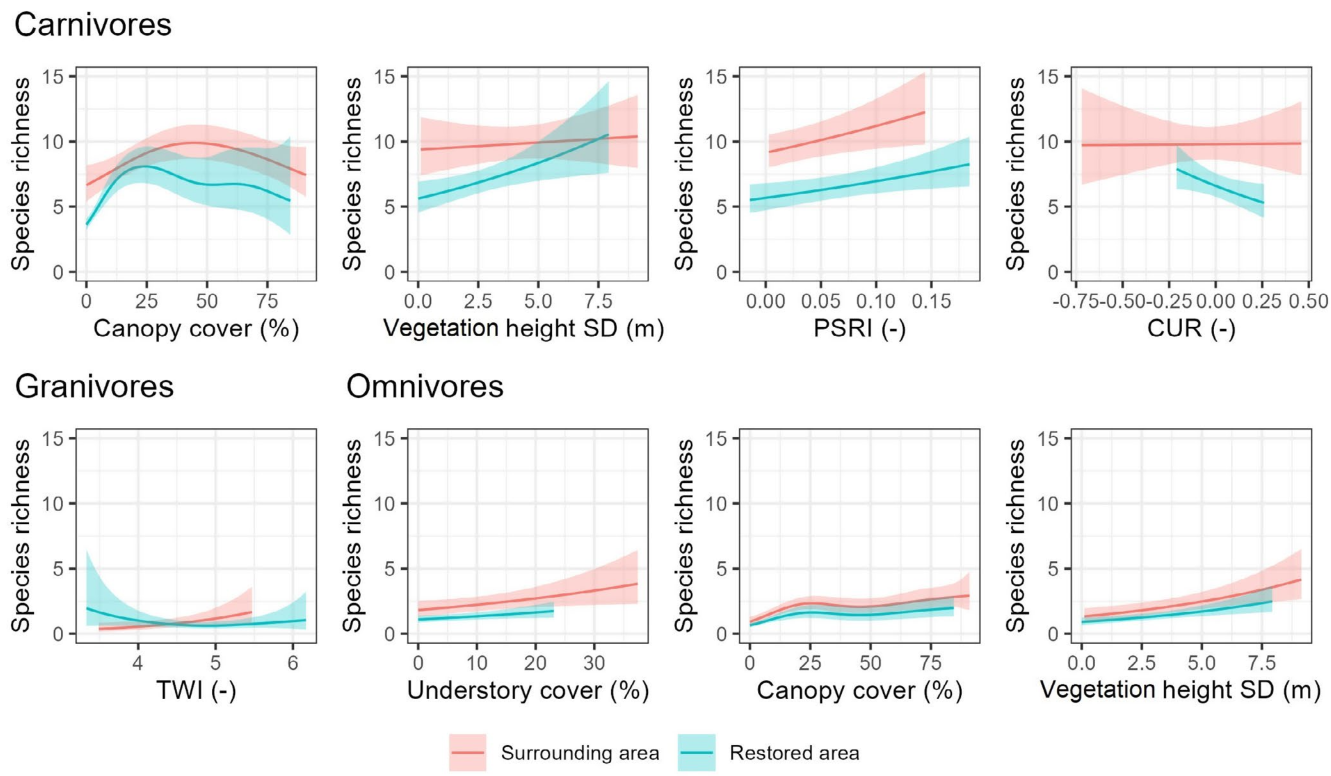

FIGURE 8 Response curves derived from generalised additive models, showing the relationship between the diet guilds richness (carnivores, granivores and omnivores) and the evaluated habitat heterogeneity variables (only the significant variables are shown) and the difference between restored and surrounding areas. CUR, curvature; PSRI, Plant Senescence Reflectance Index; SD, standard deviation; TWI, topographic wetness index.

4.3 | Implications and limitations for restoration planning and management

Understanding habitat characteristics that influence species distributions in restored/decommissioned mining areas, as well as monitoring these factors, is crucial to assuring long-term biodiversity benefits. In the EU, such monitoring capabilities will guide the development of national restoration plans, as expected within the scope of the Nature Restoration Law (European Union, 2024). In Czechia, in particular, the current phasing-out from coal-based energy production, which is to be completed by 2033, will further benefit from remote-sensing-based biodiversity monitoring capabilities such as those explored in our study.

