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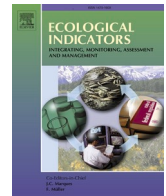
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Original Articles

Textural indices of aerial images reveal urban landscapes temporal dynamics and their effects on plants and birds

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ABSTRACT

Landscape temporal dynamics are a crucial concern in ecology to understand current biodiversity. But historical environmental data are often not easily available. This study assesses for the first time the potential of historical orthophotographs to describe past landscape conditions and determine the temporal lag between landscape changes and biotic communities responses.

This method utilizes Gray level Co-occurrence Matrix (GLCM) texture indices computed from black and white orthophotographs to construct continuous metrics of landscape composition. Metrics were first developed using present-day data, i.e. 2015, and calibrated with categorical land cover maps of the Strasbourg Eurometropolis, France. Subsequently, these metrics were applied to historical orthophotographs from 1966, 1976, 1986, and 2000. Plant and bird data from research and citizen science programs were used to estimate the time delay in which these communities respond to evolutions in built areas and high vegetation.

Obtained texture-based models reveal that built areas exhibit high contrast and homogeneity, depicted through a linear relation, and that high vegetation display low pixel brightness and high brightness diversity, better described via a nonlinear model. We successfully applied those findings to historical orthophotographs, and revealed dependencies on landscape composition up to 50 years ago for plants and up to 30 years ago for birds, with the time lag and the influence of built and high vegetation areas depending on the selected biodiversity indices.

These results demonstrate the utility of archive black and white orthophotographs' texture indices for describing urban landscapes over the past five decades, making them valuable tools for ecological research. These indices are more accessible than categorical data like land cover maps for past years. They have the potential to greatly benefit future studies investigating time lags in landscape ecology, simplifying access to historical landscape features and contributing to sustainable urban planning efforts.

1. Introduction

Past environmental conditions, including landscape characteristics, disturbances, or climate, can have a lasting impact on present-day biodiversity due to temporal lags and legacy effects (Cuddington, 2011; Haddou et al., 2022). These effects may explain the persistence of species under unsuitable conditions (i.e., extinction debt, Tilman et al., 1994) and the absence of species in suitable locations due to slow demography or restrained dispersal (i.e., colonization credit, Cristofoli and Mahy, 2010). Such relaxation times in the biodiversity response can be explained by nonstationary ecosystems achieving a new equilibrium over variable times (Kuussaari et al., 2009; Jackson and Sax, 2010;

Figueiredo et al., 2019). Quantifying such processes is challenging due to the complex interactions between environmental pressures that operate at different spatio-temporal scales.

Long-term studies are essential for unraveling the relationships between biodiversity and environmental changes, including landscape transformations (De Palma et al., 2018; Keten et al., 2020). However, there are limitations to long-term studies due to the availability and consistency of data describing past landscapes and biological patterns (Bürgi et al., 2017; Ridding et al., 2021). To overcome these limitations, researchers have frequently employed the 'space for time' substitution assumption (Pickett, 1989). This approach assumes that spatial patterns observed in different developmental stages (i.e., chronosequences,

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Walker et al., 2010) can serve as proxies for temporal patterns. However, this substitution is inadequate when organisms respond slowly compared to their evolving environment (Damgaard, 2019), for instance, in complex contexts where cumulative historical effects shape biotic communities alongside their current environment (Cortina et al., 2022; Alberti and Wang, 2022; Tappeiner et al., 2021). Therefore, there is a need for methodological frameworks that can facilitate the description of ecological habitats over temporal scales (De Palma et al., 2018). The prediction of past landscape features can be used to assess the effect of historical landscapes on current biological communities, as explained in the “past habitat” method described by Ridding et al. (2021). Additionally, recent studies have emphasized the importance of coupling spatial with temporal dimensions when describing ecosystem dynamics (Ossola et al., 2021).

The most common way of assessing landscape effects, including landscape temporal evolution, on biotic communities involves deriving landscape metrics from categorical land cover or land use maps composed of categories (forest, grassland, crops, etc.) (Luck and Jianguo (2002); Uemaa et al., 2009; Walker et al., 2009; Morelli et al., 2016). First, these maps often lack accuracy and completeness when applied to past landscapes because of the failures of classification algorithms when using historical data (Adler and Jedicke, 2022; Poterek et al., 2020; Auffret et al. (2017); Herrault et al., 2013). For instance, aerial photographs provide information at unprecedented spatial and temporal scales in Europe or North America but remain poorly exploited due to their heterogeneous specifications (scale, lens properties, spectral sensitivity, and film development) and quality (Aber et al., 2010). Consequently, they are mostly manually digitized and categorized into land cover classes, which is time consuming and may lead to misclassification errors. Second, categorical maps often provide discrete, simplistic representations of the environment, unrepresentative of ecological realities.

A recently promoted solution uses continuous variables derived from pixel values to explain biodiversity patterns (Park and Guldmann, 2020; Wood et al., 2013). This approach may solve issues such as landscape representation or image classification accuracy (Adler and Jedicke, 2022; Coops and Wulder, 2019). Among these metrics, Gray level Co-occurrence Matrix (GLCM) indices (Haralick et al., 1973) are texture-based metrics initially developed in computer vision. They were later used in image classification tasks and still serve to calibrate oriented-object approaches (Morin et al., 2022; Le Louarn et al., 2017). GLCM indices have been successfully applied in ecological studies to derive continuous variables, and used to characterize present-day vegetation and bird communities (Farwell et al., 2021; Wood et al., 2013; Culbert et al. 2012a; St-Louis et al., 2009). Park and Guldmann (2020) showed their potential as an alternative to classical composition and configuration landscape metrics from satellite images acquired above the urban tree canopy in Columbus (Ohio, United States of America). Farwell et al. (2021) extracted GLCM indices from Landsat data to describe habitat heterogeneity in the USA. Wood et al. (2013) used aerial infrared photographs and Landsat data to calculate GLCM indices as a surrogate of vegetation structure in Wisconsin (USA). These authors found that texture-based indices had variable association levels following bird taxa, while information generated using 30 m resolution (Landsat data) was generally less successful than aerial photographs in predicting bird diversity.

In this study, our objective was to explore the potential and relevance of GLCM texture indices in reconstructing past landscape changes using historical aerial photographs and examining their influence on current biodiversity. Focus was placed on the evolution of built and high vegetation areas. This choice was motivated by ecological and societal concerns since urban environments are fast evolving (Moll et al., 2019) and strongly affect species diversity and composition (Alberti and Wang, 2022). To achieve this, a collection of panchromatic orthophotographs acquired on five dates by the National Mapping Agency (*Institut national de l'information géographique et forestière*, IGN) in the Strasbourg

Eurometropolis, France, was used.

Throughout this study, three central questions were addressed: (Q1) Can GLCM indices characterize present-time urban landscape composition using grayscale aerial photographs? (Q2) Can GLCM indices depict past landscape composition from old panchromatic aerial photographs and derive consistent landscape changes over time? (Q3) Are GLCM indices relevant variables to explore time lags in the species-habitat modeling, i.e., to what extent do current species communities depend on past landscape features?

