Landscape and Urban Planning 210 (2021) 104064

Contents lists available at ScienceDirect

Landscape and Urban Planning

journal homepage: www.elsevier.com/locate/landurbplan

Research Paper

The role of the vegetation structure, primary productivity and senescence derived from airborne LiDAR and hyperspectral data for birds diversity and rarity on a restored site

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HIGHLIGHTS

- We tested the role of vegetation structure, NDVI and PSRI for bird diversity.
- Shrub cover and tree cover had strong positive effects on bird richness.
- The PSRI, shrub cover and herbaceous cover had positive effects on bird rarity.
- Heterogeneous vertical vegetation structure promotes bird richness and rarity.
- Combining forests with spontaneous succession will balance richness and rarity.

ARTICLE INFO

Keywords:
Mining
NDVI
PSRI
Senescence
Spoil heap
Vegetation structure

ABSTRACT

Management of restored areas requires ecologically meaningful spatial data providing objective measures of restoration success. Understanding relationships between species diversity on the one hand and habitat heterogeneity and productivity on the other can help establish such measures and prioritize restoration management. We used airborne LiDAR and hyperspectral data to derive characteristics of vegetation structure, primary productivity and senescent vegetation (i.e. old dead vegetation) for prediction of richness and rarity of bird communities colonizing newly available habitats restored after coal mining. In addition, we analysed, which type of restoration (i.e. agricultural, forest, or spontaneous succession) results in more favourable conditions. The boosted regression trees explained 52% and 12% of deviance of overall species richness and rarity, respectively. We found that the overall species richness was strongly affected by the variance in vegetation structure, while the rarity was also affected by the presence of senescent vegetation. The relative importance of variables differed between the richness and rarity. The shrub cover had a strong positive effect on both, while the tree cover had a strong positive effect on species richness. The herbaceous cover and presence of senescent vegetation had positive effects on species rarity. This study, therefore, supports the necessity to create a mosaic of habitats with heterogeneous vertical structure including all layers of vegetation and highlights the importance of senescent vegetation. Combination of forests restoration with sites left to spontaneous succession appears to be the best strategy to increase both bird species richness and rarity in newly restored sites after coal mining.

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https://doi.org/10.1016/j.landurbplan.2021.104064
Received 3 June 2020; Received in revised form 25 January 2021; Accepted 30 January 2021
Available online 25 February 2021

1. Introduction

The mining of various raw materials has expanded globally in the last few decades with the growing demands for various commodities and their increasing consumption (Kung et al., 2020; Lèbre et al., 2020). On the one side, economic benefits and wealth generated by the resource industry are substantial (Svobodova, Owen, Harris, & Worden, 2020); on the other side, areas under mining lease are subject to significant landscape changes (Worlanyo & Jiangfeng, 2020). The changes are often associated with negative environmental impacts, including irreversible land degradation and biodiversity loss (Giam, Olden, & Simberloff, 2018; Osenberg, 2018). However, under certain circumstances, mining and related activities can bring about also positive changes enhancing conservation value of the landscape (Šálek, Hendrychová, & Řehoř, 2010; Schulz & Wiegleb, 2000; Vanhée & Devigne, 2018).

Minimization of the negative effects of mining is typically ensured by ecological restoration, i.e. a process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed (Clewell & Aronson, 2013; Martins et al., 2020). Monitoring of restored sites is required to gather ecologically meaningful data that can provide objective and quantitative measures of the restoration success. In practice, among other ecological measures, species diversity of various taxa is frequently used and many studies evaluated the effect of habitat heterogeneity on the diversity of species on restored sites (Crouzeilles, Ferreira, Chazdon, Lindenmayer, Sansevero, Monteiro, & Strassburg, 2017; Martins et al., 2020). To model relationships between the species diversity and the heterogeneity of restored sites, however, the environment is usually represented by semiquantitative or categorical measures only (e.g. by rough subjective estimates of vegetation cover). Moreover, even these measures are usually spatially and temporarily limited as field surveys traditionally used by ecologists are extremely labour-intensive, especially over larger areas (Bejček, 1988; Gould & Mackey, 2015; Hagger, Wilson, England, & Dwyer, 2019; Kolář, Tichanek, & Tropek, 2017; Vojar et al., 2016). Although a direct field survey of habitat attributes can provide valuable information, it is unsuitable for repeated monitoring due to both labour intensiveness and limited informative value of subjective estimates, especially where detailed habitat characteristics are concerned.

In this study, we aim to identify measures that can be easily derived from airborne remote sensing data and used as a more elegant and more precisely measurable alternative to simple and subjective field surveys. Airborne remote sensing data are increasingly available from national or regional scanning campagins (Melin, Shapiro, & Glover-Kapfer, 2017; Stereńczak et al., 2020). Such technologies represent efficient and cost-effective sources for developing indicators relevant to the large-scale decision making, to the understanding of continuous processes of site restoration, and developing effective management tools that will maintain high biodiversity of restored sites (e.g., Cordell et al., 2017; Laurin et al., 2020; Prošek et al., 2020; Urban, Štroner, Křemen, Braun, & Möeser, 2018). In addition, conservation strategies for post-industrial sites are highly debated in connection with restoration approaches (Hendrychová, Svobodova, & Kabrna, 2020), including the adopted restoration method (Tropek et al., 2010; Vicentini, Hendrychova, Tajovský, Pižl, & Frouz, 2020; Vymazal & Sklenicka, 2012). Therefore, we relate evaluated indicators to the individual restoration methods and provide recommendations for restoration practice.

In the next chapter, the theoretical background of the research and ecological explanation for the selection of environmental variables derived from airborne remote sensing data will be discussed and the aims of this study will be clearly expressed. Chapter 3 introduces the study area, the data and its preprocessing, the environmental variables and statistical analyses including models evaluation. Chapters 4 and 5 then present the obtained results followed by their discussion with respect to restoration goals and informing on possible limitations. Finally, the Chapter 6 contains conclusions and recommendations for resoration practice.

2. State of the art

Birds with their high dispersal ability play an important role in the early colonization of restored sites and therefore comprise one of the best indicators for the assessment of the restoration success (Bejček & Šťastný, 1984; Cardoso da Silva & Vickery, 2002; Martins et al., 2020). One of the important factors affecting bird species richness is the habitat heterogeneity. Habitat heterogeneity is determined by the variability of environmental conditions (e.g. habitat type, dominant vegetation species, soil types, topography) and it is assumed that more complex environments may provide more niches and thus increase species diversity (so-called habitat heterogeneity hypothesis; see review by Tews et al., 2004).

A common approach of indicating heterogeneity of the habitat is to use the variability in its physical structure (physiognomy) (Davies & Asner, 2014). Physiognomy of the habitat is generally determined by plants and the debate whether bird species diversity is more affected by vegetation structure or by plant composition is still ongoing (Adams & Matthews, 2019; MacArthur & MacArthur, 1961; Müller, Stadler, & Brandl, 2010). Although some studies have shown the importance of plant composition and it is clear that it should not be ignored (Adams & Matthews, 2019), the vegetation structure has been traditionally considered the primary driver of bird diversity (Müller et al., 2010). This may be partly due to intensive research addressing relationships between bird richness and vegetation structure, which has been triggered by advances in the measurement of the vegetation structure by airborne LiDAR (see reviews by Davies & Asner, 2014; Bakx, Koma, Seijmonsbergen, & Kissling, 2019).

