GfÖ
GfÖ Ecological Society of Germany, Austria and Switzerland
Basic and Applied Ecology 70 (2023) 38–49
Basic and Applied Ecology
www.elsevier.com/locate/baae

Habitat heterogeneity promotes bird diversity in agricultural landscapes: Insights from remote sensing data

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Received 27 February 2022; accepted 25 April 2023
Available online 28 April 2023

Abstract

Understanding the main drivers of biodiversity loss in Europe's agricultural landscapes has been a research priority in the last decades. One of the most important factors promoting biodiversity in farmed landscapes is habitat heterogeneity, which has often proved crucial for avian species and communities. Birds are highly sensitive to environmental changes and make use of a broad range of ecological niches, thus being exceptionally sensitive to the loss of habitat heterogeneity. Remote sensing data are particularly suited to quantify habitat heterogeneity at fine scales over relatively large extents, allowing to consider how different measures of heterogeneity may affect biotic communities at a regional scale. Here, we used airborne LiDAR (Light Detection And Ranging) and satellite multispectral data to derive vegetation canopy height and primary productivity for 118 sites in complex agricultural landscapes in a region in the Central Alps. We computed different bird diversity indices and classified bird species into guilds according to specific traits to analyse the relationship between avian communities and different facets of habitat heterogeneity. Results confirmed that habitat heterogeneity is essential in shaping rich and diverse bird communities, and it is particularly important for several farmland birds. By comparing the effects of canopy height, primary productivity, and specific vegetation features (e.g., cover of grassland, shrub, and tree layers), we showed how different habitat characteristics as well as landscape heterogeneity affected bird richness, diversity, functional entropy, and trait patterns. Landscape and height heterogeneity, estimated by NDVI and LiDAR Rao's Q indices, strongly influenced all response variables, for example, high NDVI values promoted species diversity and ground-understory nesters, and shrub layer was important for ground-understory nesters and forest specialists. Finally, we provide recommendations for conservation practices and mitigation measures to improve bird diversity in agricultural landscapes.

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https://doi.org/10.1016/j.baae.2023.04.006
1439-1791/

Keywords: Agroecosystems; Alpine environment; Avian traits; Complex landscapes; Farming; Forest encroachment; Intensification; Land cover; Landscape metrics; Land use

Introduction

The increasing loss of biodiversity in European agricultural landscapes has been largely attributed to agricultural intensification and abandonment of marginal areas in recent decades (Assandri et al., 2019b; Botías et al., 2019; Brambilla, 2019). Understanding key environmental determinants that could help stop (and reverse) farmland biodiversity loss is particularly urgent and important (Jetz et al., 2019; Pettorelli et al., 2016).

Farmland birds are a key component of agricultural biodiversity and they are amongst the most threatened bird groups in Europe (Reif & Vermouzek, 2019). In addition, especially in farmed landscapes, birds provide crucial ecosystem services, such as natural pest control, pollination, or seed dispersal (Whelan et al., 2008), which should be guaranteed also for the future generations. Birds have been used as indicators in many ecological studies dealing with biodiversity in agro-ecosystems, because they are highly sensitive to environmental changes, occupy a wide range of ecological niches, show patterns often representative of other taxa, and are relatively easy to survey (Gottschalk et al., 2010). In 2005, even the European Union officially adopted a Farmland Bird Index (Gregory et al., 2005) as a proxy to evaluate the general status of biodiversity in agricultural landscapes in Europe.

Landscape heterogeneity is one of the most important factors driving composition and diversity of bird communities in agricultural landscapes (Anderle et al., 2022; Brambilla, 2019): complex landscapes may provide a high number of niches, increasing bird species richness and diversity (the so-called habitat heterogeneity hypothesis; Tews et al., 2004). Heterogenous landscapes increase resources available to birds (e.g., food, shelters) and may change their foraging behaviour (Schuldt et al., 2019) by influencing movement patterns (Jirinec et al., 2016) and species interactions (Seibold et al., 2013). In addition, landscape or habitat heterogeneity can also determine microclimatic conditions that could provide essential refugia in the face of climatic extremes, increasing habitat and bird resilience (Brambilla et al., 2021; Virah-Sawmy et al., 2009), allowing e.g., alpine specialist species to avoid too warm microclimates (Alessandrini et al., 2022). The loss of heterogeneity is likely one of the main drivers of the farmland birds crisis (Benton et al., 2003), especially in intensive agricultural landscapes (Batáry et al., 2011), which are currently undergoing major land use and land cover changes in many parts of Europe, including the Alps.

The effect of habitat and landscape heterogeneity is often difficult to measure over large areas, since field-based surveys have limited coverage in time and space, and mainly focus on vegetation composition. It is even more difficult in regions characterised by a wide elevational gradient (such as the Alps), which contributes to shaping diverse agricultural landscapes, and where environmental drivers may act over different spatial scales (Anderle et al., 2022).

Remotely sensed data typically provide proxies of landscape or habitat heterogeneity, and can overcome the field mapping limitations, enabling complete coverage of high-resolution data at the landscape-scale in a shorter and easier way (Rocchini et al., 2018). In the last years, LiDAR (Light Detection And Ranging) and multispectral data have been extensively applied to model biodiversity patterns (Moudrý et al., 2021; Randin et al., 2020), because they allow the quantification of the canopy height and the habitat diversity over wide areas with a high resolution (Maltamo et al., 2014), and also to explore the link between birds and primary productivity (Evans et al., 2005). LiDAR data also can be used to explore the "Height Variation Hypothesis" (HVH; Torresani et al., 2020), which assumes that a high variation in vegetation height translates into a more complex habitat or landscape structure and hence a higher species diversity (see also Appendix S2). However, few studies focusing on agricultural landscapes and vertebrate ecology have simultaneously included these two different types of variables (e.g., Sheeren et al., 2014).

Our study evaluated the effects of heterogeneity of landscape and canopy height on birds (Palmer et al., 2002) by capitalising on the increasing availability of remote sensing data encompassing topographic variables, satellite multispectral and LiDAR data. We worked at two spatial scales (100 and 400 m-radii) to consider different sizes of bird territories and because effects of some factors may be scale-dependent, e.g., microclimate conditions or spatial configuration. We focused on highly diversified agricultural alpine landscapes, along a broad elevational gradient (200−1800 m a.s.l.), which characterises the study area and shapes the local bird communities. These characteristics make the study area particularly suited to investigate heterogeneity effects across different conditions and scales (Anderle et al., 2022). We focus on the impact on bird richness and diversity indices, on different avian functional traits that are particularly relevant for ecosystem functioning (Weisberg et al., 2014), and on threat levels. We expected that (i) different remote sensing data types will provide complementary results to explain ecological requirements of alpine bird communities; (ii) due to their ecological relevance, NDVI and LiDAR Rao's Q indices will contribute most to the models since they best represent the level of heterogeneity; (iii) the different vegetation layers and the variables defining vegetation density (e.g., Mean and Maximum NDVI) can contrastingly influence different bird guilds and threat levels; (iv) independent variables will react differently at the two different scales studied, mainly due to different microclimate conditions or spatial configuration (Anderle et al., 2022).