2. Materials and methods

2.1. Study area

This study takes place in the Strasbourg Eurometropolis in north-eastern France, comprising 33 municipalities, 502,000 inhabitants with a population density of 1500 people/km² (INSEE, 2019). The survey area covers 250 km² of the northern part of the Eurometropolis due to the availability of historical spatial data. It includes built areas (7 %), artificial non built areas (mainly roadways, parking, and bare soil, 16 %), crops (31 %), low and herbaceous vegetation (16 %), high vegetation (i.e., trees, 28 %), and open water (3 %) (Fig. 1, Sertit 2017).

The study area extends over an entire urbanization gradient for 2015 landscapes. This was necessary to feed our models with non-urbanized landscapes, so we can include urban sites that were not yet urbanized at the start of the historical period under consideration (1966).

Strasbourg's urbanization pattern follows a similar trajectory to other industrial cities in Western Europe. The city, first organized around a medieval city center, experienced rapid population growth alongside industrial development in the 19th century, simultaneously with the arrival of the German administration in 1870 (Igersheim, 2011). By the late 1950 s, densely populated urban areas emerged near the initial urban core while post-World War II reconstructions occurred. The 1960–2000 decades witnessed urban expansion in the first and second rings, characterized by a discontinuous urban fabric, housing private residences, leisure facilities, and commercial and industrial activities. In the early 2000 s, densification policies aimed at curbing sprawl and promoting high-rise residential buildings appeared, marking a shift in *peri*-urban development (Héraud and Nonn, 2013). Overall, built areas increased from 400 ha in 1956 to 950 ha in 2017. Regarding Strasbourg's tree heritage, the majority of the trees lining the city's core and ornamental trees were planted in the late 20th century, influenced by the hygienic movement—an ideological and political trend implemented by Adolphe Alford in Paris during that century. Later, after the end of World War II, considerable rebuilding took place in the city, accompanied by massive tree planting and green space creation. Throughout our study period (i.e., 1956–2017), the wooded areas doubled to 4100 ha in 2017, with a sharp increase recorded after 2008 (+35 %, + 122 ha/yr).

2.2. Orthophotographs

Landscape evolution was reconstructed using panchromatic orthophotomosaics (Giordano, Le Bris, and Mallet, 2017) covering the 250 km² of the study area for five dates: 1966, 1976, 1986, 2000, and 2015 (Fig. S1). These images exhibited the highest conservation level while covering the most extensive geographical surface. The time perspective of approximately 60 years and regular time gaps of around 10–15 years between orthophotographs were crucial for reconstructing landscape dynamics over multiple decades (Fig. S1). First, this allows for the exploration of the continuous effects of profound modifications due to urban expansion in the first and second rings of the city. These changes partly led to transformations of agricultural areas towards different levels of urbanization with potential time lag effects on current biodiversity. Second, a 10–15-year frequency allows for the observation of a large gradient of changes between two dates that texture metrics can

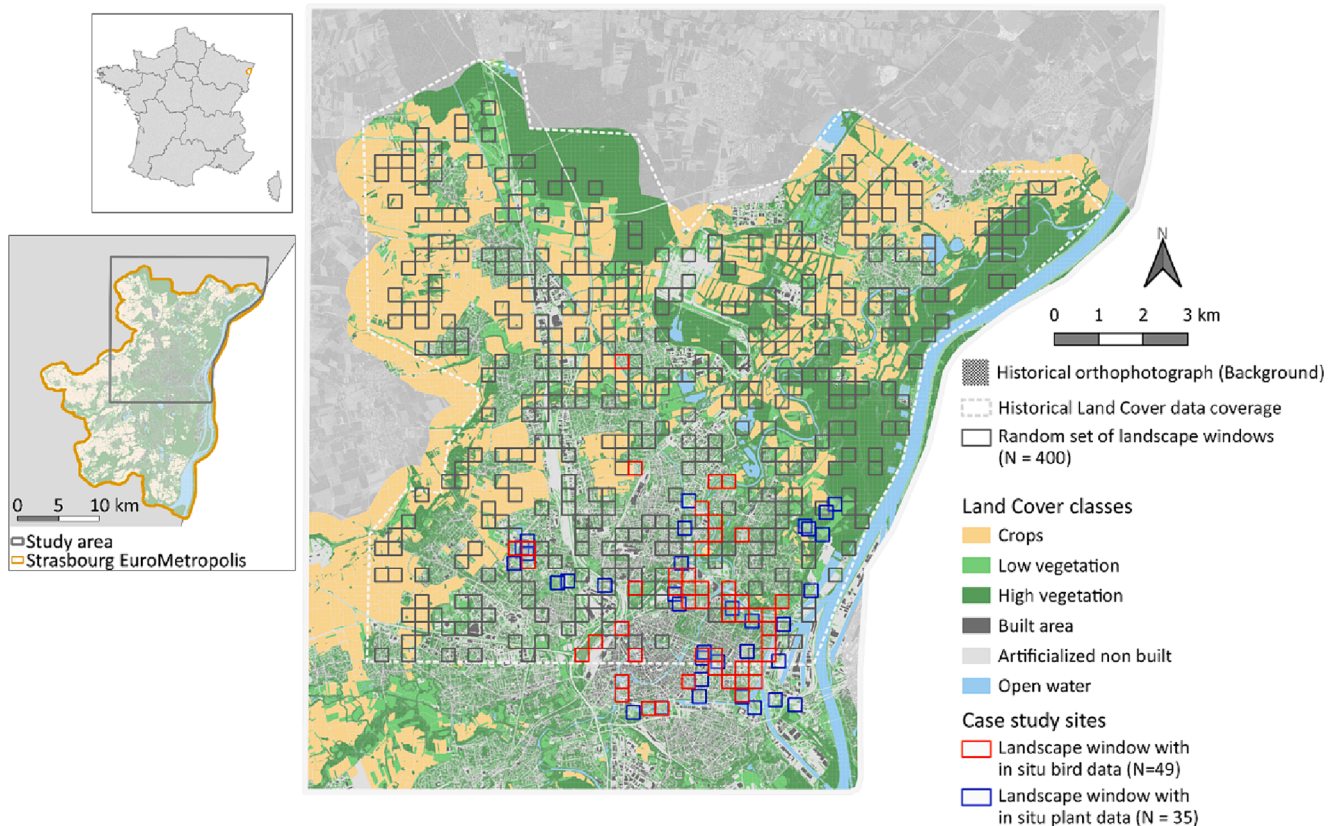


Fig. 1. Study area and spatial organization of data: vectorial map of the Strasbourg Eurometropolis (6 land cover classes) and black and white historical orthophotographs. Landscape windows used to assess the ability of texture in describing land covers, for present and past (Q1 & 2), are displayed in gray, while sites included in the ecological case studies (Q3) appear in red (birds) and blue (plants). The dotted white line highlights the spatial coverage of validation land cover data for the past.

easily capture. The RGB image from 2015 was converted to grayscale using a luminosity method and the following equation: $\text{grayscale} = 0.3 \cdot R + 0.59 \cdot G + 0.11 \cdot B$ (where R, G, and B are respectively the pixel values of red, green, and blue channels). Last, we performed two post-processing stages to increase consistency between dates: (1) all orthophotomosaics' spatial resolution were aligned on 1 m by down-sampling to calculate texture metrics on similar spatial grids over time, and (2) the histograms of pixel intensities of each orthophotomosaic were adjusted against the 2015 Gy levels histogram using histogram equalization (R package *RSToolbox*, function *HistMatch*).