Soon after the first studies showed the potential of LiDAR-derived vegetation structure for explaining species-environment associations, attempts begun to integrate LiDAR with variables derived using other complementary remote sensing data (e.g. multispectral or hyperspectral) assessing their relative importance and complementarity (Bae et al., 2018; Cooper, McShea, Forrester, & Luther, 2020; Goetz, Steinberg, Dubayah, & Blair, 2007; Vogeler et al., 2014). Such variables include, for example, the normalized difference vegetation index (NDVI; Tucker, 1979). The use of NDVI to model bird species richness is based on species-energy theory. According to that theory, species richness is limited by the quantity of available energy (Brown, 1981; Wright, 1983) and energy available to consumers is dependent on primary productivity (Evans, Warren, & Gaston, 2005). It is assumed that greater primary productivity of plants (i.e. biomass) supports higher animal species richness and NDVI is commonly used as a measure of vegetation productivity (Bailey et al., 2004; Hobi et al., 2017; Leyequien et al., 2007; Youngentob, Yoon, Stein, Lindenmayer, & Held, 2015).

On the other hand, however, many species including birds are specialists and/or poor competitors, preferring specific habitats with relatively lower habitat heterogeneity or low primary productivity (Reif, Hořák, Krištín, Kopsová, & Devictor, 2016). The occurrence of these species can be associated with early stages of spontaneous succession, which are rare in the cultural landscape but relatively common on restored sites (Šálek, 2012). These early successional habitats can, therefore, represent valuable refuges for rare and unique bird specialists and/or poor competitors.

For the early successional habitats in areas after coal mining, growths with old dead vegetation from previous vegetation season are typical (Hendrychová et al., 2020). This is particularly true for aquatic vegetation in areas left to spontaneous succession (e.g. *Phragmites australis* and *Typha latifolia*) but a similar representation of such old (dead) vegetation can be also observed in low steppe vegetation in agriculturally restored areas (e.g. *Calamagrostis epigejos* and *Arrhenatherum elatius*). For birds, the dead vegetation provides shelter, nesting, and foraging opportunities at the time when green vegetation is at minimal heights. It is, therefore, an important component of habitat heterogeneity not only in the autumn and winter but possibly even more so in the spring. The amount of old dead vegetation (i.e. senescent vegetation) can be estimated using the plant senescing reflectance index (PSRI), which was developed as a quantitative measure of leaf senescence (Merzlyak, Gitelson, Chivkunova, & Rakitin, 1999) and used as a potential predictor of species occurrence in studies published previously (e.g. Soto, Pérez-Hernández, Hahn, Rodewald, & Vergara, 2017).

Determining the attributes of the habitat heterogeneity and primary productivity of restored sites and their association with species diversity and/or rarity can help to identify ecologically valuable areas on large landscape scales. Therefore, in this study, we examined how the vegetation structure, primary productivity (i.e. NDVI) and old senescent vegetation from the previous season (i.e. PSRI) derived from airborne laser scanning and hyperspectral data predict species richness and rarity of bird communities colonizing newly available (restored) habitats after coal mining. Specifically, we focused on the following questions: (i) Is there a detectable relationship between the fine-scale habitat attributes of early succession stages obtained by airborne remote sensing and the occurrence of birds? (ii) Which is of greater importance for the occurrence of birds – the primary productivity, presence of old vegetation, or vegetation structure? And (iii) which type of restoration (i.e. agricultural, forest, or spontaneous succession) results in the development of more favourable habitats for bird species richness and rarity?

3. Data and methods

3.1. Study area, type of reclamation and habitats

The study was carried out on the Radovesická spoil heap (Fig. 1) located in the North Bohemian Brown Coal Basin, Czechia, one of the largest active brown coal mining regions in Europe. The study area was subject to various methods of restoration (i.e. agricultural, forestry, and spontaneous succession; Fig. 2). Agricultural reclamations typically include the establishment of permanent grasslands with initial sowing of a species-poor grasses mixture (*Festuca, Dactylis, Phleum, Poa, Cynosurus, Agrostis*) mixed with about 10% of legumes (*Trifolium, Coronilla, Lotus, Medicago*). Such areas are mowed twice a year even after the reclamation is completed. Afforestation includes predominantly homogenous plantations of even-aged stand combining autochtonous and allochthonous trees (*Acer, Pupulus, Quercus, Fraxinus, Tilia, Carpinus, Larix*) supplemented with shrubs (*Eonymus, Padus, Lingustrum, Cornus, Symphoricarpos, Spiraea, Lonicera, Viburnum*). Successional sites in our study area are characterized by structurally diversified bare ground with sparse annuals and biennials, followed by perennials (*Tanacetum, Artemisia, Cirsium*) and grasses (especially *Calamagrostis epigejos* and *Arrhenatherum elatius*) with scattered authochtonous shrubs (*Sambucus, Rosa, Betula, Crataegus*). The tree growths on the successional sites are dominated by birch (*Betula pendula*), mixed with other deciduous trees (*Salix, Populus*). See Fig. S1 in the Supplementary material for examples of vegetation structure.

3.2. Bird survey, richness and rarity calculation

Bird data were collected in 2012 by five experienced ornithologists (co-authors of this study). Each of the 153 survey points was visited twice during the season (5–6 and 28–29 May) to increase the likelihood of detecting the earlier and later breeding species. The survey points form a grid spaced at 300 m intervals. At each survey point, all bird individuals identified by sight or sound within a 100 m distance from the survey point were recorded. The results from both visits were pooled together and the bird diversity (species richness) for each survey point was calculated as the number of species detected on the survey point. In