Understanding such impacts is needed to support the development of conservation measures to mitigate the impact of modern agriculture on birds. Tackling the loss of landscape heterogeneity due to the intensification of the most productive areas, or to the abandonment of the marginal ones, should be pivotal to the Common Agricultural Policy (Assandri et al., 2019b), even though it largely failed in addressing such issues until now (Assandri, 2022). Adequate conservation and management measures should be implemented by the countries to promote heterogeneity through e.g., the increase of ecotonal elements, diversification of agricultural practices, reduction of fertiliser inputs, or the promotion of agriculture in marginal areas that would be abandoned without concrete support (Assandri et al., 2019a, 2019b; Fischer et al., 2008).

Materials and methods

Study area and study sites

The study was carried out in the Autonomous Province of South Tyrol (north-eastern Italy), in the Central Alps. South Tyrol covers an area of approximately 7400 km^2, with an elevation between 194 m and 3905 m a.s.l. (Fig. 1).

The territory is predominantly mountainous and primarily covered by forests (50%), pastures (22%), meadows (10%), unproductive areas (which include high mountains and glaciers; 10%), orchards (3%), vineyards (1%), annual crops (1%) and settlements (3%; Anderle et al., 2022). Annual and permanent crops are mostly located in valley bottoms, whereas grasslands (meadows and pastures) are found from low mountainsides to the subalpine and alpine belts. The

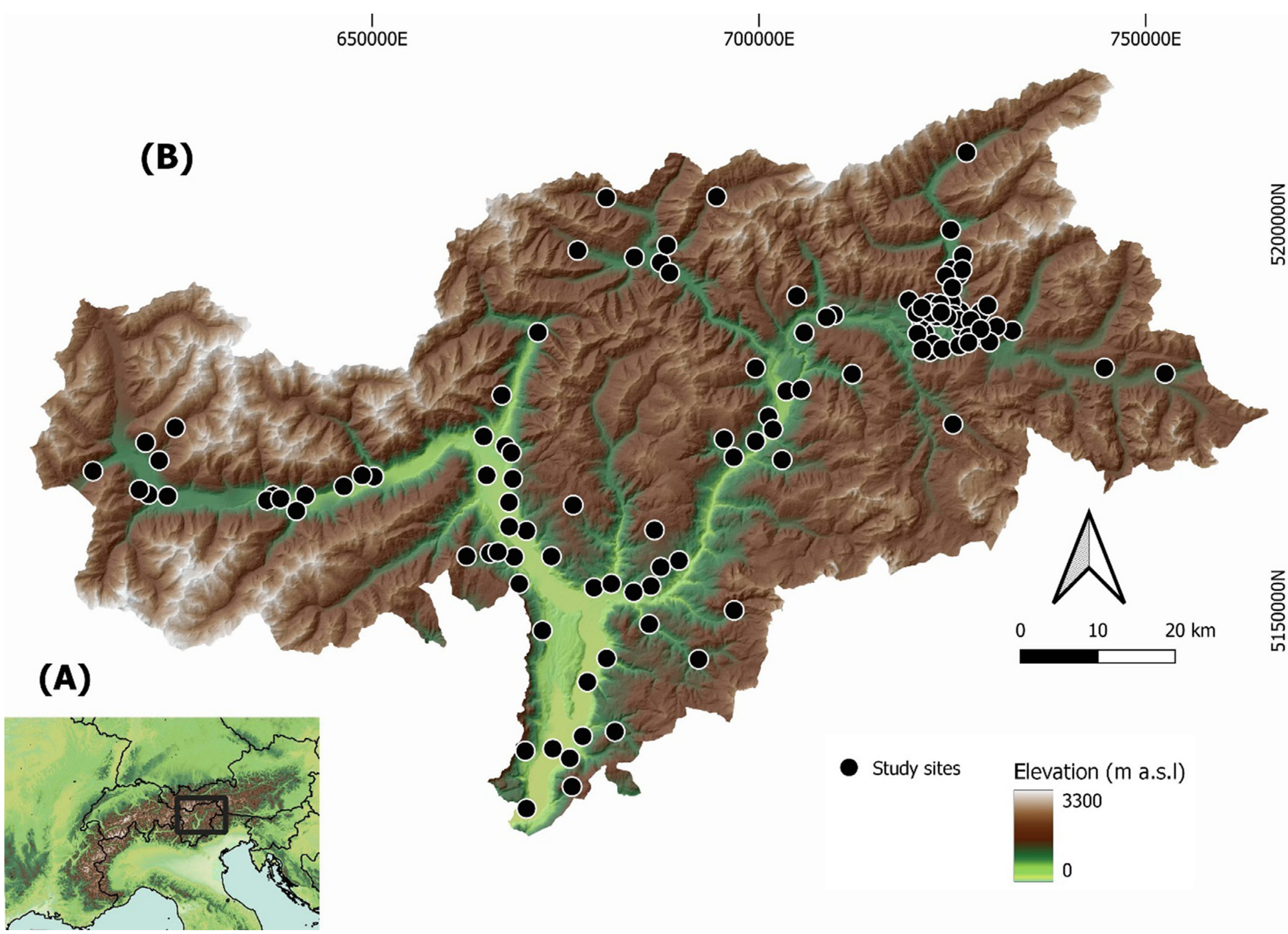

Fig. 1. (A) Study area located in the Central Alps (north-eastern Italy, Autonomous Province of South Tyrol), and (B) the 118 study sites in agricultural areas.

study was conducted within a long-term project named *Biodiversity Monitoring South Tyrol* (Hilpold et al., 2023), and sites were selected according to a stratified selection approach, using different agricultural categories of land use as strata (Table S1). We used different geographical baseline data to calculate the total area of the different habitat strata in South Tyrol; within each single stratum we performed a random site selection (Hilpold et al., 2023). Only agricultural sites from the valley floors to the montane area (1800 m a.s.l.) were selected, resulting in a total of 118 sites. Sites above that elevation are not or only weakly affected by agricultural practices.

Bird data

A single observer (MA) surveyed diurnal bird species from 15th April to 15th July, between 2019 and 2021. The survey period coincides with avian breeding season in the Alps, therefore, after the exclusion of migrants and overflying individuals, birds observed within their breeding habitats can be considered as likely breeding (Assandri et al., 2019b). Exclusively migrant species within the area were excluded from the analysis (Arbeitsgemeinschaft für Vogelkunde und Vogelschutz - Südtirol, 2010), as well as birds observed only flying over the survey sites, because they were not breeding and not closely related with the specific site, respectively. Each site was visited three times in the same year and birds were counted within a 100 m-radius from the site by means of 10-min point-counts, with at least 2 weeks between subsequent visits; the visit order of point-count sites was changed between subsequent surveys (Anderle et al., 2022). The minimum distance between two points was set at 800 m to avoid possible double counts. Counts started shortly after sunrise (5.30 a.m.) and ended at 11 a.m. Adverse weather conditions (moderate/strong wind or heavy rain/snow) were avoided.