2.3. Land cover data

The land cover evolution of high vegetation and built areas was reconstructed using digitalized maps of these two land cover classes from orthophotomosaics acquired in 1956, 1978, 1995, 2008, and 2017 (Fig. S1). These historical data did not cover the entire study area for the 5 years, eventually representing 145 km² (Fig. 1). These two contrasted classes are easily recognizable in historical orthophotographs, no matter their quality or the acquisition date. Given the scarcity of historical land cover data, this offers the opportunity to produce it at reasonable spatio-temporal scales.

2.4. Landscape descriptions

2.4.1. Texture indices calculation

To describe landscape features based on orthophotographs, texture metrics were calculated, for each year, from the gray level values in 400 randomly distributed, non-overlapping landscape windows (300 m x 300 m), accounting for 30 % of the study area (Fig. 1). This window size

represents the best compromise for fitting the floristic and avian richness variations to the urban context (Muratet et al., 2008; Morelli et al., 2013; Keten et al., 2020). Two types of texture metrics were calculated on each landscape window discretized into 18 Gy levels: (1) the mean and Shannon diversity index of pixel brightness (i.e., gray levels) at the window level as first-order indices and (2) the contrast and homogeneity metrics as second-order indices (Fig. 3.). For this purpose, a 5x5 pixel (or m²) mobile square window was used within each landscape window (R package *GLCM Textures*) derived from the Gray level Co-occurrence Matrix (GLCM) (Haralick et al., 1973). Those indices reveal spatial patterns and neighborly relationships between pixels (Farwell et al., 2021; Hall-Beyer, 2017) (Table 1, Fig. 2). Each window was analyzed for eight second-order indices, by calculating the minimum, maximum, mean, and standard deviation of contrast and homogeneity. This resulted in a total of ten texture metrics. The number of discretized gray levels and the size of the mobile square window were determined following a sensitivity analysis of the relationships between textural and landscape metrics (Fig. S2).

Three main assumptions supported the selection of these texture metrics: (1) high vegetation exhibits dark, rough texture and should correlate with homogeneity and brightness (Park and Guldmann, 2020), (2) built areas display crisp edges (building footprint) and smooth surfaces (rooftop), which would likely correlate with homogeneity and contrast, and (3) diversity of gray levels should reveal the diversity of ecological habitats as illustrated in the spectral diversity theory (Rocchini and Neteler, 2012).

2.4.2. Vectorial land cover metrics computing

To evaluate the ability of texture-based metrics to describe landscape features, they were compared to three vectorial land cover metrics:

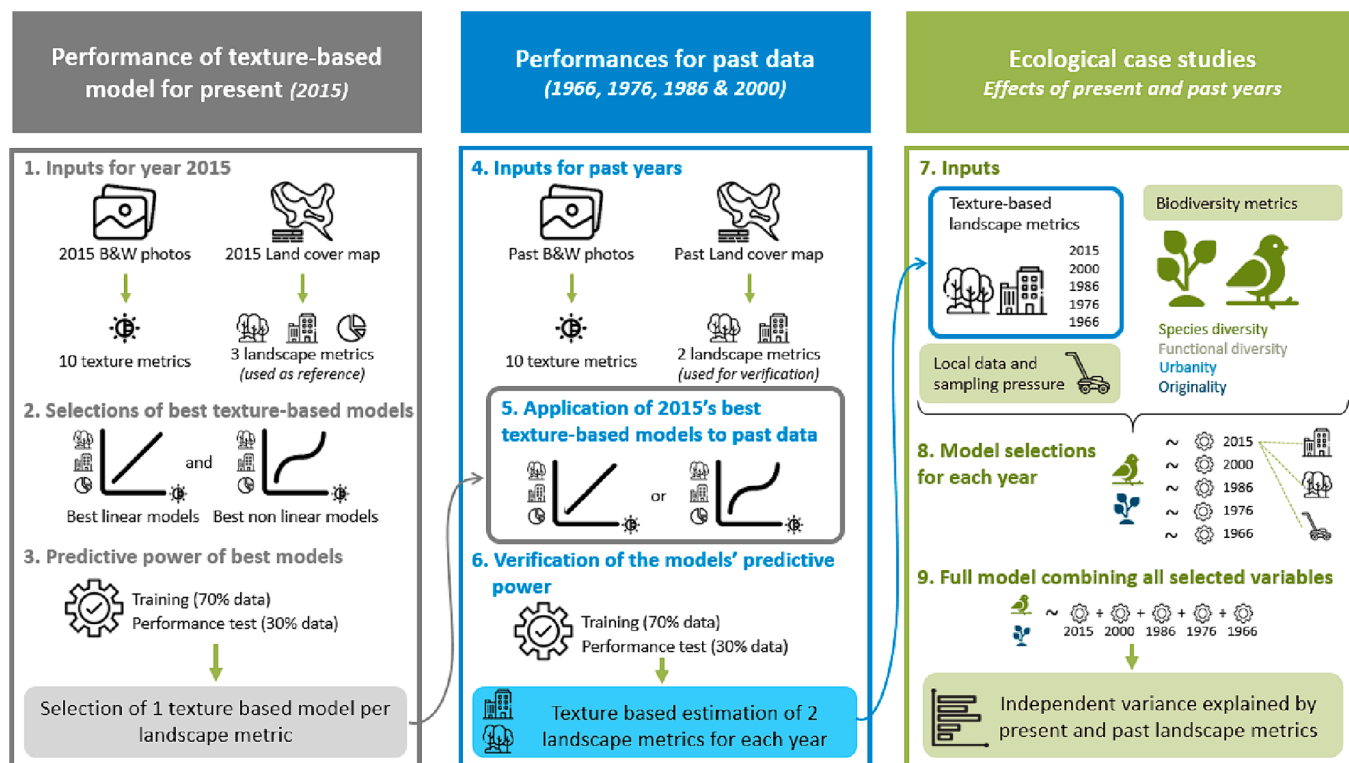


Fig. 3. Schematic and conceptual representation of the materials and methods used in the article.

ratios of (1) high vegetation and (2) built areas (in %) and (3) landscape diversity (Table 1) (R package *landscapemetrics*, Hesselbarth et al., 2019). Landscape diversity was computed for the present (2015) across six land cover classes: low vegetation, high vegetation, built area, non built artificialized area, cropland, and water. However, due to the availability of only two land cover classes in the historical data, past landscape diversity indices for previous years could not be derived.

Given the unavailability of categorized and continuous material (i.e., land cover maps and orthophotographs) for the same years, it was presumed that land cover metrics evolved approximately linearly between two dates. To enable the comparison of past texture metrics with land cover metrics, texture metrics were linearly interpolated between the two closest years of land cover data. These estimations were then used to compute and evaluate the model's performances.

2.5. Study case

2.5.1. Botanical data

Plant data were collected on 35 herbaceous sites of the study area covering a range of urbanization levels, from densely built areas to semi-natural forests (Fig. 1). The mean site area was 0.6 ha (min = 0.1 ha, max = 3.3 ha), and local management varied from no action to 15 mowings a year. Plants were surveyed between 2020 and 2022, during three consecutive years for 17 sites, two years for 15 sites, and one year for 3 sites, making up 84 site-year individuals. Vascular plants were systematically sampled in 15 quadrats (1 m x 1 m), distributed along three lines separated by 4 m, between June and July once a year.