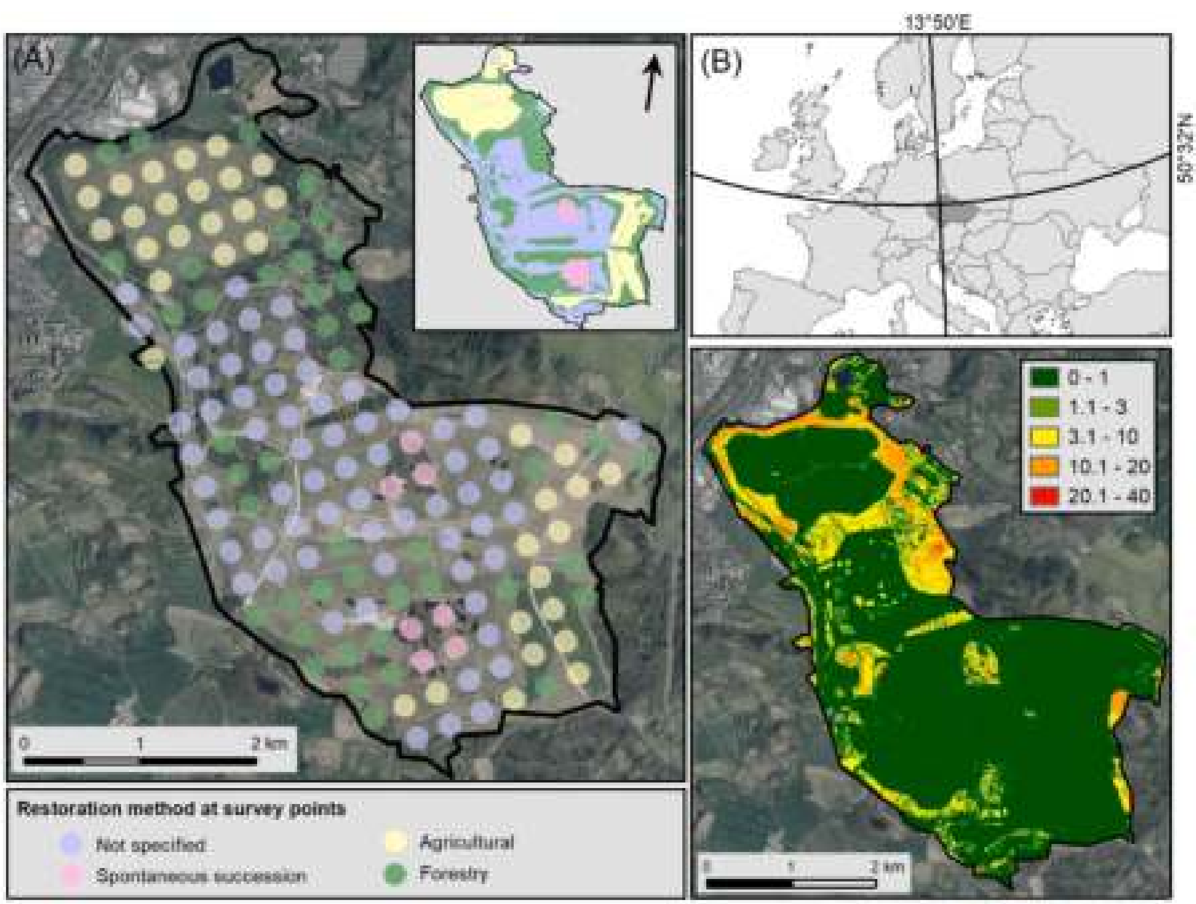

Fig. 1. Study area; (A) Location of survey points and adopted restoration method (forestry, agriculture, and naturally regenerating systems called “spontaneous succession”). The survey points represent a 100 m buffer; (B) Location of the study area in the Czech Republic; (C) Canopy height model (meters).

Fig. 2. Aerial photos of the study area. The two photos in the top row were taken on the 10th of May 2020 and show the two areas left to spontaneous succession surrounded mostly by agriculturally restored areas. The three bottom images were taken on 25th of April 2020 and show the areas after agricultural restoration (left), forest restoration (middle), and the area left to spontaneous succession (right). Note the presence of old dead vegetation even at this time of the year, particularly in areas left to spontaneous succession, near water bodies and other terrain depressions.

addition, we calculated an index of species rarity for each survey point reflecting the scarcity of species throughout the Czech Republic based on the large-scale quadrat mapping of birds (Šťastný, Bejček, & Hudec, 2006). For each species, the rarity index was calculated using the formula 1-*N*/628 where *N* represents the number of quadrats occupied by the species from 628 in total (Šálek, 2012; Table S2 in Supplementary material). The overall rarity for each survey point was then calculated as the sum of index values for all species recorded at a point. Individuals recorded while flying over the site or beyond the defined distance were excluded from the analysis.

3.3. Airborne data collection and pre-processing

The airborne LiDAR and hyperspectral data were acquired simultaneously on 18th May 2017 using a remote sensing platform FLIS (The Flying Laboratory of Imaging Spectroscopy; Hanuš, Fabiánek, & Fajmon, 2016). Flights for data collection were conducted at 1030 m above ground at 110 knots (ground speed). Data from the hyperspectral (Visible Near Infrared, VNIR, CASI-1500), and LiDAR sensor (Riegl LMS Q-780) were used in this study. Although there was a time lag between the field survey and LiDAR and hyperspectral data campaign, we assume that data were still useful for describing birds' habitats in terms of vegetation structure, vegetation productivity and presence of old dead vegetation as it has not changed substantially over the five years (but see more on this topic in Discussion).

3.3.1. Hyperspectral data

The hyperspectral imagery consisted of 48 bands covering the visible near-infrared range from 380 to 1050 nm (CASI-1500) with a bandwidth of 7.2 nm. Pre-processing of the hyperspectral images (i.e., radiometric correction, georeferencing and atmospheric corrections) were all carried out by the provider (CzechGlobe). Radiometric corrections were performed in the RadCorr software by converting spectral radiances to physical radiance units based on calibration parameters from the CzechGlobe spectroscopic laboratory (Hanuš et al., 2016). Radiance images were geometrically corrected, orthorectified using a digital terrain model (DTM), and georeferenced to the local Datum of Uniform Trigonometric Cadastral Network (EPSG: 5514). Data were corrected for atmospheric conditions using a radiative model MODTRAN and the BREFCOR method was used for correcting the bidirectional reflectance distribution function (BRDF) effect (ATCOR-4 software; Richter & Schläpfer, 2016).

3.3.2. LiDAR data

Airborne LiDAR data were acquired with a Riegl LMS Q-780 laser scanner. The scanner has a rotating polygon mirror and scans in parallel lines. The scan field of view is 60° and the wavelength is 1064 nm. The LiDAR data were provided in LAZ format with an average point density of 8 points per square meter. The LiDAR point cloud was processed using a proprietary software by the Global Change Research Institute CAS and referenced to the local Datum of Uniform Trigonometric Cadastral Network (EPSG: 5514) and Baltic Vertical Datum – After Adjustment (EPSG: 5705). We further processed the point cloud using LAStools (http://lastools.org) and classified the point cloud into ground and vegetation classes (Klápště et al., 2020; Moudrý et al., 2020). We divided the study area into 36 tiles and classified each tile separately to allow different settings and thus a better identification of ground and vegetation returns. In addition, we identified noise returns (e.g. returns from birds) and within the distance of 100 m from the grid survey points, we manually checked and edited point clouds for obvious errors (e.g. high voltage poles classified as vegetation). Returns other than vegetation and ground were removed from subsequent analyses. Prior to the calculation of vegetation structure variables, we height-normalized the LiDAR point cloud (i.e. the returns' height above the DTM was calculated).

3.4. Primary productivity and habitat heterogeneity variables

To investigate the importance of primary productivity and habitat heterogeneity, we derived two vegetation indices from the hyperspectral data and six variables from the LiDAR data; all these indices and variables bear a potential relevance to the bird diversity (Table 1). The two

Table 1
Overview of 8 potential explanatory variables derived from LiDAR and hyperspectral data within a 100 m vicinity of survey points. Rx denotes the reflectance at the wavelength of x nm. We excluded areas of water bodies from calculations of NDVI and PSRI. Variables in bold were used in our final models (i.e. after excluding collinear variables).