Using the '*vegan*' package in R (Oksanen et al., 2020), we calculated species richness as the total number of species observed at a site, and the Shannon diversity index using the maximum number of individuals observed during the three visits per species at a site (Anderle et al., 2022). Using one characteristic value (maximum) per site (over the three visits) allowed to consider the actual composition of the breeding bird community at sample sites, while avoiding treating data collected over single visits in the same site as independent. Bird species were assigned to guilds based on two functional traits representing different types of key species-habitat interactions (nest location and habitat specialisation), and were also grouped according to the level of threat within the study area. Nest locations were grouped in four categories, aligned along a gradient of vegetation development: rock and building nesters, ground-understory nesters (nesting directly on or close to the ground), mid-story and canopy nesters (closed and open arboreal), and tree cavity nesters (Storchová & Hořák, 2018). Habitat specialisation included farmland, alpine grassland or forest specialists, generalist or synanthropic species, based on the list of species used to assess the Common farmland bird indicator for Europe (https://pecbms.info/trends-and-indicators/indicators/indicators/E_C_Fa/); we slightly adjusted the list to mirror the local context by integrating also the Italian indicator (Rete Rurale Nazionale & LIPU, 2020; Table S3). Threat level involved threatened (near threatened, vulnerable, endangered, critically endangered), non-threatened (least concern) birds and species with unidentified status were listed as unknown (Ceresa & Kranebitter, 2020). We limited all trait and threat levels between 0 and 1 to account for the different number of categories (Korányi et al., 2021; Marcolin et al., 2021). Community Weighted Mean (CWM) for traits and threat level, and Rao's functional entropy were calculated using the '*FD*' package in R (Laliberté et al., 2014; Marcolin et al., 2021). A comprehensive list of species recorded, including the values of each trait per species, is available in Table S3.

Environmental variables

Topographical, LiDAR, and multispectral variables were calculated at two spatial scales (100 and 400 m) to estimate habitat and environmental features. The smaller scale reflects the territory size of passerine birds during the breeding season (e.g., Pestka et al., 2018), while the larger one approximates the wider home ranges of larger birds (e.g., Bocca et al., 2007). Furthermore, the effects of some factors may be scale-dependant (e.g., microclimate conditions or spatial configuration; Anderle et al., 2022). For a detailed explanation of all environmental variables refer to Tables 1 and S2.

Topographical variables

We derived topographical variables from the Digital Terrain Model based on Airborne Laser Scanning campaign carried out in 2006 by the Province of Bolzano (http://geocatalogo.retecivica.bz.it/geokatalog/). In addition, elevation, slope, and potential solar radiation were used with a spatial resolution of 2.5 m (Table S2).

LiDAR variables

We derived LiDAR variables from an airborne laser scanning campaign carried out in 2004−2006 (Tamburlin et al., 2021); the Canopy Height Model (CHM) derived from the original point cloud had a 2.5 m spatial resolution. Human artifacts were removed from the CHM using a shapefile of the buildings falling within the study sites (Fig. S3). At 100 and 400 m scales we calculated at each site the following indices: herb layer, shrub layer, tree layer, mean canopy height, maximum canopy height, standard deviation of canopy height, canopy cover (Torresani et al., 2020), and LiDAR Rao's Q index (Rocchini et al., 2017; Table 1 and S2; Appendix S2).

Multispectral variables

Using Google Earth Engine (Moore & Hansen, 2011) in R (R Development Core Team, 2021) we computed a Sentinel-2-derived NDVI (Normalized Difference Vegetation Index) map with a spatial resolution of 10 m for the years 2019, 2020, and 2021 (Fig. S4, S5, S6). Each map was obtained as a composite mean NDVI value of all the available cloud-free images for the period from 15 April to 15 July. For multispectral variables, we used a map of the year consistent with the period when birds were surveyed. Multispectral data allows the measurement of plant characteristics and vegetation diversity. In addition, texture metrics derived from multispectral data quantify spectral and spatial variation in pixel values of an image, and thus suggest information on spectral and spatial vegetation heterogeneity (Haralick et al., 1973; Tuanmu & Jetz, 2015). The mean NDVI, maximum NDVI, standard deviation of NDVI and NDVI Rao's Q index were calculated at each study site (Appendix S2, Table 1 and S2).

Table 1. Environmental variable type, full name, descriptions, units, interpretation, for those entered in the averaged most supported models. For references and all variable descriptions see Table S2.

Type	Full name	Description	Interpretation	Value range (Unit)
Topographical	Slope	Mean slope within 100 and 400-m buffer using QGIS (QGIS Development Team, 2020)	Site average slope (larger values indicate greater slope)	0−46 (°)
	Potential solar radiation	Sum of direct, diffuse, and reflected radiation due to sun irradiance, according to incidence solar angle, and the shadowing effect of topography. It was computed for a reference day (21st June) using the command "*r.sun*" in GRASS GIS (GRASS Development Team, 2020)	Site average sun radiation (larger values indicate greater radiation)	7413−9367 (Wm^{-2})
	Elevation	Site elevation extracted from a DTM using QGIS (QGIS Development Team, 2020)	Site elevation (larger values indicate greater elevation)	200−1800 (m a.s.l.)
Multispectral	NDVI Rao's Q index	Rao's q index calculated in R within 100-m and 400-m buffers extracted from the NDVI maps $Q_{rs} = \sum_{i,j=1}^{N} d_{ij \times p_i \times p_j}$ Qrs = Rao's Q applied to remote sensing data $pi = pj = 1/N$ = relative abundance of pixel *i, j* in a selected area composed of *N* pixels (buffer areas) dij = spectral (distance/dissimilarity) between pixel *i* and *j* ($dij = dji$ and $dii = 0$)	Vegetation heterogeneity (larger values indicate greater heterogeneity)	0.02−0.42
	Mean NDVI	Mean of values within 100-m and 400-m buffers extracted from the NDVI maps	Vegetation density (larger values indicate denser vegetation)	0.43−0.88
	Maximum NDVI	Maximum value within 100-m and 400-m buffers extracted from the NDVI maps	Vegetation density (larger values indicate denser vegetation)	0.65−0.96
LiDAR	Shrub layer	Percentage of area within 100-m and 400-m buffers with vegetation height between 1 and 4 m	Percentage of shrub layer within the site	0−100 (%)
	LiDAR Rao's Q index	Rao's q index calculated in R within 100-m and 400-m buffers extracted from the LiDAR map $Q_{rs} = \sum_{i,j=1}^{N} d_{ij \times p_i \times p_j}$ Qrs = Rao's Q applied to remote sensing data $pi = pj = 1/N$ = relative abundance of pixel *i, j* in a selected area composed of *N* pixels (buffer areas) dij = spectral (distance/dissimilarity) between pixel *i* and *j* ($dij = dji$ and $dii = 0$)	Vegetation height heterogeneity (larger values indicate greater heterogeneity)	0.02−9.85

Analyses

Firstly, we standardised data by scaling all the independent variables to better interpret the relative outcomes (Zuur et al., 2010; Table 1 and S2). Predictors were checked for collinearity and highly correlated variables were excluded (Spearman's Rho $\geq$ 0.65, Dormann et al., 2007; see in Apendix S1 and Table S2). The adequacy and completeness of bird sampling was assessed with accumulation curves using the '*iNEXT*' package (Hsieh et al., 2016; Fig. S7).