In each site-year, species and functional richness were computed using a set of seven relevant traits that represent various functions and performances (see Fig. S3). The dbFD function (package FD, Laliberté et al. (2014)) was used in this purpose. Additionally, the Bioflor urbanity trait (Kühn and Klotz, 2006) was included to classify plant species into five urbanity categories and assess the weighted mean for each site. Site plant community uniqueness was evaluated by calculating its local contribution to beta diversity (LCBD) using the function `beta.div`

(package *adespatial*, Legendre and De Cáceres, 2013).

2.5.2. Bird data

Opportunistic data from citizen observations of bird occurrences were compiled by the "Ligue pour la Protection des Oiseaux" and obtained via the "Odonat" platform (Baouch and Gardet, 2022). Citizens reported species observations from various locations and times, resulting in large volumes of data. Only observations collected during the breeding season, specifically from March 15th to June 15th, between 2015 and 2018, were selected. Each observation was georeferenced, and bird occurrences were aggregated within a grid covering the study area. The grid displayed windows similar to the ones previously used to assess textural and land cover metrics (Fig. 1). This approach provided a unique list of bird observations for each window. To minimize observational biases, windows with insufficient data were excluded (less than ten days of accumulated observations and less than two years of data, $n = 49$ remaining windows). The species richness was computed for each window based on the number of species detected. Similarly to the botanical data, the functional richness metric was computed using eight traits from the life history characteristics of European birds (Storchová and Hořák, 2018, Fig. S3). The functional richness was calculated using the function `dbFD` (package FD, Laliberté et al. (2014)). Additionally, the urbanity score of French species (Guetté et al., 2017) was included in this study as the abundance-weighted mean for each site. Finally, the local contribution to beta diversity (LCBD) was added using the same methodology as for plant data (Bennett et al., 2014).

2.6. Statistical analyses

2.6.1. Textural metrics' organization

To understand the organization and potential redundancy among texture metrics, a Principal Component Analysis (PCA) was conducted with the ten texture metrics as variables and the four hundred landscape windows as individuals (Fig. S4). The R package used was *FactoMineR* (Lê et al., 2008).

Table 1
Description and formulas of studied land cover and texture metrics calculated at the window level (300 m x 300 m).

Type	Metric/Index name	Description	Formula
Vectorial Land cover Metrics	Built area	Percentage of Built area	$\frac{\text{Built area}}{\text{Total area}} \hat{A} \cdot 100$
	High vegetation	Percentage of High vegetation area	$\frac{\text{High vegetation area}}{\text{Total area}} \hat{A} \cdot 100$
	Landscape diversity	Shannon Diversity Index	$-\sum_{c=1}^{N_c} p_c \log_2(p_c)$
Continuous Texture Metrics	Homogeneity (Mean, min, max, and sd)	Describes image homogeneity and emphasizes the diagonal of the GLCM, which represents no change in gray levels between adjacent pixels.	$\sum_{i=0}^{N_g-1} \sum_{j=0}^{N_g-1} \frac{1}{1+(i-j)^2} \hat{A} \cdot g(i,j)$
	Contrast (Mean, min, max, and sd)	Describes the brutal changes in gray levels between adjacent pixels by emphasizing coefficients away from the diagonal of the GLCM.	$\sum_{i=0}^{N_g-1} \sum_{j=0}^{N_g-1} (i-j)^2 \hat{A} \cdot g^2(i,j)$
	Mean brightness	Measures the average gray level value of the image	$\sum_{i=0}^{N_g-1} \sum_{j=0}^{N_g-1} i \hat{A} \cdot g(i,j)$
	SHDI brightness	Diversity of represented gray levels	$-\sum_{g=1}^{N_g} p_g \hat{A} \cdot \log_2(p_g)$

With: N_c the number of classes in land cover data (here $N_c = 6$), N_g the number of gray levels in discretized images (here $N_g = 18$), p_c or p_g the proportion of class c or gray level g in the cell, $g(i, j)$ the coefficient of the GLCM matrix of indices i and j .

The size of the moving square window used in GLCM texture computation is 5 by 5 pixels (Fig. S2).

2.6.2. Present and past relationships between texture and land cover metrics

Model selection on current data – For 2015, the power of texture metrics (Homogeneity, Contrast, Mean brightness and SHDI Brightness) to predict the three land cover metrics (High vegetation, Built area, Landscape diversity) was evaluated. We standardized all variables before analysis. Generalized linear models and nonlinear generalized additive models were run separately for each land cover metric, leading to six model selections in total. For this purpose, the package *mgcv* was used (Wood, 2017). Within each selection, to enhance interpretability and prevent overfitting, we included only one or two texture metrics and their interactions ($n = 55$ models each). These models were ranked using the corrected Akaike information criterion (AICc) and those with $\Delta AICc < 2$ were retained (Fig. S5).

Predictive power assessment – For each land cover metric, the predictive power of the two best models (one linear and one nonlinear) was assessed by reporting R^2 , slope and intercept of the linear relationship between predicted values and observed values. We repeated this process 100 times using 70 % of the images randomly selected ($n = 280$) as

calibration data, while the remaining 30 % ($n = 120$) served as test data (Fig. S6). The texture-based model with the highest mean predictive power for each land cover metric was used for the rest of the study.

Application to past data – The selected models were applied to analyze past years' texture metrics, testing the consistency of the identified relationships with images from 1966, 1976, 1986 and 2000. The same bootstrapping method as described above was employed to obtain corresponding predictive power scores (Fig. S6).

2.6.3. Temporal trends in textural and land cover metrics

Using present and historical metrics datasets, annual growth rates of predicted and observed land cover metrics were estimated over the study period (1966–2015) using linear models with the year as the explanatory variable. The consistency of these metrics through time was assessed by examining the correlation between predicted and observed trends of land cover metrics.

2.6.4. Study case modeling

We assessed the influence of predicted land cover metrics (built area and high vegetation) for 1966, 1976, 1986, 2000 and 2015 in combination with site data (i.e. mowing frequency, sampling year for plants and sampling effort for birds) on four biodiversity metrics (species richness, functional richness, urbanity, and LCBD) for both plants and birds.

Variable selection for each year and each biodiversity metric – We compared (1) the full model, which included the predicted built area and high vegetation metrics for a given year and, site data, (2) every partial model derived from the full one and (3) the null model. We ranked models by the corrected Akaike information criterion (AICc, delta AICc < 2) and retained the corresponding variables.

Hierarchical partitioning – The selected variables for each year were included in a comprehensive cross-year model for each biodiversity metric. To avoid multicollinearity among explanatory variables, we performed a hierarchical partitioning using R package *hier.part* (Nally and Ralph, and Christopher J. Walsh. (2004)). This procedure assessed the independent and joint contributions of each explanatory variable. The statistical significance of the independent contribution was determined by computing a pseudo Z-score with 200 randomizations (function *hp.rand*, of package *hier.part*). To identify the direction of each effect – which is not provided by hierarchical partitioning – we modeled the relationship between each variable and the studied biodiversity metric in simple regression using linear models (Fig. S8).