Hyperspectral and LiDAR derived metrics	Description	Category according to Bakx et al. (2020)
Primary productivity		
Normalized Difference Vegetation Index (NDVI)	$(R_{862} - R_{662})/(R_{862} - R_{662})$; sensitive to vegetation greenness	–
Old dead vegetation from the previous vegetation season		
Plant senescing reflectance index (PSRI)	$(R_{678} - R_{500})/R_{750}$; sensitive to senescent vegetation	–
Vegetation structure (Total vegetation)		
Mean height	Average height of vegetation returns	Total vegetation - Height
Standard deviation of height	Standard deviation of vegetation returns heights above 1 m	Total vegetation - Vertical variability
Canopy cover	Number of first returns above 1 m divided by the sum of all first returns	Total vegetation - Cover
Vegetation structure (Single layers)		
Cover of the herbaceous layer	Number of points between 0.1 m and 1 m divided by the total number of points	Single layer (Understorey) - Cover
Cover of the shrub layer	Number of points between 1 m and 3 m divided by the total number of points	Single layer (Understorey) - Cover
Cover of the tree layer	Number of points > 3 m divided by the total number of points	Single layer (Canopy) - Cover

calculated vegetation indices included 1) NDVI $(R_{862} - R_{662})/(R_{862} - R_{662})$, which corresponds to plant chlorophyll content and hence increases with vegetation productivity (i.e. the green component of biomass), and 2) PSRI $(R_{678} - R_{500})/R_{750}$, which is a measure of the leaf senescence and is sensitive to the carotenoid/chlorophyll ratio. PSRI is in this study used as an estimate of the amount of old dead (senescent) vegetation from the previous vegetation season, which is present in the study area even in May when both bird and airborne data were collected (see Fig. 2). The old dead vegetation from the previous season is mainly present in the aquatic vegetation (e.g. *Phragmites australis* and *Typha latifolia*) and, to a somewhat lesser extent, in low steppe vegetation (e.g. *Calamagrostis epigejos* and *Arrhenatherum elatius*).

In order to assess the effect of habitat heterogeneity on bird species richness and rarity, we described habitat heterogeneity using the variance in vegetation structure. We used vegetation structure variables adopted in the previous bird diversity studies (see Bakx et al., 2018 for the conceptual categorization of LiDAR-derived vegetation metrics). To describe the total vegetation (*sensu* Bakx et al., 2018) we used the mean, standard deviation of vegetation returns, and canopy cover (Table 1). We calculated these metrics to describe the structural variability of the vegetation directly from the point cloud (e.g. Bae et al., 2018); but note that some other studies calculated these metrics from the rasterized canopy height model (CHM) to describe a horizontal variation in the canopy cover (e.g. Müller, Moning, Baessler, Heurich, & Brandl, 2009; 2010). In addition, we used variables characterising the individual vegetation layers (single layer *sensu* Bakx et al., 2018). Three layers of vegetation are typically recognized; the herbaceous layer, the shrub layer, and the tree layer (e.g. Lesak et al., 2011; Jones, Arcese, Sharma, & Coops, 2013). The same vegetation layers are typically assessed during field inspections on postmining sites (e.g. Šálek, 2012). Therefore, we calculated the cover for three vegetation layers: first, we counted the number of points between 0.1 m and 1 m and divided this number by the sum of all points to estimate the cover of the herbaceous layer. Second, we counted the number of points between 1 m and 3 m and divided the result by the sum of all points to estimate the cover of the shrub layer. In the same way, the number of points between 3 m and 40 m was divided by the sum of all points to estimate the cover of the tree layer (in our study area, there are no trees higher than 40 m). It should be noted that the heights of these vegetation layers are selected arbitrarily based on our field experience (e.g. Šálek, 2012) and can thus greatly vary among different areas (e.g. Lesak et al., 2011). All primary productivity and habitat heterogeneity metrics were calculated within a 100 m radius of grid survey points using ENVI (version 5.5) and LAStools (version 200112), respectively.

3.5. Statistical analyses

We used boosted regression trees (BRT) implemented in the R package gbm version 2.1.5 (Greenwell, Boehmke, Cunningham, Developers, & Greenwell, 2019) and some additional features available in the package dismo version 1.1–4 (Hijmans, Phillips, Leathwick, Elith, & Hijmans, 2017) to assess how primary productivity and habitat heterogeneity were associated with species richness and rarity. First, we examined the collinearity among all variables to reduce the number of input variables (Fig. S3 in Supplementary material). Canopy cover and mean height were highly correlated with vertical vegetation structure metrics. As it has been highlighted that birds show a higher preference for the structural variability of the vegetation than for canopy cover (Davies & Asner, 2014) and as the vertical vegetation variability was of our primary concern, we retained the three vertical layers (i.e. herbaceous, shrub and tree cover) and excluded the canopy cover and mean vegetation height from further analyses. Another highly correlated pair of variables were NDVI and PSRI; however, as they represent unique components of the aboveground biomass and were essential for our study, we decided to retain both variables in the model. However, to evaluate whether retaining both NDVI and PSRI affected our results, we ran the models also individually with PSRI and NDVI, respectively (see the Supplementary material, Figs. S5–S8). Therefore, our final set of variables consisted of four variables representing the habitat heterogeneity and two variables representing the primary productivity (Table 1).

Two most important parameters that need to be specified for BRT are the tree complexity (which controls whether interactions are fitted) and learning rate (shrinkage) as they determine the number of trees required for the prediction. As a rule of thumb, a combination of tree complexity and learning rate that results in a model with at least 1000 trees is recommended. For models with less than 500 records, it is preferred to model simple trees (i.e. tree complexity 1–3) with a small learning rate to allow the model to grow enough trees. We fine-tuned the settings in preliminary testing and used models with tree complexity (the number of splits in a tree) of 1 (i.e. without interaction terms, as allowing interactions did not lead to a model improvement), shrinkage (learning rate) of 0.001, bag fraction (the proportion of data used when selecting optimal tree number) of 0.5, and the maximum number of trees of 5000. To estimate the optimal number of trees, we used 10-fold cross-validation. At each iteration, the residual deviance was calculated and the number of trees giving the best model (i.e. lowest deviance) was identified (Elith, Leathwick, & Hastie, 2008; Hastie, Tibshirani, & Friedman, 2001; Leathwick, Elith, Francis, Hastie, & Taylor, 2006). Species richness and rarity were modelled specifying the Poisson and Gaussian error distribution, respectively. All models were fitted in R, version 3.6.0 (R Development Core Team, 2019)

