



Distance from industrial complex, urban area cover, and habitat structure combine to predict richness of breeding birds in southeastern Tunisian oases

Foued Hamza^{1,2} · Asma Kahli³ · Mohammed Almalki⁴ · Mohamed-Ali Chokri¹

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Abstract

The rapid expansion of urban areas and industrial units has put much strain on natural environments and biodiversity. Quantifying the impact of human pressures on avian biodiversity is vital for the identification, preservation, and restoration of important areas. Here, data collected in 11 coastal Mediterranean oases were used to assess the impact of urban and industrial landscapes and habitat structure on the richness of breeding birds. Results of generalized linear mixed models analyses showed a quadratic effect of distance to the industrial complex on breeding bird richness, being optimal (6.41 ± 0.89) at 24 km. The results also showed a negative effect of the cover of urban areas. Our analysis also emphasized the importance of southern oases for breeding bird richness mostly because of their remoteness from the industrial complex and their significant coverage of fruit trees and natural ground cover. Variation partitioning analysis revealed that the shared fraction of industrial landscape, oasis habitat structure, and space was relevant in explaining the richness of breeding birds. It is highly recommended to (i) uninstall the Gabès industrial complex from this Mediterranean area, (ii) enhance the habitat quality in southern oases by planting other fruit trees, such as pomegranate and olive, and (iii) pursue scientific research in these Mediterranean coastal oases, as they offer a good opportunity for assessment and improvement of knowledge on both the impact of industrialization on quality of habitats and the richness of bird species.

Keywords Anthropogenic landscapes · Avian biodiversity · Conservation · Habitat features · Mediterranean oases

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✉ Foued Hamza
fouedhamza2010@gmail.com

Asma Kahli
asmakahli@hotmail.com

Mohammed Almalki
m11m116@hotmail.com

Mohamed-Ali Chokri
medali.chokri@gmail.com

¹ Département Des Sciences de La Vie, Faculté Des Sciences de Gabés, Université de Gabés, 6072 Zrig, Gabés, Tunisia

² Association Sauvegarde Des Zones Humides du Sud Tunisien, BP 86, Avenue Tayeb Mhiri, 6001 ,Gabés, Tunisia

³ Laboratoire Écologie Fonctionnelle Et Évolutive, University of Chadli Bendedid, El Tarf, Algeria

⁴ Department of Biology, College of Science, Taif University, P.O. Box 11099, Taif 21944, Saudi Arabia

Introduction

A remarkable acceleration in urban growth has been recorded during the recent decades (United Nations 2018a, b). The world's urban population has increased from 751 million people to 4.2 billion people between 1950 and 2018 (United Nations (2018a) Revision of world urbanization prospects, 2018). Also, this figure is expected to increase to 6.7 billion people by 2050, representing about 68% of the global population (United Nations 2018b). This accelerated human population growth has led to several adverse effects on natural environments, including deforestation, degradation of wetlands, and land conversion mainly in favor of human-modified landscapes, such as urban and agricultural areas (Brown et al. 2014; Hosonuma et al. 2012; Hansen et al. 2013). This rapid urban expansion has also led to the development of transport infrastructures, such as highways, roads, and railways, which have spawned habitat fragmentation and isolation (Li et al. 2010; Scolozzi and Geneletti 2012). These anthropogenic alterations have resulted in (i)

dramatic decline in biodiversity (McDonald et al. 2008; Reis et al. 2012) and (ii) significant impacts on the health and functioning of ecosystems (Clergeau et al. 2006; McKinney 2006; McDonald et al. 2008; Brose and Hillebrand 2016).

Industrialization, considered as one of the most extreme forms of environmental alteration, is now admitted as a major threat to biodiversity (Bernanke and Köhler 2008; Häder et al. 2020; Yuan et al. 2020). The rapid progress in the industrial sector has brought with it an increase in pollutant discharge. Several studies have reported that industrial waste leads to deteriorating environmental quality through air, soil, and water pollution (Khan and Ghouri 2011; Sujaul et al. 2013; Gupta and Shukla 2020; Yuan et al. 2020). Industrial pollution, namely, persistent organic pollutants, heavy metals, and gaseous pollutants, has exposed wildlife to toxicants and caused profound behavioral changes and adverse physiological effects (Steyn and Maina 2015; Sanderfoot and Holloway 2017). Exposure to industrial pollution may also reduce density and species richness in wildlife communities (Sanderfoot and Holloway 2017).