3. Results

3.1. Texture metrics correlation

The two first axes of Principal Component Analysis (PC1 and PC2) explained 69 % of texture metrics variance (Fig. S4). On the one hand, PC1 is mainly driven by contrast standard deviation and maximum (contribution = 19 % and 15 % respectively) and by brightness SHDI and mean (15 % and 12 % respectively). PC2, on the other hand, depends mainly on homogeneity mean and maximum (26 % and 19 % respectively) and is opposite to contrast minimum and mean (20 % and 19 % respectively). When placing the landscape windows onto the PCA plan, they organize themselves according to the type of land cover, from agricultural to densely urbanized landscapes along PC1 and from forest to agricultural landscapes along PC2.

3.2. Selection and performances of texture-based landscape metrics for year 2015

The model selections consistently ranked in the highest positions models with two texture metrics and their interactions (Fig. 4 & Fig. S5). The models used for the rest of the study were selected by comparing the predictive performances (predictive R^2) between the linear and

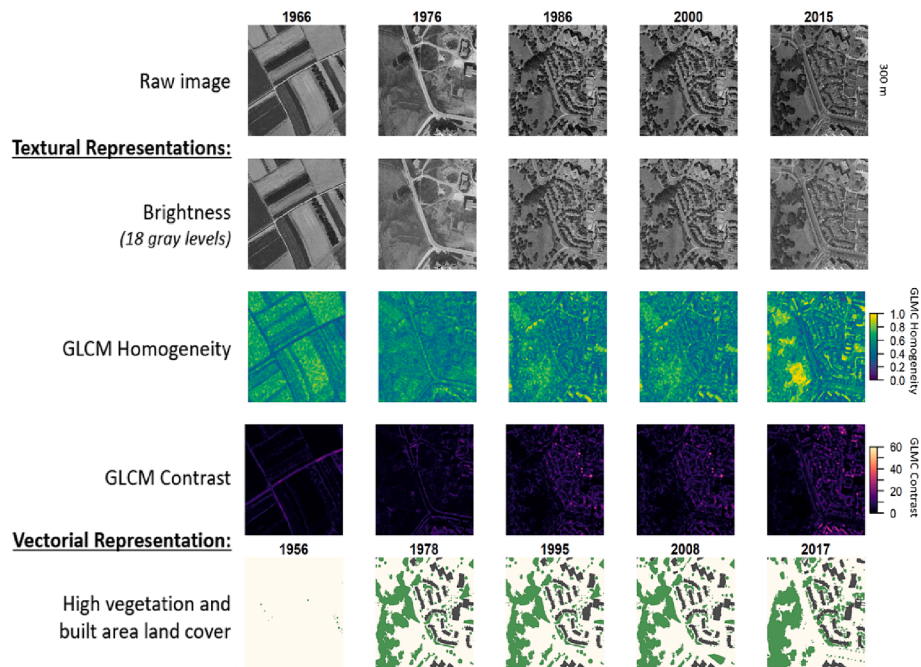


Fig. 2. Visual representation of landscape descriptions implemented in this study at window level. We represented raw images and landscape metrics (rows) across all years (columns) for one single landscape window (id point 1411; coordinates: 1046080, 6843312; Lbt93). Note that years of orthophotographs and vectorial land cover do not match.

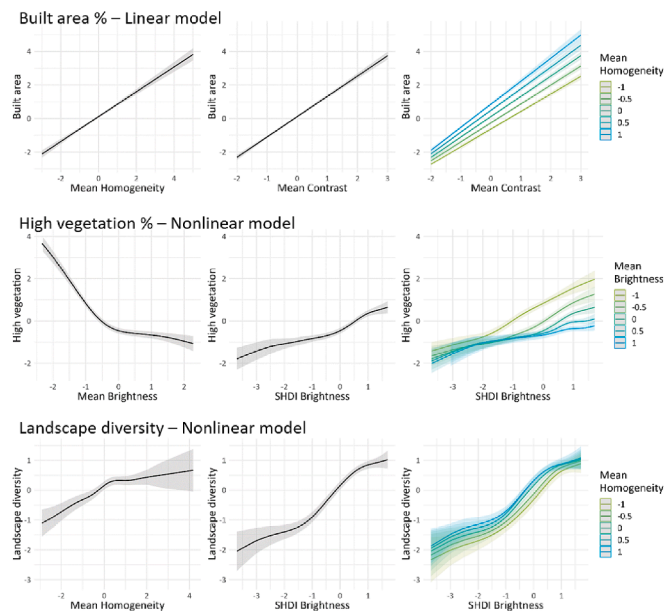


Fig. 4. Relationships between land cover and textural metrics issued from best selected models. Values for land cover and texture metrics were normalized. Represented slopes are for single variable models (or interaction only models).

nonlinear models. The linear relationship with mean homogeneity and mean contrast was the best to approach the built area (predictive $R^2 = 0.75$, Table 2), both being positively correlated with it, as well as their interaction term. The more homogeneous and contrasted the landscape, the more built-up it should be. The best high vegetation model combined nonlinear relationships with mean brightness and brightness SHDI, respectively having a negative and a positive correlation (predictive $R^2 = 0.85$). The interaction term modulated the role of brightness diversity where the darker the landscape, the higher the positive role of brightness SHDI. Landscape windows with high brightness diversity but low

mean pixel brightness values are more likely to be highly covered by high vegetation. The landscape diversity nonlinear model was the most efficient and was composed of two texture metrics from the previous models where mean homogeneity combined with brightness SHDI (predictive $R^2 = 0.74$), with positive relations and an interaction effect not as high as in the previous models.

Nonlinear effects modulated the impact of extreme values, except for the relation between the built area and homogeneity, where the model had a high effective degree of freedom (Table 2), producing a highly nonlinear relation.

The mean predicted values obtained via the selected models were 6.8 % for built areas with a confidence interval of [-3.7; 23.5 %] and 27.1 % [CI = 0.9; 92.6 %] for high vegetation, while for landscape diversity, the mean was 0.98 [CI: 0.11; 1.38]. For each land cover metric, the average values are in the same magnitude and range as for validation data. The intervals comprising 95 % of validation data are, for comparison purposes, [0.0 %; 30.3 %] for the built area, [0.0 %; 99.3 %] for high vegetation and [0.04; 1.55] for landscape diversity.

3.3. Application of the selected models over past years' data

When applying the selected models to past land cover metrics for the built area and high vegetation, the relationships between estimated and observed data followed the same patterns as for 2015 ($R^2 \geq 0.5$ for all years), except for 1966's estimation of the built area ($R^2 = 0.49$, Fig. S6). For all past years, the intercepts for the built area were consistently higher than 0 (min = 2 %, max = 6 %). In contrast, high vegetation intercepts showed negative values (Fig. S6) (min = -7.8 %, max = -4.5 %). A similar pattern was observed for the variations of the slope coefficient throughout the years. When there was a significant difference with the value of 2015, the coefficient tended to be higher than 1 for the built area and lower than 1 for high vegetation.