Regression models

We analysed the effects of heterogeneity across different conditions and scales on bird diversity indices, different bird functional traits, and threat levels, by means of linear and generalised linear models. For all models we evaluated the variance inflation factors (VIFs) to account for multicollinearity and excluded the most problematic variables (VIF > 3; Zuur et al., 2010) from the dataset (Appendix S1). We also checked for potential patterns of spatial autocorrelation in models' residuals by means of a variogram (Dormann et al., 2007). We did not detect any patterns, suggesting a lack of spatial autocorrelation. We related six bird response variables (species richness, Shannon diversity, Rao's functional entropy, and the Community Weighted Mean for nest location, habitat specialisation, and level of threat) to topographic, LiDAR and multispectral variables. After checking for normality and heteroscedasticity of residuals we used Linear Models for all variables, except for species richness (count data), for which we used a Generalized Linear Model with a Negative Binomial distribution to handle over-dispersion (Zuur et al., 2013). We built all possible models for each scale and response variable with the 'dredge' function in the R package '*MuMIn*' (Barton, 2020). An information-theoretic approach to perform a model selection based on the Akaike's information criterion (Burnham & Anderson, 2004) corrected for small sample size (AICc) was applied. The most supported models were selected (ΔAICc < 2), after excluding uninformative parameters (i.e., variables that were included only in models that comprised more parsimonious and simpler models as nested ones; Arnold, 2010). A total of 12 models (one for each dependent variable and scale) were obtained by averaging the most supported ones (ΔAICc < 2), or by taking the most supported if there were no alternative models with similar support.

Results

A total of 3794 individuals belonging to 91 species (Table S3) were counted; the accumulation curves suggested that the sampling was adequate and complete (Fig. S7). The most common species was blackbird (*Turdus merula*) with 309 records, followed by common chaffinch (*Fringilla coelebs*; 265); some of the rarest were corncrake (*Crex crex)*, ortolan bunting (*Emberiza hortulana)* and woodlark (*Lullula arborea)*. Ground-understory nesters accounted for 38.5% of the species surveyed, mid-story and canopy nesters for 23.1%, tree cavity nesters for 19.8% and rock and building nesters accounted for 18.7%. Farmland and alpine grassland specialists accounted for 29.7%, while 26.4% were forest specialists, the remaining (44.0%) were generalist and synanthropic species. Half of the species (51.0%) were non-threatened birds, threatened birds (mainly farmland specialists) were 23.7% and the remaining (25.3%) had unknown status (for bird species classification please refer to Table S3).

Concerning remote sensing data, the NDVI Rao's Q index was selected in more than half of the final models and was the most frequently significant multispectral variable in the models. LiDAR Rao's Q index was retained in 10 out of 12 final models, and it was the most frequently included variable (for variable description and interpretation please see Table 1 and S2).

Bird species richness and diversity

Species richness was positively affected at both scales by solar radiation and LiDAR Rao's Q, and at 400 m by NDVI Rao's Q (see Fig. 2 and Table S4). Shannon diversity was also mainly positively influenced by environmental variables. In fact, solar radiation, and LiDAR Rao's Q showed positive effects at both scales, while NDVI Rao's Q and mean NDVI only at 100 m, and Maximum NDVI only at 400 m. Only Elevation showed contrasting effects on Shannon diversity: positive at 100 m and negative at 400 m. Rao's functional entropy was positively influenced at both scales by solar radiation and by NDVI Rao's Q, while it was negatively affected by shrub layer at both scales.

Nest location

Nest location index was positively influenced at both scales by LiDAR Rao's Q, while negatively by NDVI Rao's Q. Elevation had negative effects on nest location at 400 and 100 m. Nest location at 400 m was influenced positively by Maximum NDVI. With decreasing elevation, the community composition changed at both scales from species nesting on ground or close to the ground to species nesting in the canopy and in tree cavities. The same happened with decreasing NDVI Rao's Q at both scales. The community composition also changed from species nesting on ground or close to the ground to species nesting in the canopy and in tree cavities with increasing LiDAR Rao's Q at both scales and maximum NDVI at 400 m (see Fig. 2 and Table S4).

Habitat specialisation

Habitat specialisation index was influenced positively at both scales by LiDAR Rao's Q, by slope at 100 m, and by

Variables	Species richness		Shannon		Rao's functional entropy		Nest location		Habitat specialisation		Level of threat	
	100 m	400 m	100 m	400 m	100 m	400 m	100 m	400 m	100 m	400 m	100 m	400 m
Slope									**0.041**		**0.049**	
Potential solar radiation	**0.070**	**0.081**	0.075	**0.099**	**0.148**	**0.127**				-0.004		
Elevation			0.017	-0.016			**-0.026**	-0.020				
NDVI Rao's Q		**0.070**	0.043		**0.139**	**0.124**	**-0.034**	-0.017	**-0.018**			-0.012
Mean NDVI			**0.103**								0.018	
Maximum NDVI				0.040				0.010		0.005		0.021
Shrub layer					-0.044	**-0.148**				0.011		0.024
LiDAR Rao's Q	**0.089**	**0.157**	**0.131**	**0.186**			**0.038**	0.020	**0.047**	**0.077**	0.019	**0.067**

Fig. 2. Graphical representation of different responses to predictors shown by the dependant variables, based on the final models at the two different spatial scales (100 m and 400 m). "+" and "−" represent positive (red colour) and negative (blue colour) effects. Numbers represent coefficients (based on models with ΔAICc < 2, bold, if parameters do not include zero in their confidence intervals); blank cells denote no effects (see Table S4 for a complete view of different models).

maximum NDVI and shrub layer at 400 m. Concurrently, it was negatively affected by solar radiation at 400 m and by NDVI Rao's Q at 100 m. The community changed from farmland and alpine grassland specialists to forest specialist with increasing slope at 100 m, maximum NDVI and shrub layer at 400 m, and LiDAR Rao's Q at both scales. The community composition changed from forest specialists to farmland and alpine grassland specialists with increasing NDVI Rao's Q at 100 m and potential solar radiation at 400 m (see Fig. 2 and Table S4).

Threat level

Level of threat was positively influenced by LiDAR Rao's Q at both scales, by shrub layer and maximum NDVI at 400 m, and by mean NDVI and slope at 100 m. NDVI Rao's Q had negative effects at 400 m on threat level. The community changed from threatened to non-threatened birds increasing slope and mean NDVI at 100 m, increasing maximum NDVI and shrub layer at 400 m and increasing LiDAR Rao's Q at both scales. While the community changed from non-threatened to threatened birds with increasing NDVI Rao's Q at 400 m. For more details, please refer to Fig. 2 and Tables S1 and S3.