The region of Gabès, in southeastern Tunisia, is listed among the top most polluted cities in North Africa and the Mediterranean region (UNEP, MAP, 2012; Majdoub et al. 2018). Since the installation of the Tunisian Chemical Group (TCG) of phosphate treatment for fertilizer and acid production in the early 1970s, approximately 50 million tons of phosphogypsum have been released into the environment (Guillaumont et al. 1995). This industrial waste inherits several toxic and harmful substances, such as heavy metals (e.g., cadmium, copper, zinc, lead) and radionuclides (El Zrelli et al. 2018a, b). The TCG and related units are the main emitters of many gaseous pollutants, namely, sulfuric oxides (SO_x), nitric oxides (NO_x), ammonia (NH_3), and hydrogen fluoride (HF) (Majdoub et al. 2018). It is estimated that 17,652 tons of sulfur dioxide (SO_2), 717 tons of NO_x , and 311 tons of sulfur dioxide (NH_3) are released into the region of Gabès every year (Majdoub et al. 2018). The TCG also ejects a large quantity of particulate matter (PM) with a diameter $\leq 10 \mu\text{m}$ (PM_{10}) (Majdoub et al. 2018). It is estimated that 1,750 t/year of PM_{10} is discharged directly into the air (Majdoub et al. 2018). These industrial wastes result in a deterioration of air quality (Taieb and Ben Brahim 2014; Majdoub et al. 2018), ecosystems (El Zrelli et al. 2017; Majdoub et al. 2018), and biodiversity (Rabaoui et al. 2015; El Kateb et al. 2016).

In the Mediterranean basin, Gabès maritime oases are among the rarest in the world (Abaab 2012; Fayeche and Tarihouni 2020). They are characterized by the development of a mixture of cultivated and spontaneous plants organized into three main layers: palm trees, fruit trees, and herbaceous plants (Rhouma et al. 2020; Hamza and Hanane 2021). This agriculture system has been created by local farmers to exploit the available water in different ways and to diversify

the agricultural yield. Palm trees (*Phoenix dactylifera*) constitute the pillar of oases and form the upper floor (Twiti et al. 2009; Rhouma et al. 2020; Hamza and Hanane 2021). This layer is characterized by the predominance of common varieties, such as Bouhattam, Rochdi, and Lemsi (Twiti et al. 2009; Rhouma et al. 2020). The intermediate layer is mainly dominated by many species of fruit trees, such as pomegranate (*Punica granatum*), olive (*Olea europaea*), apricot (*Prunus armeniaca*), and common fig (*Ficus carica*), which grow in the shade of date palms (Twiti et al. 2009; Rhouma et al. 2020; Hamza and Hanane 2021). The lowest layer consists of various vegetable crops, fodder crops, industrial crops, and spontaneous plants (e.g., tomato (*Solanum lycopersicum*), alfalfa (*Medicago sativa*), the henna tree (*Lawsonia inermis*), tobacco (*Nicotiana tabacum*), and Bermuda grass (*Cynodon dactylon*) (Twiti et al. 2009). With more than 300,000 date palms and a large diversity of fruit trees (Ben Salah 2011), the oases of Gabès provide central ecosystem services and benefits, such as food resources (Abaab 2012; MEDD 2015), resistance to land erosion (Haj-Amor et al. 2020), and climate change (Haj-Amor et al. 2020).

Oases of Gabès constitute hotspots for birds where exceptional richness is observed (Isenmann et al. 2005; Hamza and Hanane 2021). They provide a suitable habitat for several species during wintering season (Isenmann et al. 2005; Hamza and Hanane 2021). Gabès oases are also recognized as the key stopover for many trans-Saharan migratory birds in the Black Sea/Mediterranean flyway (Isenmann et al. 2005). Many Afro-Palaeartic migrant species use this agroecosystem both during spring migration on their way to the breeding areas in the Northern Hemisphere and during autumn migration when they return to wintering sites south of the Sahara (Isenmann et al. 2005). Many desert and non-desert-adapted bird species, such as common blackbird (*Turdus merula*), common chaffinch (*Fringilla coelebs*), and European serin (*Serinus serinus*), also depend on these oases during the breeding period (Isenmann et al. 2005; Hamza and Hanane 2021). Despite their importance, these oases have been strongly modified, degraded, or lost as a consequence of anthropogenic activities (Medhioub 2002; Abaab 2012; MEDD 2015; Arfa et al. 2017; Fargette et al. 2019; Katlane et al. 2020). Urbanization remains among the most pressing threats for this agroecosystem (MEDD 2015; Arfa et al. 2017; Carpentier 2017; Carpentier and Gana, 2017; Fargette et al. 2019). Indeed, human population density within the Gabès region has increased by 12.4% between 2004 and 2014 (Municipality of Gabès 2020). This rapid increase has led to the expansion of urban areas while bringing profound changes in the structure and function of the oasis system (Abaab 2012; Katlane et al. 2020; Rhouma et al. 2020). It is estimated that the oases of Gabès have lost 30% of their palm trees since the colonial era (Ben Salah 2011; Carpentier and Gana 2017). According to Carpentier