The linear regression between the temporal trends of actual and estimated land cover metrics returned an adjusted R-squared coefficient of 0.25 for high vegetation and 0.49 for the built area, with intercepts each time significantly different from 0 (0.17 ± 0.01 and -0.03 ± 0.01 respectively) and slope coefficients significantly different from 1 (0.39

Table 2

Linear and nonlinear models selected to predict land cover metrics through texture metrics for 2015. The Landscape Shannon Diversity Index was computed over six land cover classes. For linear models (Generalized Linear Model – GLM), coefficient values are given with mean +/- standard deviation based on a single simulation run over the total plot sample and according to the model's output. For nonlinear models, input models were Generalized Additive Models (GAM). edf stands for effective degree of freedom. The higher the edf value, the stronger the nonlinearity. The relationship was considered to be linear when $\text{edf} \leq 1$.

LINEAR SELECTED MODEL							
Vectorial Land cover Metric	Continuous Textural Metrics	Coefficients	P-value	AIC	Δ AIC	df	Predictive R ²
% Built area	Intercept	0.11 ± 0.03	<0.001 (***)	594	60	396	0.75[0.68 – 0.80]
	Mean Homogeneity	0.74 ± 0.04	<0.001 (***)				
	Mean Contrast	1.21 ± 0.04	<0.001 (***)				
	Mean homogeneity x Mean Contrast	0.16 ± 0.02	<0.001 (***)				
% High vegetation	Intercept	−0.08 ± 0.03	<0.01 (**)	642	61	396	0.71[0.61 – 0.78]
	Mean Homogeneity	−0.33 ± 0.03	<0.001 (***)				
	Mean Brightness	−0.46 ± 0.03	<0.001 (***)				
	Mean Homogeneity x Mean Brightness	0.25 ± 0.03	<0.001 (***)				
Landscape diversity	Intercept	−0.01 ± 0.03	0.86	623	39	396	0.72[0.66 – 0.78]
	Mean Homogeneity	0.28 ± 0.03	<0.001 (***)				
	SHDI Brightness	0.82 ± 0.03	<0.001 (***)				
	Mean Homogeneity x SHDI Brightness	−0.06 ± 0.03	<0.05 (*)				
NONLINEAR SELECTED MODEL							
Vectorial Land cover Metric	Continuous Textural Metrics	edf	P-value	AIC	Δ AIC	df	Predictive R ²
% Built area	S(Mean Homogeneity)	9	<0.001 (***)	487	132	393	0.73[0.42 – 0.85]
	S(Mean Contrast)	1	<0.001 (***)				
	S(Mean Homogeneity, Mean Contrast)	17	<0.001 (***)				
% High vegetation	S(SHDI Brightness)	1	<0.001 (***)	391	205	388	0.85[0.79 – 0.89]
	S(Mean Brightness)	1	<0.001 (***)				
	S(SHDI Brightness, Mean Brightness)	16.43	<0.001 (***)				
Landscape diversity	S(Mean Homogeneity)	1	<0.01 (**)	588	16	391	0.74[0.68 – 0.80]
	S(SHDI Brightness)	3.66	<0.001 (***)				
	S(Mean Homogeneity, SHDI Brightness)	9.31	<0.001 (***)				

± 0.03 and 0.65 ± 0.03).

3.4. Ecological case study: Textural indices explaining plant and bird communities

All models retained local and sampling data, and those variables were significant in seven of them (Fig. 5), explaining up to 18 % of plant metrics variations for mowing frequency, 10 % of plant metrics' variance for the sampling year, and 21 % of variance of bird metrics for sampling effort. The mowing frequency consistently negatively affected all plant metrics (Fig. S8) except urbanity, for which it was positive. The sampling effort positively affected bird species and functional diversity but negatively affected LCBD.

Six out of eight models explaining current bird and plant communities included estimated land cover metrics, with at least one playing a significant role in each case. The built area exhibited a better explanatory power of plants and birds than high vegetation. The predicted built area for 2015 accounted for up to 31 % of the variance across all groups and biodiversity metrics (Fig. 5). The past built area significantly explained plants' urbanity and birds' functional richness, with an explained variance up to 24 %. In most cases, the effects of the built area were negative (Fig. S8), with a lesser impact in past years, except for urbanity measures, where the built area had a positive effect, which was more pronounced in 2000 and 1986.

The high vegetation metric appeared in three models. It consistently negatively impacted plant species richness, with the past explaining more variance than the present metric (i.e., up to 5 % of explained variance). High vegetation also negatively impacted the bird urbanity score; this effect was stable for 2015, 2000, and 1986 and was responsible for up to 18 % of the variance. Finally, past years' high vegetation positively impacted plants' LCBD, explaining 11 % of the variance (Fig. S8, Fig. 5).

Urbanity relied on the past with higher explanatory factors than other biodiversity metrics, with plants' urbanity score impacted by the built area of years 1976–1986 and birds' urbanity score relying equally on high vegetation of years 1986–2015.

4. Discussion

In this study, we aimed to characterize present and past urban landscape composition (built and high vegetation areas) to measure the effects of historical landscapes and their temporal changes on current biodiversity. For this purpose, we used texture metrics derived from grayscale aerial photographs. Past texture metrics proved to be relevant variables to assess the effects of past landscapes on current plant and bird communities. However, we did not find temporal changes of texture metrics consistent with land cover changes across years, making them poor predictors of the landscape's temporal trends over a long-term period.

4.1. Texture characterization of urban landscapes

Overall, relationships between land cover and texture metrics showed high predictive performances for linear and nonlinear models. Our results demonstrated the potential for black and white photographs to assess some basic landscape features composing the urban – non urban gradient. Meanwhile, continuous descriptions of landscapes usually use complex data derived from remote sensing, such as NDVI (St-Louis et al., 2009; Wood et al., 2013; Park and Guldmann, 2020), requiring multi-band material, that is not commonly available before the rise of satellite imagery.

The selected models relied on brightness, mean homogeneity, and mean contrast, suggesting that other measures of texture indices (standard deviation, min, and max) have less explanatory power at the landscape level over a 300 m x 300 m window. Following our hypothesis, we found that homogeneity and contrast were significantly positively associated with built-up areas. Their combination may offer the advantage of reproducing spatial gradients of built areas in urban landscapes with their ability to characterize sharp differences among neighboring features and smooth surfaces. Our findings support the conclusion of a previous study exploring the potential of texture-based classification in urban landscapes using multispectral aerial photos (Mhangara and Odindi, 2013). The discrimination between high vegetation and built areas was more effective using homogeneity, while