Monitoring in restored ecosystems often requires a combination of in-situ field surveys focused on species richness and vegetation characteristics (see reviews by Martins et al., 2020; Wortley et al., 2013). However, vegetation characteristics alone, particularly vegetation structural diversity derived from remote sensing data, can be used as a rapid and effective measure for assessing the condition of restored sites and informing management practices (Gibbons & Freudenberger, 2006; LaRue et al., 2023). Our study demonstrates that habitat heterogeneity characteristics—such as terrain characteristics, vegetation structure and senescence—derived from remote sensing data offer useful variables that can be used for restoration success (sensu biodiversity support), assessment and planning. Compared to field surveys, hyperspectral and lidar data offer greater potential for delivering information that can be directly applied to management actions (Anderle et al., 2023; Cooper et al., 2020; Jones et al., 2013; Moudrý et al., 2021; Rigo et al., 2024). Although we focused our study on a single site, we used a standardised, data-driven workflow that can be extended to monitor restoration beyond the mining regions (e.g. Anderle et al., 2022; Latif et al., 2020).

With the continuous increase in remote sensing data availability, its application in restoration ecology is highly promising, particularly for assessing vegetation characteristics (Martins et al., 2020; Moudrý, Gdulová, et al., 2019; Szostak et al., 2020). However, it should be noted that although data availability has been steadily increasing due to national and regional scanning initiatives (see Moudrý et al., 2023 for a list of countries with accessible lidar data in Europe), the acquisitions for the same area (e.g. a state) are often limited by high acquisition costs and long repetition intervals (see Moudrý et al., 2025 for a list of European countries with multiple lidar acquisitions). In areas where multiple acquisitions exist, assessment of the temporal development of vegetation structure and associated species assemblages is possible (Korejs et al., 2023). Typically, however, studies like the presented one are conducted under suboptimal conditions, often with a time lag between field surveys and remote sensing data acquisition. For example, this gap was 6 years in Goetz et al. (2007) or 10 years in the studies by Huber et al. (2016) and Wallis et al. (2016). On the other hand, gaps of a few years do not lead to significant errors, as vegetation structure changes relatively slowly (Hill & Hinsley, 2015; Vierling et al., 2014), and it is therefore recommended to use ALS data rather than predicted vegetation structure metrics whenever possible (Moudrý et al., 2024, 2025).

5 | CONCLUSIONS

Spoil heaps represent valuable early successional habitats that are otherwise disappearing from the human-managed landscape. We demonstrated how vegetation and terrain characteristics of such restored sites and their surroundings influence bird species richness. Additionally, we showed how remote-sensing-based continuous variables on habitat heterogeneity can be used for extensive monitoring of mining regions in transition, enabling managers to assess habitat characteristics within a broader landscape. Our findings highlight the importance of creating a diverse mosaic of habitats with complex vertical structures, and emphasise the vital role of senescent vegetation and natural terrain characteristics in enhancing biodiversity conservation on restored sites and their surroundings.

AUTHOR CONTRIBUTIONS

Lucie Moudrá, Miroslav Šálek and Vítězslav Moudrý conceived the ideas; Vojtěch Barták and Vítězslav Moudrý designed the methodology; Vladimír Bejček, Karel Šťastný, Ondřej Volf, Petr Musil, and Miroslav Šálek collected the data; Vojtěch Barták and Lucie Moudrá analysed the data; Lucie Moudrá and Vítězslav Moudrý led the writing of the manuscript. Lucie Moudrá, Vojtěch Barták, Vítězslav Moudrý, Ruben Remelgado, Stephanie Roilo, Duccio Rocchini, Vladimír Bejček, Karel Šťastný, Ondřej Volf, Petr Musil and Miroslav Šálek contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare that there are no conflicts of interest regarding the publication of this manuscript.

DATA AVAILABILITY STATEMENT

The dataset used in this study is available at https://doi.org/10.6084/m9.figshare.27161958 (Moudrá et al., 2025), and the code for the analysis can be accessed at https://doi.org/10.6084/m9.figshare.27161994 (Barták, 2025).

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SUPPORTING INFORMATION

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

Figure S1. Species accumulation curve based on 1000 randomization of the sites order.

Figure S2. Correlograms for species richness of each species group as well as for residuals from a corresponding generalized additive model.

Figure S3. Species richness per guild.

Figure S4. Venn diagrams showing the percentage of explained (and unexplained) deviance in the richness of (a) nesting, (b) foraging and (c) diet guilds, as explained by the three groups of predictors: vegetation characteristics (understorey cover, canopy cover, standard deviation of vegetation height, PSRI), reclamation status (restored vs. surrounding area) and terrain characteristics (curvature, topographic wetness index).

Table S1. Table of coefficients of the parametric terms of the GAM models. Individual models are in columns.

Table S2. Significance of smooth terms of the GAM models.

Appendix S1. List of observed species and their attribution to individual guilds.

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