Discussion

In our study we assessed the effects of the heterogeneity of both landscape and canopy height on bird richness and diversity, on selected avian traits, and threat levels. As expected, (i), different data types provided complementary results to explain ecological requirements of the alpine bird communities studied. For example, increasing slope and elevation mainly favoured a bird community with more forest specialists, while high solar radiation favoured a diverse and rich community and was particularly important for farmland birds. High NDVI and LiDAR Rao's Q correlated with high richness and diversity, and NDVI Rao's Q also with functional entropy of bird communities in agricultural landscapes. The former was more important for agricultural and threatened species, and the latter for forest species. As we predicted (iii), increasing mean and maximum NDVI mainly triggered a shift in the bird community from farmland to forest nesters, from threatened to non-threatened birds, and from ground-understory to forest nesters (both mid-story and canopy and tree cavity nesters). The shrub layer supported forest species at the 400 m-scale. Contrary to what we assumed (iv), only once one variable (elevation on Shannon diversity) showed different effects at the two different scales. As in our expectations (ii), RAO's Q index seems promising, despite being still under-explored in animal ecology studies (Rocchini et al., 2018); therefore, we recommend its use as a good proxy for habitat heterogeneity in future studies addressing the effect of heterogeneity on biological communities.

Heterogeneous landscapes, mainly revealed by NDVI Rao's Q, promoted richness, diversity, and functional entropy of bird communities. The canopy height heterogeneity, expressed by LiDAR Rao's Q, promoted more mid-story and canopy nesters and forest specialists in the community, offering more niches, resources, and nesting opportunities (Bohn & Huth, 2017; Ceresa et al., 2012). The negative effects that LiDAR Rao's Q had on bird communities with ground-understory nesters, farmland specialists, and threatened birds, suggest that increasing canopy heterogeneity is detrimental to species more closely associated with open habitats, which often rely on short vegetation with no or scarce trees (e.g., skylark *Alauda arvensis*, or red-backed shrike *Lanius collurio*; Brambilla et al., 2020; Ceresa et al., 2021). The effects exerted by both Rao's Q indices and shrub layer, highlighted the importance of landscape heterogeneity, e.g., the occurrence of marginal elements (such as hedges, single trees, rows of trees, woodlands) and diversification of agricultural practices, for breeding birds, which is in line with many other studies providing consistent evidence from the same sector of the Alps (Assandri et al., 2019b) and other regions (Barbaro et al., 2021). Additionally, not only the whole community was richer and more diverse, but also farmland and alpine grassland specialists (which included the most threatened species in this study), ground-understory nesters and functional entropy benefited from increasing landscape heterogeneity (Smith et al., 2022). The greatest number of species detected, 23 in total, was obtained from two orchard meadows, a hay meadow, and a pasture. This result highlights the key role of extensively managed grasslands, a 'traditional' habitat with high natural and cultural values, for the conservation of farmland biodiversity, especially for farmland specialists (Brambilla, 2019; Smith et al., 2022). Furthermore, more complex grasslands can offer greater resources, both in terms of food and shelters available, especially to farmland specialists. Indeed, our results showed that an increase of Rao's Q, or maximum NDVI (that respectively may reflect an increase in the landscape heterogeneity and in the presence of e.g., hedges, tree rows, or bushes) led to an increase in diversity of the bird community, functional entropy, farmland and alpine grassland specialists, probably because NDVI reflected the abundance of above-ground invertebrates (e.g., food for insectivores and chicks of most species) and the quantity and quality of available plant-based foods (e.g., for granivores and omnivores; see Ding et al., 2021; Pettorelli et al., 2011). Higher NDVI heterogeneity (e.g., alternation of grassland, forest and different habitats) might provide particularly suitable conditions for many species, being associated with the co-occurrence of food-rich (micro)habitats with dense vegetation, and (micro)habitats suitable for food collection, with sparser or less dense vegetation (e.g., Brambilla & Gatti, 2022).

The presence of dense vegetation, as indicated by maximum and mean NDVI values, had different effects on threatened birds and forest nesters and specialists. While the maximum NDVI values were beneficial for the latter two groups, they had a negative impact on threatened birds. This is likely because dense vegetation is a preferred nesting habitat for forest birds, but it is not exploited by species that nest in open areas (as many threatened ones). An increasing NDVI Rao's Q index, depicting heterogeneous landscapes, showed a negative influence on forest specialists, mid-story and canopy, and tree cavity nesters, as they are mainly associated with continuous forest areas embedded in agricultural landscapes (Anderle et al., 2022; Bełcik et al., 2020). Shrub layer exerted negative effects on functional entropy, and on a bird community with more farmland and grassland specialists and threatened birds (mainly farmland specialists) at 400 m. However, it had positive effects on a community with more forest specialists. These effects could be related to intensive apple orchards and vegetation at intermediate climax stages (which due to their height were classified as shrub layer). These habitats were mainly found in the valley floors and in montane areas within the study area, respectively. Both those habitats are non-optimal for farmland and alpine grassland specialists but suitable for generalists and some forest specialists (Rime et al., 2020).

Some other topographical characteristics contributed to shaping avian communities in Alpine agricultural landscapes. Slope emerged as a rather important driver by promoting more forest specialists and negatively impacting farmland and alpine grassland specialists, and threatened birds (which were mainly farmland specialists). The topographically most favourable areas (flat or gently sloping) are usually exploited for agriculture, while steeper slopes are hardly accessible and consequently left uncultivated or are covered by forest. As elevation increases, management intensity of agricultural practices decreases (Assandri et al., 2019b; Brambilla et al., 2021), while the number of seminatural elements generally increases, as does the risk of land abandonment (Brambilla, 2019). This pattern was mirrored by the opposite effects that elevation had on Shannon diversity at different scales, positive at the 100, and negative at the 400 m-scale, and by the positive effect on functional entropy. Solar radiation was also important for birds, mainly exerting positive effects, something expectable in this rather cold Alpine region. This effect was particularly evident for farmland specialists, who could benefit from targeted management or conservation initiatives implemented in areas with a favourable exposition. For example, some species normally confined to the valley floor are shifting upwards, where they find better sites that best suit their microclimatic needs (e.g., the Corncrake; Brambilla et al., 2021).

Our results showed that habitat heterogeneity derived from LiDAR and multispectral data can provide ecologically important variables and can thus become an alternative to field surveys, especially at larger scales. The availability of LiDAR and multispectral data is continuously increasing, as is their potential to provide large-scale species distribution models (Rocchini et al., 2022). There is also a high potential for using similar models to provide information that can lead to management and conservation actions, such as the identification of target areas for the conservation of farmland biodiversity, providing important management information for the improvement of agricultural landscapes (Cooper et al., 2020; Moudrý et al., 2021). Therefore, we suggest that such data should be increasingly included in ecological and conservation studies to optimise their use in land planning, management, and conservation.

Conclusions

Many studies showed the efficiency of using LiDAR or multispectral variables as proxies for environmental factors shaping bird communities in relation to land use and other landscape characteristics; nonetheless, only very few have combined such variables while focussing on agricultural landscapes. Our findings suggested that a combination of LiDAR and multispectral images, also accounting for topographical aspects, can best predict characteristics of bird communities in agricultural landscapes. In our models, many factors were only important at a single scale, others at both, highlighting the importance of modelling ecological patterns at different scales. The ongoing dynamics of intensification in agricultural profitable areas and abandonment in marginal, high-elevation ones, are thus reflected in the association between elevation and avian traits, with forest specialists being favoured by abandonment at higher elevation. On the other side, management intensification of valley floors is also forcing farmland specialists to shift towards upper elevations. However, climatic conditions are sub-optimal, and suitable habitats, even if of potential high-quality, are less available on a wide landscape scale due to the abandonment of agricultural practices (and subsequent forest encroachment).