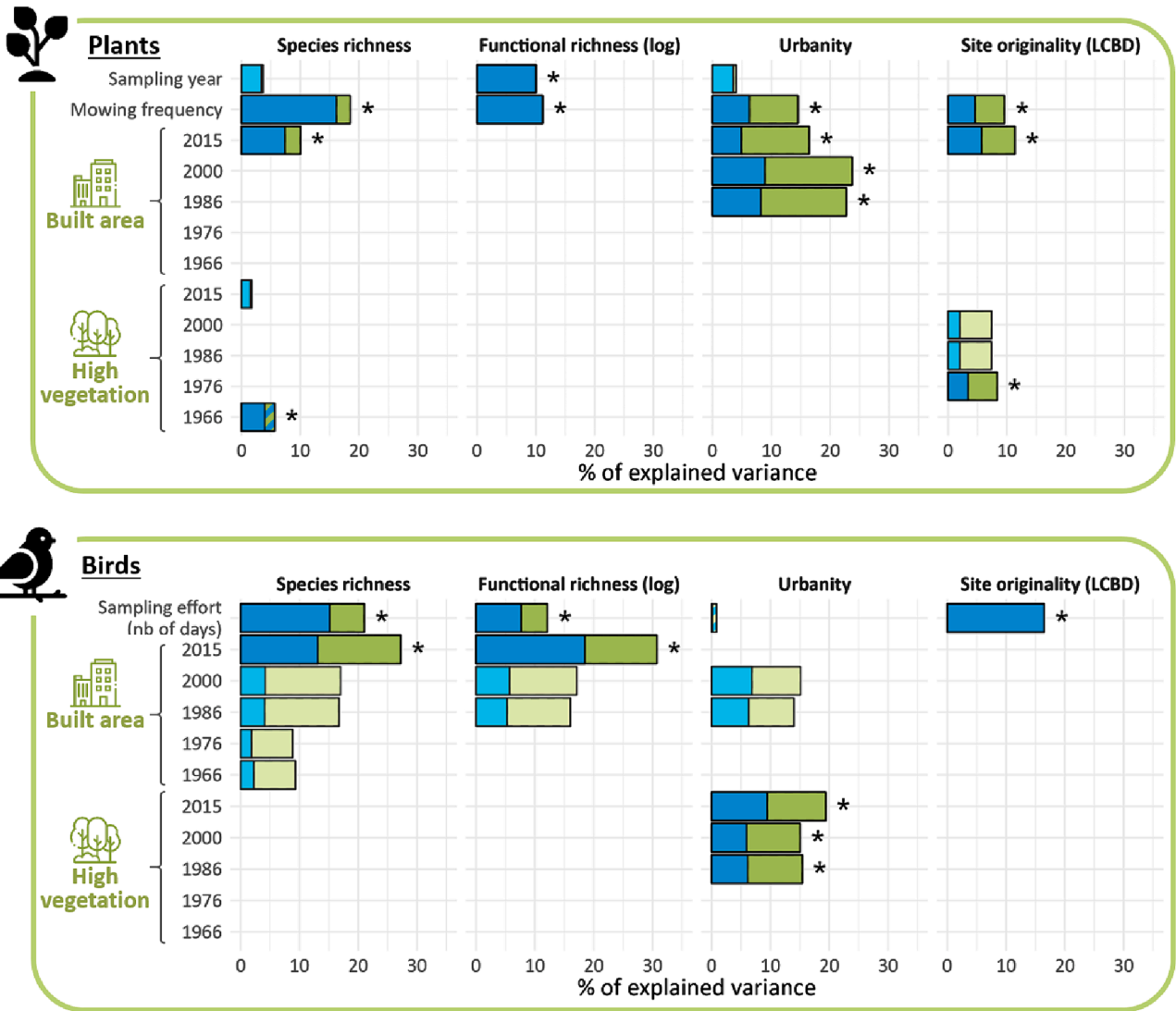


Fig. 5. Result of hierarchical partition for plants and birds. Each taxon was represented through four biodiversity metrics and included only the variables identified through the model selections for each year. The colored bars correspond to the relative influence of landscape variables on the assessed biodiversity metrics. Blue stands for independent contribution, while green represents the joint contribution. The model selection for birds’ site originality only returned sampling effort and did not include any landscape variable. Asterisks and darker colors mean a variable has a significant independent contribution (200 repetitions via hp.rand). Striped parts represent a negative joint contribution.

contrast was the most efficient metric for separating buildings from grass areas. Homogeneity and brightness were strongly related to high vegetation areas, as previously suggested by Park and Guldman in 2020, and Herold *et al.* in 2003 already noted homogeneity’s generalized contribution to characterizing different land cover classes with similar spectral characteristics. In this study, the latter texture metric contributes to separating all urban land use categories, underlying its essential role in characterizing the different elements of the urban matrix. In urban landscapes, high vegetation areas exhibit lower brightness values than others (except for water areas) (Avery and Berlin, 1992), making this texture metric effective for quantifying tree cover. Rough surfaces such as high vegetation cover were also well captured by homogeneity that quantifies the smoothness of an image with low values yielding high feature complexity. This is also consistent with previous studies, in addition to Mhangara and Odindi (2013) and Herold *et al.* (2003) cited above, that used homogeneity as a descriptor of vegetation complexity or heterogeneity (Farwell *et al.*, 2021; Culbert *et al.*, 2012). In Farwell *et al.* (2021), homogeneity was the best metric for estimating total bird richness across forests, grasslands, and vegetation sites in the United States. Lastly, we found that landscape diversity was significantly

associated with brightness SHDI, indicating that gray level diversity correctly reproduced land cover diversity in the orthophotographs.

Interactions between texture metrics were key variables for predicting spatial gradients of high vegetation, built-up areas, and landscape diversity in urban landscapes. Models with interactions systematically outperformed models with individual texture metrics. For instance, we found that homogeneity mitigated the effect of contrast on the percentage of built area. Although contrast may be sufficient to capture built-up areas, homogeneity may offer the advantage of better fitting specific built-up area types. We hypothesize that for similar levels of contrast, different levels of homogeneity featuring building rooftops may correspond to other classes, such as residential areas (moderate homogeneity) or industrial/commercial areas (high homogeneity). Following the same reasoning, in the linear model, the interaction between homogeneity and brightness was strongly related to the percentage of high vegetation. This may reflect that for high vegetation areas (low homogeneity), the interaction with brightness contributes to better capturing the tree composition by describing different vegetation types (e.g., species or management regime). In the nonlinear model predicting high vegetation areas, brightness SHDI, in combination with

mean brightness, replaced homogeneity. Brightness SHDI was decisive in discriminating dark and uniform plots, corresponding to agricultural landscape windows, from dark and diversified ones, related to high vegetation cover. Lastly, besides the role of metrics' interactions, our results also showed that the nonlinear effects in the models allowed us to capture more complex features with texture metrics. We found flattening yield relationships between texture and land cover metrics for extreme values (Fig. 4). This suggests that nonlinear models can correctly adjust orthophotographs saturation problems for very low or high values of land cover metrics.

Our results promote the interest of rethinking processes using spatial archives to reconstruct ecological habitat dynamics (Coops and Wulder, 2019) over a long period. Indeed, our texture-based modeling framework was successful in predicting past landscapes. We propose an alternative to the paradigm of producing discrete maps to calculate past land cover metrics to include a historical perspective in ecology studies. The texture-based approach greatly facilitates past landscape characterization by offering the opportunity to maximize the potential of long-time spatial archives. The proposed methodology paves the way for studying possible time lags of biodiversity in response to habitat disturbances.

We, however, found a decline in the performance of texture models over time, indicating substantial impacts of decreasing quality in orthophotographs on landscape description. On the one hand, this is particularly true for built-up areas. Crisp edges of buildings tend to be less clearly defined over time due to blurring effects and conservation levels in orthophotographs. It could negatively impact the computation of texture metrics, such as contrast featuring sharp transitions among pixels. On the other hand, brightness mean and diversity were more performant in capturing high vegetation areas due to the higher robustness of brightness derived variables to noisy black and white photographs. Given the sensitivity of texture metrics, we suggest that aerial missions should be carefully chosen to ensure a minimum quality threshold before applying the developed approach.