3.6. Assessment of model performance

The identified best models were fitted to the entire dataset and used to produce partial dependency plots that show the effect of each variable after accounting for the average effects of all other variables (De'Ath, 2007; Elith et al., 2008). In addition, we assessed the relative importance of each variable (i.e. the contribution of each variable to the model fit scaled so that the sum adds to 100) using formulae developed by Friedman (2001) and implemented in the gbm package (Greenwell et al., 2019). The overall performance of BRT models was evaluated using the total deviance explained, which was calculated by dividing the difference between the mean total deviance and the estimated 10-fold cross-validated residual deviance by the mean total deviance. The cross-validated residual deviance is a measure of the deviance left unexplained by the model. Because results from the k-fold cross-validation can vary depending on the random selection of points for the folds, this

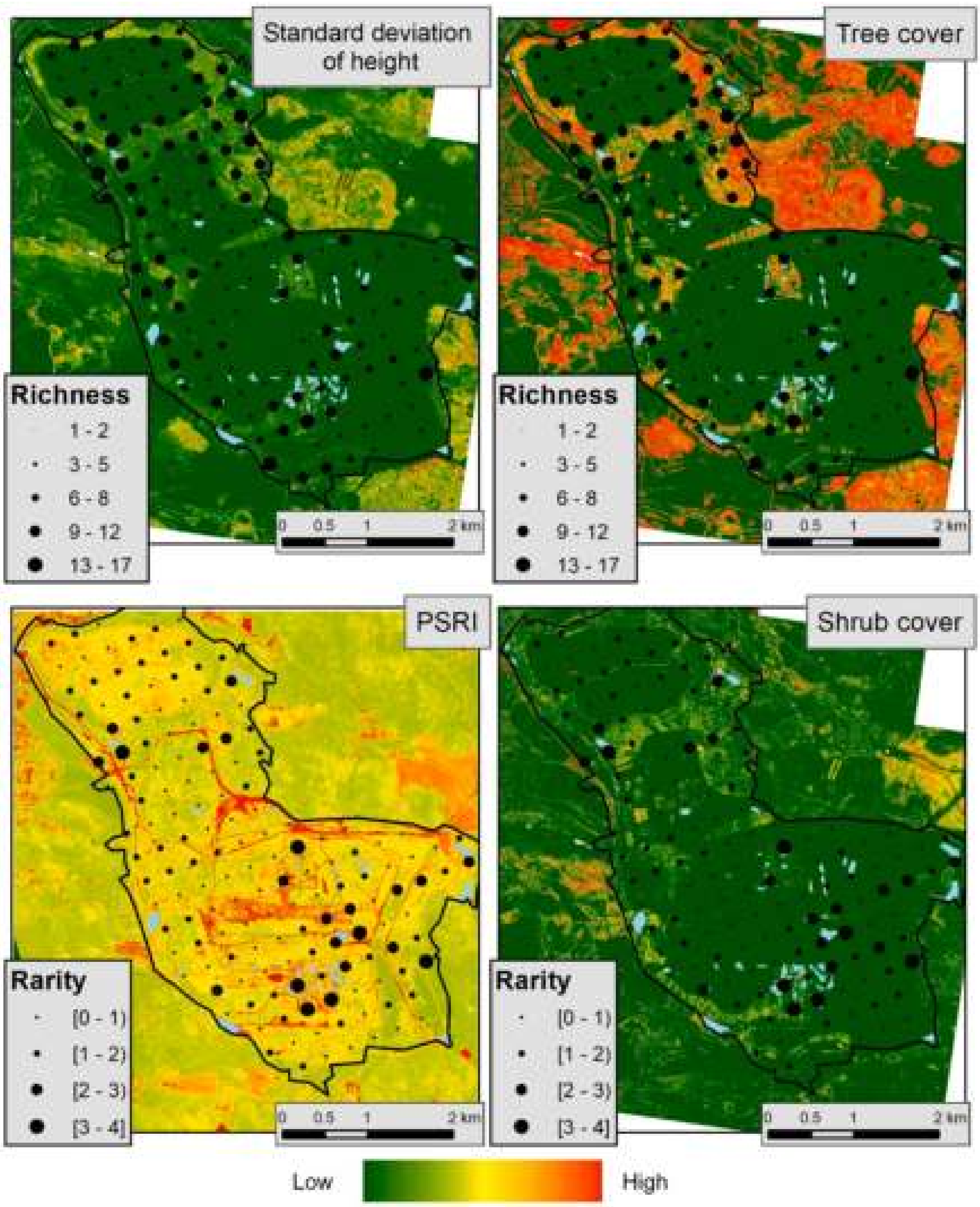

Fig. 3. Spatial distribution of species richness (upper images) and rarity (lower images) along with the four most influential explanatory variables (Standard deviation of height, Tree cover, PSRI, and Shrub cover).

procedure was repeated 5 times for each model, and overall means were calculated for the relative importance of each variable and total deviance explained by the models (Leathwick et al., 2006).

4. Results

4.1. Bird richness

We observed 83 bird species from a total of 1340 individual bird records. The overall bird species richness ranged from 1 to 17 species per survey point with a median of 6 species (Fig. 3). The BRT model of overall species richness explained 52% of deviance. The overall species richness was strongly affected by the habitat heterogeneity while primary productivity had only a minimal effect (Table S4 in Supplementary material). The effects of the midstory density and canopy density were the strongest and jointly accounted for most of the explained variability. The standard deviation of height had a moderate effect, and the effects of herbaceous cover, NDVI and PSRI were weak (Fig. 4). The partial dependency plots of the individual variables showed a rapid increase of species richness at relatively low values of the shrub cover and tree cover with only a minimal change as these variables continued to increase. The ranges of the shrub cover and herbaceous cover associated with the steepest increase in the bird richness were 0–5% and 0–20%, respectively. The standard deviation of height had a positive effect with an increase in overall richness for values between 2 m and 3 m and no effect above that value (Fig. 4).

4.2. Bird rarity

The bird rarity index ranged from 0.04 to 3.81 per survey point with a median rarity of 1 (Fig. 3). The BRT model of bird rarity explained 12% of deviance and the rarity was strongly affected by both habitat heterogeneity and primary productivity (Table S4 in Supplementary material). The shrub cover, herbaceous cover and PSRI had the strongest effects and jointly accounted for most of the explained variability. The effects of the standard deviation of height and NDVI were moderate, and the canopy density had a weak effect (Fig. 5). The partial dependency plots of the single variables showed a rapid increase in rarity for PSRI values above 0.10. A rapid increase in rarity was also shown at relatively low values of shrub cover and herbaceous cover with a minimal change as these variables continued to increase. The ranges of the shrub cover and herbaceous cover associated with the steepest increase of the bird rarity were 0–5% and 10–15%, respectively (Fig. 5).

4.3. Heterogeneity and productivity with respect to the restoration technique

Our results show a clear effect of the adopted restoration technique on habitat heterogeneity and primary productivity (Fig. 6). Most importantly, the spontaneous succession considerably differs from other sites when looking at primary productivity. The values of NDVI (i.e. vegetation greenness) and PSRI (i.e. senescent vegetation) were relatively similar for the agricultural and forest restoration but compared to them, the sites left to spontaneous succession had much lower values of NDVI and clearly higher values of PSRI (Fig. 6). The structural measures show a distribution of values commensurate with the individual habitat types. Note that the sites with unspecified restoration method were similar to agricultural restoration and mostly consisted of low vegetation.