The effects of habitat heterogeneity and characteristics on avian communities may help define conservation measures, as e.g., within the framework of the new Common Agricultural Policy (2023−30). Increasing habitat heterogeneity, especially in the impoverished valley floors, where landscape intensification and homogenisation are massive, is key to farmland bird conservation. High habitat heterogeneity, e.g., diversification of farming practices and high availability of landscape elements between fields, such as dry-stone walls, individual trees, hedges, tree rows, or small woodlands, should be conserved and restored. An increase in heterogeneity would largely benefit the overall biodiversity while also contributing to increasing the cultural value of agricultural landscapes.

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.

Acknowledgments

We thank Thomas Marsoner for cartographic support. We thank the Department of Nature, Landscape and Spatial Development, in particular the Office of Nature, and to the Forestry Department provided logistic support. We thank one anonymous reviewer, Dr. Arne Wenzel, and Dr. Péter Batáry for thorough and helpful reviews. This work is part of M.A.'s PhD at the University of Innsbruck. This work is part of the *Biodiversity Monitoring South Tyrol*, financed by the Autonomous Province of Bozen/Bolzano-South Tyrol. The authors thanks the Department of Innovation, Research University and Museums of the Autonomous Province of Bozen/Bolzano for covering the Open Access publication costs.

Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.baae.2023.04.006.

References

Alessandrini, C., Scridel, D., Boitani, L., Pedrini, P., & Brambilla, M. (2022). Remotely sensed variables explain microhabitat selection and reveal buffering behaviours against warming in a climate-sensitive bird species. *Remote Sensing in Ecology and Conservation*. doi:10.1002/rse2.265.

Anderle, M., Paniccia, C., Brambilla, M., Hilpold, A., Volani, S., Tasser, E., . . . Tappeiner, U. (2022). The contribution of landscape features, climate and topography in shaping taxonomical and functional diversity of avian communities in a heterogeneous Alpine region. *Oecologia*, *199 (3)*, 499–512.

Arbeitsgemeinschaft für Vogelkunde und Vogelschutz - Südtirol. (2010). *Atlante degli uccelli nidificanti dell'Alto Adige*. www.vogelschutz-suedtirol.it

Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's information criterion. *Journal of Wildlife Management*, *74*(6), 1175–1178. doi:10.2193/2009-367.

Assandri (2022). Editorial - do ornithologists still play a role in reversing the crisis of farmland biodiversity? *Avocetta*, *46*, 3–5. doi:10.30456/AVO.2022E1.

Assandri, G., Bogliani, G., Pedrini, P., & Brambilla, M. (2019a). Species-specific responses to habitat and livestock management call for carefully targeted conservation strategies for declining meadow birds. *Journal for Nature Conservation*, *52*, 125757. doi:10.1016/J.JNC.2019.125757 July.

Assandri, G., Bogliani, G., Pedrini, P., & Brambilla, M. (2019b). Toward the next common agricultural policy reform: Determinants of avian communities in hay meadows reveal current policy's inadequacy for biodiversity conservation in grassland ecosystems. *Journal of Applied Ecology*, *56*(3), 604–617. doi:10.1111/1365-2664.13332.

Barbaro, L., Assandri, G., Brambilla, M., Castagneyrol, B., Froidevaux, J., Giffard, B., Pithon, J., Puig-Montserrat, X., Torre, I., Calatayud, F., Gaüzère, P., Guenser, J., Macià-Valverde, F., Mary, S., Raison, L., Sirami, C., & Rusch, A. (2021). Organic management and landscape heterogeneity combine to sustain multifunctional bird communities in European vineyards. *Journal of Applied Ecology*, *58*(6), 1261–1271. doi:10.1111/1365-2664.13885.

Barton, K. (2020). *Package ' MuMIn'. Multi-Model Inference R Package Version 1.43.17* (Version 1.43.17).

Batáry, P., Fischer, J., Báldi, A., Crist, T. O., & Tscharntke, T. (2011). Does habitat heterogeneity increase farmland biodiversity? *Frontiers in Ecology and the Environment*, *9*(3), 152–153. doi:10.1890/11.WB.006.

Bełcik, M., Lenda, M., Amano, T., & Skórka, P. (2020). Different response of the taxonomic, phylogenetic and functional diversity of birds to forest fragmentation. *Scientific Reports*, *10*(1), 20320. doi:10.1038/s41598-020-76917-2.

Benton, T. G., Vickery, J. A., & Wilson, J. D. (2003). Farmland biodiversity: Is habitat heterogeneity the key? *Trends in Ecology & Evolution*, *18*(4), 182–188. doi:10.1016/S0169-5347(03)00011-9.

Bocca, M., Carisio, L., & Rolando, A. (2007). Habitat use, home ranges and census techniques in the Black Woodpecker Dryocopus martius in the Alps. *Ardea*, *95*(1), 17–29. doi:10.5253/078.095.0103.

Bohn, F. J., & Huth, A. (2017). The importance of forest structure to biodiversity−productivity relationships. *Royal Society Open Science*, *4*,(1) 160521. doi:10.1098/rsos.160521.

Botías, C., Basley, K., Nicholls, E., & Goulson, D. (2019). Impact of pesticide use on the flora and fauna of field margins and hedgerows. *The Ecology of Hedgerows and Field Margins*, 90–109. doi:10.4324/9781315121413-5.

Brambilla, M. (2019). Six (or nearly so) big challenges for farmland bird conservation in Italy. *Avocetta*, *43*(2), 101–113.

Brambilla, M., & Gatti, F. (2022). No more silent (and uncoloured) springs in vineyards? Experimental evidence for positive impact of alternate inter-row management on birds and butterflies. *Journal of Applied Ecology*, *59*(8), 2166–2178. doi:10.1111/1365-2664.14229.

Brambilla, M., Gubert, F., & Pedrini, P. (2021). The effects of farming intensification on an iconic grassland bird species, or why mountain refuges no longer work for farmland biodiversity. *Agriculture, Ecosystems & Environment*, *319*, 107518. doi:10.1016/j.agee.2021.107518.

Brambilla, M., Gustin, M., Cento, M., Ilahiane, L., & Celada, C. (2020). Habitat, climate, topography and management differently affect occurrence in declining avian species: Implications for conservation in changing environments. *Science of the Total Environment*, *742*, 140663. doi:10.1016/j.scitotenv.2020.140663.

Burnham, K. P., & Anderson, D. R. (2004). Model selection and multimodel inference. *Model Selection and Multimodel Inference*. doi:10.1007/b97636.

Ceresa, F., Bogliani, G., Pedrini, P., & Brambilla, M. (2012). The importance of key marginal habitat features for birds in farmland: An assessment of habitat preferences of Red-backed Shrikes Lanius collurio in the Italian Alps. *Bird Study : the Journal of the British Trust for Ornithology*, *59*(3), 327–334. doi:10.1080/00063657.2012.676623.