Applying the present texture-based models to past years showed a reverse trend in error estimates of built-up and high vegetation areas. Texture metrics generally overestimated built areas due to a positive systematic error corresponding to the intercept difference with 2015's model (Fig. S6.a). Also, the slopes of past coefficients were higher than 2015's, meaning that this overestimation was even greater for high percentages of built-up areas. In addition to radiometric quality issues, profound modifications in the global aspect of built-up areas through the years may explain the difficulties of the present texture-based models to perform in past years. Secondly, the high vegetation area was underestimated (Fig. S6.b). Seasonal differences between the present and past aerial missions may help understand this error. Compared to most recent orthophotographs taken in spring, the two oldest orthophotographs were acquired in winter, when most trees had no leaves, which could explain the underestimation. We also hypothesize that temporal mismatches existing between validation databases and the selected aerial missions may partly explain the differences. Although we had performed linear interpolation of land cover metrics between dates to match orthophotographs' years, changes occurring during these periods may be nonlinear.

Past land cover estimates based on texture metrics allow the reproduction of relevant spatial gradients at each date. However, error propagation through the years makes it challenging to assess landscape changes. The intercept of linear regression between texture-based and land cover based change coefficients did not equal zero for built-up or high vegetation areas. Uncertainty in the direction of changes made temporal trends from estimated land covers unreliable. It reduced its potential for understanding the role of land use history on biodiversity and ecological systems (i.e., legacy effect, Yang et al., 2017). However, we could evaluate which years were most involved in shaping present biotic communities (i.e., a time lag assessment, Kuussaari et al., 2009).

4.2. Ecological case studies

We validated our hypothesis that texture-based land cover estimates, for both present and past, significantly affected birds and plant communities. This demonstrates that texture-based metrics effectively describe urban landscapes which themselves shape composition and diversity of species communities. Although our estimated metrics for the present had a higher explicative power than past ones on communities, we still identified an impact of urban landscape history on current biodiversity patterns. Time lags were longer for plants than for birds (e.g., 50 year versus 30 year time lags on plant and bird species richness respectively). This discrepancy in time lag differences was already evidenced in previous works, between 25 and 90 years for plants (Ridding et al., 2021; Cortina et al., 2022; Yang et al., 2017; Lindborg, 2007) and between 10 and 15 years for birds (Gauzère and Devictor, 2021; Haddou et al., 2022). We however improved precision of temporal lag estimation by using five different years instead of one, two or three dates in the other studies.

Our results demonstrate that community responses to current and past landscapes vary according to the community indices. We recorded a longer time lag for the urbanity score than for the functional richness for birds and plants, suggesting functional metrics to be more dynamic and quicker to adapt than urbanity. This latter metric's dependency on the past implies that some species with a high urban score, while preferring highly built landscapes, may need those landscapes to have experienced several decades since urbanization to benefit from them. This also indicates that land cover changes affect ecological communities with variable time dynamics, depending on the facet of the community considered.

The effect of texture-based landscape description on each biodiversity metric (Fig. S8) were consistent with the findings of numerous previous studies. Increasing built areas reduced the species number and the functional richness of bird assemblages. It also decreased the species richness and the β -diversity of plants. These patterns are likely due to the loss of ecological niches available for plants and birds in the most urbanized environments (see Keten et al., 2020; Padilla and Sutherland (2021) for birds and Ruas et al., 2022 for plants). We found that the urbanity score increased with built area (for plants) and decreased with high vegetation cover (for birds) (Guetté et al., 2017). We speculate that these different responses of the urbanity score between taxa may be due to the sensibility of forest birds to areas covered by high vegetation, whereas herbaceous plants are adapted to urban areas in our studied sites and mainly affected by the building's density. For birds, we did not find any landscape influence on birds' β -diversity, while we could have expected a positive effect of high vegetation (Bennett et al., 2014). Finally, we did not find any link between landscape composition and plants' functional richness. We however found a strong effect of mowing frequency on this metric, which may exceed landscape effect as plants' functional richness has been shown to be very sensitive to management intensity (Gros et al., 2023; Hall et al., 2020). All effects were consistent over the years – i.e., we did not find opposed effects for different years of the same landscape metric.

4.3. Perspectives and areas for improvement

Our work provides new insights into continuous metrics in biodiversity study as an alternative to more often used categorical metrics, but it is not without limitations. First, we limited our study to compositional metrics, focusing on two highly contrasted land use classes, the high vegetation, and the built areas, and did not investigate the potential to predict less distinctive ones, such as crops, low vegetation or water areas, which can appear similar on black and white aerial orthophotographs (Herold et al., 2003). Second, we did not explore the potential of texture metrics to predict landscape configuration (e.g., shape and mean patch size or connectivity), which is at least as important for biodiversity as compositional metrics (Moore et al., 2022; Lindborg, 2007). This

limitation is due to the lack of historical data on other land cover classes not studied here and needed for validating configurational texture metrics. In addition, the data was unsuitable for inter-annual comparisons as the historic orthophotographs presented many differences between years. This made it challenging to disentangle the interyear variations due to each year's specificities from the differences attributed to actual landscape changes. We look forward to updates on the treatment of this material, for which this is a common pitfall (Kataev et al., 2021), as such advancement could allow future studies to include continuous temporal gradients.

Finally, as we worked in a city undergoing some patterns in its spatial and temporal dynamics of landscapes, the sites included in our case studies only represented a subset of the conceivable landscape compositions and temporal evolution. For instance, we did not have any example of sites where the built area decreased with time, which prevented us from exploring the potential effects of this scenario on biodiversity. Furthermore, as Strasbourg has had a consistent history at the city level, the sites displayed a high level of multicollinearity in their present and historical landscapes.

5. Conclusion

In conclusion, we reiterate the interest and novelty of this study, which tackles the challenge of using historical orthophotographs, often overlooked in ecological studies, as source material. Its unique approach highlights the potential of texture metrics to describe current and past urban landscapes. We insist on the interest of using non-linearity and interaction terms in our statistical approach, as those two additions significantly improved the predictive performance of our models.

Our results provide new evidence of the lasting impact of landscape trajectories on biotic communities – up to several decades time-lag – that combine with effects of current landscapes and management practices on communities. Further studies should also consider biodiversity temporal dynamics and assess how they are inflected by spatio-temporal patterns of urbanization and urban densification as human-induced unbalance in biodiversity is a dynamic process unfolding through space and time.

Author contributions

All authors have conceived the article's ideas and methodology. S D has conducted the analysis and led the manuscript writing. F C, PA H, and A M have provided the data and supervised the analysis. All the authors reviewed and revised the manuscript during and after the writing process, and gave their final approval for publication.

CRedit authorship contribution statement

Suzie Derminon: Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization. **François Chiron:** Writing – review & editing, Supervision, Resources, Methodology, Conceptualization. **Audrey Muratet:** Writing – review & editing, Supervision, Resources, Methodology, Conceptualization. **Pierre-Alexis Herrault:** Writing – review & editing, Supervision, Resources, Methodology, Conceptualization.

Declaration of competing interest

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

Data availability

Data and code produced by the authors are available in an online repository following this link: <https://zenodo.org/records/10940024>.

Data not produced by the authors are referenced in the article and are to be requested directly from their producers.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2024.112002>.

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