5. Discussion

In this study, we evaluated the effect of the variance in vegetation structure, primary productivity and senescent vegetation on bird communities colonizing newly available (restored) habitats after coal mining (Fig. 3). We found a detectable relationship between fine-scale habitat attributes of early succession stages derived from airborne LiDAR and hyperspectral data and the occurrence of birds. The models with six variables representing the vegetation structure, primary productivity and the presence of senescent vegetation explained 52% and 12% of the variability in species richness and rarity, respectively, which is comparable to prior studies. The previous studies combining LiDAR data with the indices derived from passive optical sensors (e.g. NDVI) typically explained the variability in species richness between 15% and

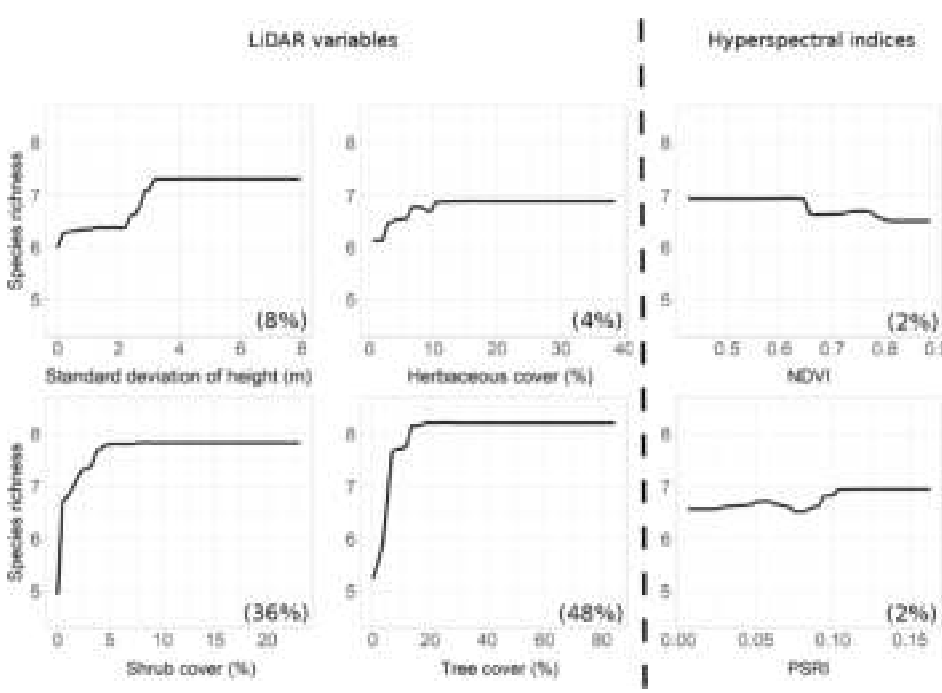

Fig. 4. Partial dependency plots for boosted tree analyses of overall species richness. The partial plots show the modelled relationships between species richness and standard deviations of height, herbaceous cover, shrub cover, tree cover, NDVI, and PSRI. The relative importance of the variable in the model is given in parentheses.

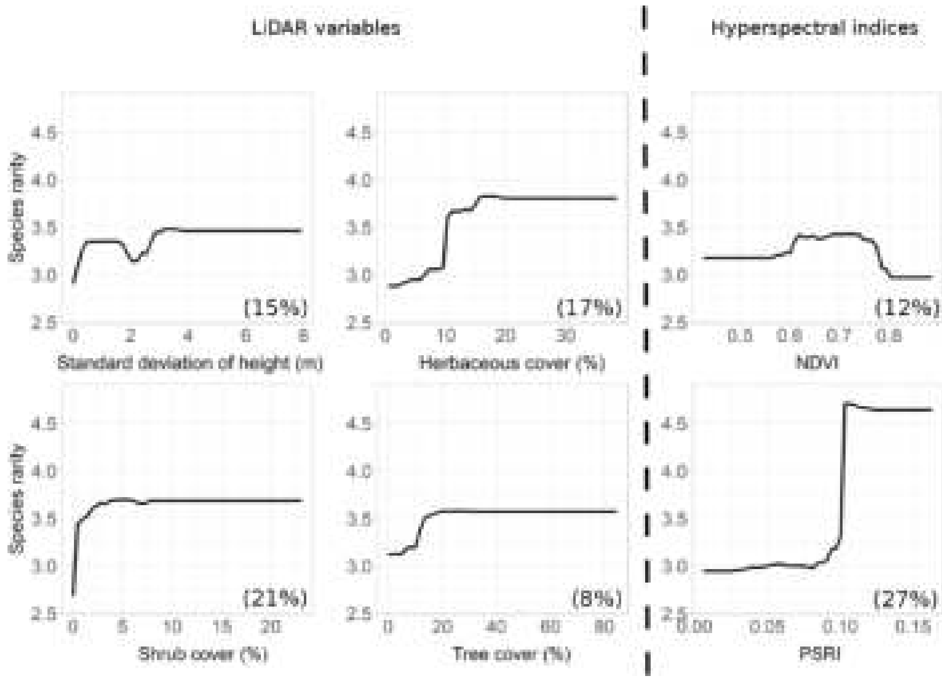

Fig. 5. Partial dependency plots for boosted tree analyses of species rarity. The partial plots show the modelled relationships between the species rarity and standard deviations of height, herbaceous cover, shrub cover, tree cover, NDVI, and PSRI. The relative importance of the variable in the model is given in parentheses.

55% (Goetz et al., 2007; Jones et al., 2013; Vogeler et al., 2014).

5.1. Importance of vegetation structure, NDVI and PSRI for bird species richness

Variance in vegetation structure had a positive effect on species richness and explained most of the explained variablity (Fig. 4). While NDVI and PSRI showed almost no effect on species richness, shrub cover (i.e. the cover of shrubs and saplings between 1 m and 3 m high) and tree cover (i.e. cover of vegetation >3 m high) exhibited a strong positive effect on species richness. The standard deviation of height and herbaceous cover (cover of vegetation up to 1 m high) had minor effects on species richness. Species richness climbed steeply at low values of shrub cover (0%–5%), low values of tree cover (0%–20%), and the standard deviation of height between 2 m and 3 m (Fig. 4). Such conditions are typical of forest restoration and sites left to spontaneous succession (Fig. 5). These findings are in accordance with prior studies such as Goetz et al. (2007) and Vogeler et al. (2014) who combined LiDAR with NDVI and more recently Melin, Hill, Bellamy, and Hinsley (2019) who combined LiDAR with variables derived from hyperspectral data and showed that the vegetation structure (i.e. LiDAR derived variables) is more important for the assessment of bird species richness at local scales than variables derived from passive remote sensing.