Ceresa, F., & Kranebitter, P. (2020). Lista Rossa 2020 degli uccelli nidificanti in Alto Adige. *Gredleriana*. doi:10.5281/ZENODO.4245030.

Ceresa, F., Kranebitter, P., Monrós, J. S., Rizzolli, F., & Brambilla, M. (2021). Disentangling direct and indirect effects of local temperature on abundance of mountain birds and implications for understanding global change impacts. *PeerJ*, *9*, e12560. doi:10.7717/peerj.12560.

Cooper, W. J., McShea, W. J., Forrester, T., & Luther, D. A. (2020). The value of local habitat heterogeneity and productivity when estimating avian species richness and species of concern. *Ecosphere (Washington, D.C)*, *11*(5). doi:10.1002/ecs2.3107.

Ding, Z., Hu, H., Cadotte, M. W., Liang, J., Hu, Y., & Si, X. (2021). Elevational patterns of bird functional and phylogenetic structure in the central Himalaya. *Ecography*, *44*(9), 1403–1417. doi:10.1111/ecog.05660.

Evans, K.L., Warren, P.H., & Gaston, K.J. (n.d.). *Species-energy relationships at the macroecological scale: A review of the mechanisms*. https://doi.org/10.1017/S1464793104006517

Dormann, F., M. McPherson, C., B. Araújo, J., Bivand, M., Bolliger, R., Carl, J., Davies, G., G., Hirzel, R., Jetz, A., Daniel Kissling, W., Kühn, W., Ohlemüller, I., Peres-Neto, R., R., Reineking, P., Schröder, B., Schurr, F, B., M., & Wilson, R. (2007). Methods to account for spatial autocorrelation in the analysis of species distributional data: A review. *Ecography*, *30*(5), 609–628. doi:10.1111/j.2007.0906-7590.05171.x.

Fischer, M., Rudmann-Maurer, K., Weyand, A., & Stöcklin, J. (2008). Agricultural land use and biodiversity in the Alps. *Mountain Research and Development*, *28*(2), 148–155. doi:10.1659/mrd.0964.

Gottschalk, T. K., Dittrich, R., Diekötter, T., Sheridan, P., Wolters, V., & Ekschmitt, K. (2010). Modelling land-use sustainability using farmland birds as indicators. *Ecological Indicators*, *10*(1), 15–23. doi:10.1016/j.ecolind.2009.05.008.

GRASS Development Team. (2020). Geographic Resources Analysis Support System (GRASS). *Software. Open Source Geospatial Foundation Project. http://grass.osgeo.org*.

Gregory, R. D., van Strien, A., Vorisek, P., Gmelig Meyling, A. W., Noble, D. G., Foppen, R. P., & Gibbons, D. W. (2005). Developing indicators for European birds. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *360*(1454), 269–288. doi:10.1098/rstb.2004.1602.

Haralick, R. M., Dinstein, I., & Shanmugam, K. (1973). Textural features for image classification. IEEE Transactions on Systems, Man and Cybernetics, SMC, *3*(6), 610–621. doi:10.1109/TSMC.1973.4309314.

Hilpold, A., Anderle, M., Guariento, E., Marsoner, T., Mina, M., Paniccia, C., Plunger, J., Rigo, F., Rüdisser, J., Scotti, A., Seeber, J., Steinwandter, M., Stifter, S., Strobl, J., Suarez-Muñoz, M., Vanek, M., Bottarin, R., & Tappeiner, U. (2023). Handbook biodiversity monitoring south tyrol. *Eurac Research*. doi:10.57749/2qm9-fq40.

Hsieh, T. C., Ma, K. H., & Chao, A. (2016). iNEXT: An R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution*, *7*(12), 1451–1456.

Jetz, W., McGeoch, M. A., Guralnick, R., Ferrier, S., Beck, J., Costello, M. J., Fernandez, M., Geller, G. N., Keil, P., Merow, C., Meyer, C., Muller-Karger, F. E., Pereira, H. M., Regan, E. C., Schmeller, D. S., & Turak, E. (2019). Essential biodiversity variables for mapping and monitoring species populations. *Nature Ecology and Evolution*, *3*(4), 539–551. doi:10.1038/s41559-019-0826-1.

Jirinec, V., Isdell, R. E., & Leu, M. (2016). Prey availability and habitat structure explain breeding space use of a migratory songbird. *The Condor*, *118*(2), 309–328. doi:10.1650/CONDOR-15-140.1.

Korányi, D., Gallé, R., Donkó, B., Chamberlain, D. E., & Batáry, P. (2021). Urbanization does not affect green space bird species richness in a mid-sized city. *Urban Ecosystems*, *24*, 789–800. doi:10.1007/s11252-020-01083-2/Published.

Laliberté, E., Legendre, P., & Shipley, B. (2014). *FD: measuring functional diversity (FD) from multiple traits, and other tools for functional ecology. R package version 1.0-12.1*.

Maltamo, M., Næsset, E., & Vauhkonen, J. (2014). Forestry applications of airborne laser scanning. Concepts and case studies. *Managing For Ecosystems.* Springer, *27*, 460.

Marcolin, F., Lakatos, T., Gallé, R., & Batáry, P. (2021). Fragment connectivity shapes bird communities through functional trait filtering in two types of grasslands. *Global Ecology and Conservation*, *28*. doi:10.1016/j.gecco.2021.e01687.

Moore, R. T., & Hansen, M. C. (2011). Google Earth Engine: A new cloud-computing platform for global-scale earth observation data and analysis. AGU Fall Meeting Abstracts, 2011 IN43C-02.

Moudrý, V., Moudrá, L., Barták, V., Bejček, V., Gdulová, K., Hendrychová, M., Moravec, D., Musil, P., Rocchini, D., Šťastný, K., Volf, O., & Šálek, M (2021). 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. *Landscape and Urban Planning*, *210*, 104064. doi:10.1016/j.landurbplan.2021.104064.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, B., Simpson, G.L., Solymos, P., Stevens, M.H.H., & Wagner, H. (2020). *The vegan R package version 2.5.7: community ecology*.

Palmer, M. W., Earls, P. G., Hoagland, B. W., White, P. S., & Wohlgemuth, T. (2002). Quantitative tools for perfecting species lists. *Environmetrics*, *13*(2), 121–137. doi:10.1002/env.516.

Pestka, Z., Jakubas, D., & Wojczulanis-Jakubas, K. (2018). Habitat preferences of Red-backed Shrikes Lanius collurio and Barred Warblers Sylvia nisoria breeding sympatrically in a wetland/farmland mosaic. *Bird Study : the Journal of the British Trust for Ornithology*, *65*(3), 317–328. doi:10.1080/00063657.2018.1503996.

Pettorelli, N., Ryan, S., Mueller, T., Bunnefeld, N., Jedrzejewska, B., Lima, M., & Kausrud, K. (2011). The Normalized Difference Vegetation Index (NDVI): Unforeseen successes in animal ecology. *Climate Research*, *46*(1), 15–27. doi:10.3354/cr00936.