5.2. Importance of vegetation structure, NDVI and PSRI for bird species rarity

In contrast to species richness, our results show that combining information from LiDAR and passive optical sensors might be important when species rarity is of concern. We found a positive effect of both habitat heterogeneity and primary productivity on species rarity (Fig. 5). PSRI (i.e. old dead vegetation from the previous vegetation season) was the most important predictor with a strong positive effect on species rarity, followed by shrub and herbaceous cover. The greatest increase in rarity was associated with PSRI values higher than 0.10, above 2% for the shrub cover, and above 10% for the herbaceous cover (Fig. 5); above these values, the rarity remained more or less constant. This is likely because the senescent vegetation and relatively high herbaceous and shrub covers provide shelter and enhance the diversity of insect communities and hence food availability for birds (e.g. Müller, Bae, Röder, Chao, & Didham, 2014; Soto et al., 2017; Vergara et al., 2017).

It is, however, important to note that the model of bird rarity explained only 12% of deviance. This is likely related to the fact that typical rare species that occur in our study area are ground-nesting or foraging birds. Such species include, for example, Wheatear *Oenanthe oenanthe*, Montagús Harrier *Circus pygargus*, Bluethroat *Luscinia svecica cyanecula*, Whinchat *Saxicola rubetra*, Stonechat *Saxicola torquata*, Great Reed Warbler *Acrocephalus arundinaceus* or Meadow Pipit *Anthus pratensis*. These specialists require specific and mutually different conditions such as bare grounds (Wheatear), unmanaged grassy patches (Montagús Harrier, Whinchat, Stonechat, Meadow Pipit) or reedbeds (Bluethroat, Great Reed Warbler) that are neither adequately represented by the variance in the vegetation structure nor by NDVI and PSRI indices, respectively. Indeed, ground-nesting or foraging species are typically reported to be poorly modelled using habitat heterogeneity and productivity variables (Cooper et al., 2020; Weisberg et al., 2014). The five-year time lag between the data acquisitions and difficulties to distinguish old dead vegetation from bare surfaces might represent alternative explanations for the relatively low deviance explained by these factors (see Chapter 5.4. below).

5.3. Which type of restoration results in the development of more favourable habitats?

It is evident that all vertical levels of habitat heterogeneity (i.e. herbaceous, shrub and tree covers) are important either for species richness or rarity. This supports the necessity to create the mosaic of habitats with heterogeneous vertical structure during restoration to support high species richness as suggested e.g. by Harabiš, Tichanek, and Tropek (2013). However, the high variance in vegetation structure alone is not sufficient to support rare species. Indeed, management and restoration goals can change considerably depending on whether the aim is to support high species richness or rare species (Cooper et al., 2020). It seems that a high herbaceous and shrub cover combined with the presence of old dead vegetation promote rarity. However, this

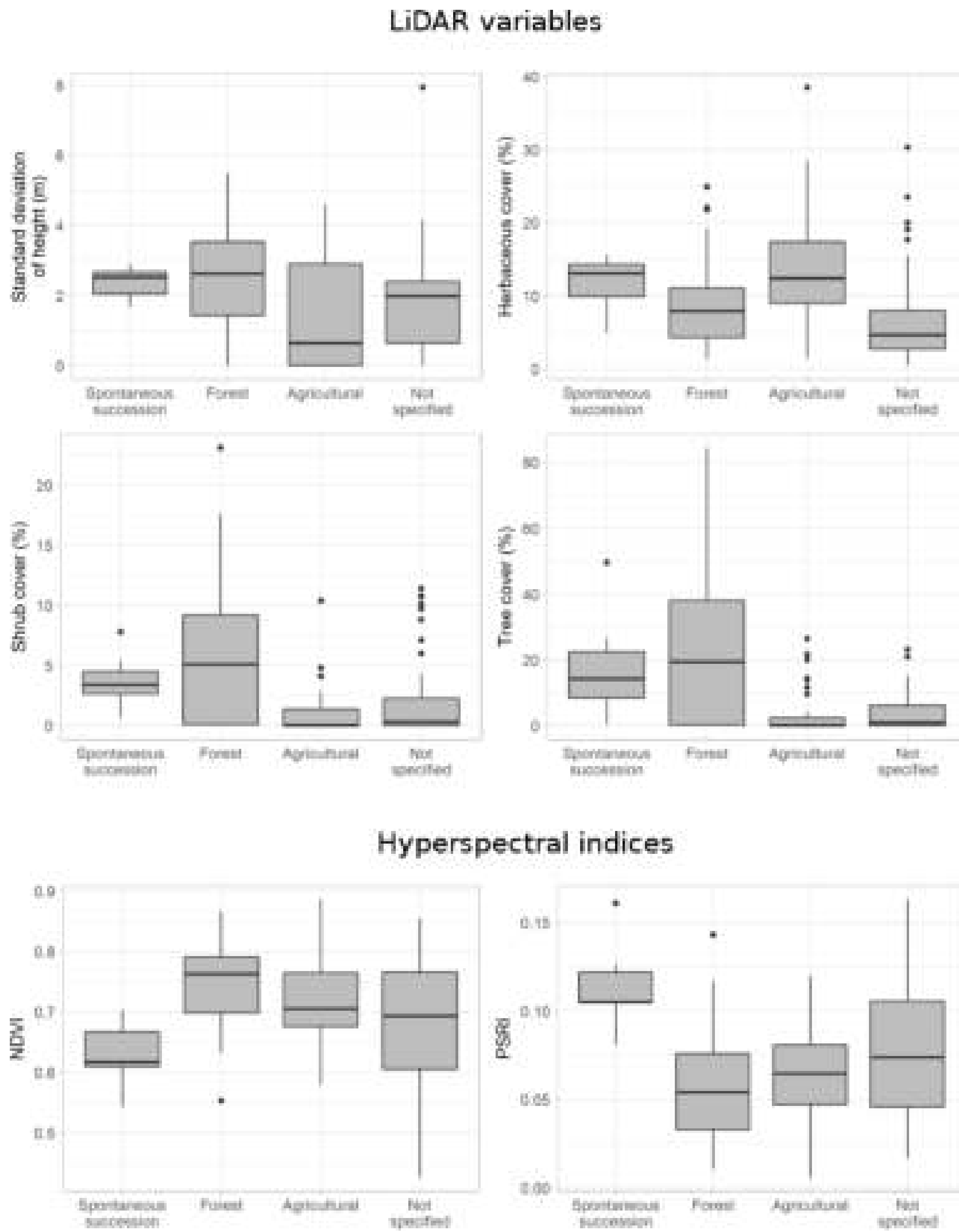

Fig. 6. Comparison of the vegetation structure (LiDAR variables), NDVI and PSRI indices depending on the adopted restoration techniques. The central horizontal line in the box marks the median. The boxes show the interquartile range (25th to 75th percentile) and the whiskers indicate 1.5 times the interquartile range.

combination is rare on technically reclaimed sites, i.e. after agricultural and forest restoration. In contrast, this study shows that such conditions are typically present on sites left to spontaneous succession (Fig. 5). This is a likely explanation for the fact that the spontaneous succession sites are particularly favoured by rare vertebrates (Šálek, 2012; Vojar et al., 2016).