Pettorelli, N., Wegmann, M., Skidmore, A., Mücher, S., Dawson, T. P., Fernandez, M., Lucas, R., Schaepman, M. E., Wang, T., O'Connor, B., Jongman, R. H. G., Kempeneers, P., Sonnenschein, R., Leidner, A. K., Böhm, M., He, K. S., Nagendra, H., Dubois, G., Fatoyinbo, T., . . . Geller, G. N. (2016). Framing the concept of satellite remote sensing essential biodiversity variables: challenges and future directions. *Remote Sensing in Ecology and Conservation*, *2*(3), 122–131. doi:10.1002/rse2.15.

QGIS Development Team. (2020). QGIS geographic information system. Open source geospatial foundation. http://qgis.osgeo.org.

R Development Core Team, R.. (2021). R: A language and environment for statistical computing. Ed., *R foundation for statistical computing* Ed.. (p. 409). R Foundation for Statistical Computing. doi:10.1007/978-3-540-74686-7 Vol. 1.

Randin, C. F., Ashcroft, M. B., Bolliger, J., Cavender-Bares, J., Coops, N. C., Dullinger, S., Dirnböck, T., Eckert, S., Ellis, E., Fernández, N., Giuliani, G., Guisan, A., Jetz, W., Joost, S., Karger, D., Lembrechts, J., Lenoir, J., Luoto, M., Morin, X., . . . Payne, D. (2020). Monitoring biodiversity in the anthropocene using remote sensing in species distribution models. *Remote Sensing of Environment*, *239*, 111626. doi:10.1016/j.rse.2019.111626.

Reif, J., & Vermouzek, Z. (2019). Collapse of farmland bird populations in an Eastern European country following its EU accession. *Conservation letters: 12*Wiley-Blackwell. doi:10.1111/conl.12585.

R.R. Nazionale, & LIPU. (2020). *Common breeding farmland birds in Italy. Update of population trends and Farmland Bird Indicator for National Rural Network 2000-2015*. www.birdlife.org

Rime, Y., Luisier, C., Arlettaz, R., & Jacot, A. (2020). Landscape heterogeneity and management practices drive habitat preferences of wintering and breeding birds in intensively-managed fruit-tree plantations. *Agriculture, Ecosystems & Environment*, *295*, 106890. doi:10.1016/j.agee.2020.106890.

Rocchini, D., Luque, S., Pettorelli, N., Bastin, L., Doktor, D., Faedi, N., Feilhauer, H., Féret, J., Foody, G. M., Gavish, Y., Godinho, S., Kunin, W. E., Lausch, A., Leitão, P. J., Marcantonio, M., Neteler, M., Ricotta, C., Schmidtlein, S., Vihervaara, P., . . . Nagendra, H. (2018). Measuring β-diversity by remote sensing: A challenge for biodiversity monitoring. *Methods in Ecology and Evolution*, *9*(8), 1787–1798. doi:10.1111/2041-210X.12941.

Rocchini, D., Marcantonio, M., & Ricotta, C. (2017). Measuring Rao's Q diversity index from remote sensing: An open source solution. *Ecological Indicators*, *72*, 234–238.

Rocchini, D., Torresani, M., Beierkuhnlein, C., Feoli, E., Foody, G. M., Lenoir, J., Malavasi, M., Moudrý, V., Šímová, P., & Ricotta, C. (2022). Double down on remote sensing for biodiversity estimation: a biological mindset. *Community Ecology*. doi:10.1007/s42974-022-00113-7 Akademiai Kiado ZRt..

Schuldt, A., Ebeling, A., Kunz, M., Staab, M., Guimarães-Steinicke, C., Bachmann, D., Buchmann, N., Durka, W., Fichtner, A., & Fornoff, F. (2019). Multiple plant diversity components drive consumer communities across ecosystems. *Nature Communications*, *10*(1), 1–11.

Seibold, S., Hempel, A., Piehl, S., Bässler, C., Brandl, R., Rösner, S., & Müller, J. (2013). Forest vegetation structure has more influence on predation risk of artificial ground nests than human activities. *Basic and Applied Ecology*, *14*(8), 687–693. doi:10.1016/j.baae.2013.09.003.

Sheeren, D., Bonthoux, S., & Balent, G. (2014). Modeling bird communities using unclassified remote sensing imagery: Effects of the spatial resolution and data period. *Ecological Indicators*, *43*, 69–82. doi:10.1016/j.ecolind.2014.02.023.

Smith, O. M., Kennedy, C. M., Echeverri, A., Karp, D. S., Latimer, C. E., Taylor, J. M., Wilson-Rankin, E. E., Owen, J. P., & Snyder, W. E. (2022). Complex landscapes stabilize farm bird communities and their expected ecosystem services. *Journal of Applied Ecology*. doi:10.1111/1365-2664.14104.

Storchová, L., & Hořák, D. (2018). Life-history characteristics of European birds. *Global Ecology and Biogeography*, *27*(4), 400–406. doi:10.1111/geb.12709.

Tamburlin, D., Torresani, M., Tomelleri, E., Tonon, G., & Rocchini, D. (2021). Testing the height variation hypothesis with the R Rasterdiv package for tree species diversity estimation. *Remote Sensing*, *13*(18), 3569. doi:10.3390/rs13183569.

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M. C., Schwager, M., & Jeltsch, F. (2004). Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography*, *31*(1), 79–92. doi:10.1046/j.0305-0270.2003.00994.x.

Torresani, M., Rocchini, D., Sonnenschein, R., Zebisch, M., Hauffe, H. C., Heym, M., Pretzsch, H., & Tonon, G. (2020). Height variation hypothesis: A new approach for estimating forest species diversity with CHM LiDAR data. *Ecological Indicators*, *117*, 106520. doi:10.1016/j.ecolind.2020.106520.

Tuanmu, M. N., & Jetz, W. (2015). A global, remote sensing-based characterization of terrestrial habitat heterogeneity for biodiversity and ecosystem modelling. *Global Ecology and Biogeography*, *24*(11), 1329–1339. doi:10.1111/geb.12365.

Virah-Sawmy, M., Gillson, L., & Willis, K. J. (2009). How does spatial heterogeneity influence resilience to climatic changes? Ecological dynamics in southeast Madagascar. *Ecological Monographs*, *79*(4), 557–574. doi:10.1890/08-1210.1.

Weisberg, P. J., Dilts, T. E., Becker, M. E., Young, J. S., Wong-Kone, D. C., Newton, W. E., & Ammon, E. M. (2014). Guild-specific responses of avian species richness to LiDAR-derived habitat heterogeneity. *Acta Oecologica*, *59*, 72–83. doi:10.1016/j.actao.2014.06.002.

Whelan, C. J., Wenny, D. G., & Marquis, R. J. (2008). Ecosystem services provided by birds. *New York Academy of Sciences*. doi:10.1196/annals.1439.003.

Zuur, A. F., Hilbe, J. M., & Ieno, E. N. (2013). *A Beginner's Guide to GLM and GLMM with R*. Newburgh: Highland Statistics Limited Beginner's Guide Series.

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, *1*(1), 3–14. doi:10.1111/j.2041-210X.2009.00001.x.