5.4. *Use and limitations of airborne remote sensing data in restoration practice*

We have shown that the measurement of the habitat heterogeneity derived from airborne laser scanning point clouds can provide ecologically meaningful variables. As field-based estimates of vegetation structure are used as a rapid and efficient way of assessing the condition of restored sites (Gibbons & Freudenberger, 2006), LiDAR can become an alternative to such field surveys. Compared to field surveys, however, LiDAR has a higher potential for providing information that can lead to management action. As LiDAR data availability is increasing continuously due to national or regional scanning campaigns (see Melin et al., 2017; Stereńczak et al., 2020 for the list of countries and regions with LiDAR data available) and thanks to the more common adoption of open data policies (Rocchini et al., 2017), there is a high potential to use it in restoration ecology, especially for assessment of vegetation structure (Guo et al., 2017; Koska et al., 2017; Moudrý, Gdulová, et al., 2019; Moudrý, Urban, et al., 2019; Szostak, Pietrzykowski, & Likus-Cieślik, 2020). Therefore, we suggest that such data should be increasingly utilized by managing authorities for optimizing the restoration success assessment and enhancing the ecological value of reclaimed areas.

It should be, however, noted that despite the increase of LiDAR data availability, acquisitions for the same area (e.g. state) have, due to high acquisition costs, long repetition times. Therefore, studies such as the presented one are often being done under suboptimal conditions and the time lag between field surveys and LiDAR data acquisition is common (Lesak et al., 2011). For example, Goetz et al. (2007) – 6 years; Wallis et al. (2016) – 10 years. Huber, Kienast, Ginzler, and Pasinelli (2016) – 10 years. It has been shown that several years time lag is not a fundamental source of error in mature woodland ecosystems as the changes in vegetation structure are usually relatively slow (Hill & Hinsley, 2015; Vierling, Swift, Hudak, Vogeler, & Vierling, 2014). This is, however, not the case of our study area that consists of agricultural, forest, and successional sites and the time lag between remotely sensed and bird data collection might be a potential source of error. While this is certainly not a problem for agriculturally restored sites, differences in vegetation structure might have arisen during the 5 years at sites restored through forestry and those left to spontaneous succession. On the other hand, the two sites left to spontaneous succession in our study area are 16 and 26 years old, respectively, and the current rate of changes in the vegetation structure is relatively slower than during the early stages of succession. Moreover, the spontaneous succession is often blocked by sandy soils and dense grass cover (e.g. *Calamagrostis epigejos*). Therefore, the main differences can be expected in vegetation within the 1 – 3 m height range that could have grown over 3 m.

It is even more important to minimize the time lag when hyperspectral data are used. This is especially true when indices related to the vegetation biochemistry (which can change in a matter of weeks across a vegetation season) are used, it is much preferable if the hyperspectral data collection and bird survey are performed at the same time (e.g. Melin et al., 2019). Whit this in mind, we did not use any indices related directly to vegetation biochemistry and concentrated only on indices that are positively correlated to the characteristics that should have remained relatively stable over the five years (i.e. NDVI for vegetation productivity and PSRI for the amount of old dead vegetation). Besides, the bird occurrences and remotely sensed data were both collected in May, which was particularly important for the ecological relevance as this allowed accurate estimates of the amount of old dead vegetation present during the breeding season. The old dead vegetation is typical for terrain depressions (e.g. *Phragmites australis* and *Typha latifolia*) and agriculturally restored areas (e.g. *Calamagrostis epigejos* and *Arrhenatherum elatius*) and its detectability is changing more within a year than between years due to the pronounced seasonality (see also the note above on blocked succession). The amount of old dead vegetation is actually constantly growing and such sites might have become even more favourable for rare species as Whinchat, Stonechat, Montagús Harrier or Bluethroat in 2017 (the year of remote sensing data acquisition) than they were in 2012 (the year of bird data collection).

There is, however, another potential source of error, which might possibly also have been the reason why the model of bird rarity explained only 12% of deviance, namely the fact that the PSRI is high also in areas completely without vegetation, such as roads (Fig. 2). On the other hand, however, old dead vegetation, which forms an important habitat for Whinchat or Stonechat, is often present in the ditches along the roads (e.g. *Arrhenatherum elatius*) and it is, therefore, difficult to separate their effects.

For future studies and especially for monitoring practice, it would be beneficial to agree on several LiDAR-derived metrics proven to be effective for explaining species diversity and to recommend them as standard structural indicators. To facilitate comparisons, Bakx et al. (2019) recently grouped LiDAR-derived variables into 24 classes defined by six categories of vegetation (total vegetation, single trees, canopy, understorey, other single layers, and multi-layer) and four categories of the structural type (cover, height, horizontal variability and vertical variability). Our results show that the total vegetation vertical variability (i.e. standard deviation of returns height) and canopy and understory cover (i.e. herbaceous, shrub and tree covers) are potentially relevant for the assessment of conditions on early successional restored sites.

6. Conclusions

Understanding drivers of species distributions across restored landscapes and identifying areas that have the potential for supporting high species richness, vulnerable or rare species, is important for successful management of restored sites. Overall, our results show that both habitat heterogeneity and primary productivity play an important role in bird species diversity on restored sites. Shrub cover had a strong positive effect on both species richness and rarity, while tree cover had a strong positive effect on species richness. Herbaceous cover and the presence of senescent vegetation had both positive effects on species rarity. This highlights the necessity of creating a mosaic of habitats with heterogeneous vertical structure during restoration or to design the vegetation structure in a way supporting preferred species. To support this, we suggest to reduce intensive mowing of agriculturally restored areas (e.g. by creating unmowed strips of vegetation), preserve naturally formed waterlogged areas, plant trees with different growth rates and combine them with shrub vegetation. Sites left to spontaneous succession play an important role in creating restored ecosystems of high ecological value as they represent a unique combination of vegetation density and presence of senescent vegetation that, in combination, promote high species rarity.

In our opinion, airborne remote sensing, particularly laser scanning, should constitute an integral part of restoration success assessment and should be acquired with reasonable repetition rate (e.g. 5–10 years) over the restored areas, as the information derived from such data can be more easily implemented in management actions than subjective semi-quantitative or categorical measures collected during intensive fieldwork. We suggest a wider use of vegetation structure and productivity indices derived from remotely sensed data in restoration success assessment. Our results show that the total vegetation vertical variability (i.e. standard deviation of returns height) and various vertical layers of vegetation cover (i.e. herbaceous, shrub and tree cover) in combination with senescent vegetation (i.e. PSRI) are potentially relevant for monitoring of early successional restored sites.

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.

Acknowledgements

We are grateful to three anonymous reviewers for their constructive comments that significantly improved the quality of the manuscript. This work was supported by the Internal Grant Agency of the Faculty of Environmental Sciences, Czech University of Life Sciences Prague (project No. 2020B0029), and by the Czech Science Foundation (project No. 17-17156Y).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.landurbplan.2021.104064.

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