and Gana (2017), the oases of Gabès have lost about 10 ha yearly since the 1980s (Carpentier and Gana 2017). This rate has doubled after the Tunisian revolution in 2011, mainly due to the weak rule of law (Carpentier 2017; Carpentier and Gana 2017). As a result, many oases have been transformed into city oases (Abdedaiem and Veyrac-Ben Ahmed, 2014). In addition to urbanization, the growing industrial development in the Gabès region has also posed the loss of the soil and vegetation of oases (Medhioub, 2002; Abaab 2012; Rhouma et al. 2020). Furthermore, the overexploitation of groundwater by industrial and urban areas has decreased water availability in oases, which caused the abandonment of some plots (Abaab 2012; Katlane et al. 2020; Rhouma et al. 2020). These anthropogenic transformations have harmful consequences on bird communities inhabiting these oases. Understanding how intense human activities affect bird communities is essential for their management strategies.

In recent years, increasing efforts have been devoted to understanding the effects of urbanization on avian biodiversity (e.g., Evans et al. 2018; Palacio et al. 2018). However, to our knowledge, less attention has been paid to the possible impacts of industrialization. Several research works on the effect of urbanization on the ecology of birds were conducted in North America (e.g., Green and Baker 2003; Minor and Urban 2010), South America (e.g., Silva et al. 2016; Leveau et al. 2017), and Europe (e.g., Jokimäki et al., 2002; Meffert and Dzioczek 2013). Less attention has been paid to North African ecosystems, like Tunisian oases, despite their socioeconomic contrasts and anthropogenic pressures. An accurate assessment of the impact of anthropogenic land uses, such as urbanization and industrialization, on bird communities is crucial to preserve biodiversity in this threatened ecosystem.

In this study, we used bird count data collected in 11 Tunisian coastal oases to investigate the effects of anthropogenic pressures and ecological factors on breeding bird species richness. More specifically, we evaluated the influence of urban and industrial landscapes, structure of oases' habitats, and spatial structure in shaping local bird richness. As it is admitted that air pollution affects birds' physiology and their breeding performance negatively (Eeva et al. 1997; Sanderfoot and Holloway 2017; Amri et al. 2018), we hypothesized that the richness of breeding birds increases as the distance from TCG increases. Given that in this studied region urban areas are expanded at the expense of oases (Abdedaiem and Veyrac-Ben Ahmed, 2014; Carpentier 2017; Carpentier and Gana 2017; Katlane et al. 2020), we hypothesized the presence of a higher breeding bird richness far away from urban areas. Previous works in the studied oases have also shown that the breeding success of birds depends on the structure of their habitats (Selmi 2007; Boukhriss and Selmi 2019). We, therefore, hypothesized the presence of higher avian species richness in oases with a high cover of fruit trees and natural

herbaceous layer compared to those dominated by date palm trees and cultivated ground.

Materials and methods

Study area

Our study area is located in the governorate of Gabès in the southeast of Tunisia (33°52' N 10° 4' E). This city has 374,300 inhabitants and covers an area of 7,175 Km² (Municipality of Gabès, 2020). This region is characterized by an arid climate with low average rainfall (100 to 200 mm) and an annual average temperature ranging between 18 and 20 °C (Jemai et al. 2016). The annual average evaporation ranges between 1500 and 2000 mm (Jemai et al. 2016).

In the region of Gabès, coastal oases cover approximately 7,000 ha and are considered among the fundamental components of the landscape (Kassah 1996; MEDD 2015). These ecosystems, mainly characterized by a high diversity of fruit trees (i.e., date palm trees and other fruit trees) and natural and cultivated herbaceous species, consist of small and contiguous plots belonging to several farmers. This region is also characterized by a high industrial activity focused mainly on chemical industries. The TCG is the main pollution source in the region with more than 95% of atmospheric pollution comes from its factories (Medhioub, 2002). In addition, the governorate of Gabès has experienced rapid urbanization over the recent decades, and the urban population has increased from 311,713 inhabitants in 1994 to 401,895 inhabitants in 2019 (ODS 2012, 2019). As a result, drastic changes have occurred in the oases (MEDD 2015; Majdoub et al. 2018).

In this study, 11 oases of different sizes were selected (mean surface areas (ha) 689.05 ± 461.92) (Fig. 1; Suppl. Table 1). These oases extend along the coasts of the Gulf of Gabès which give them a maritime climate. Kettana is the largest oasis, while Zarate is the smallest (Suppl. Table 1).

Bird survey

Bird surveys were carried out between 7th of June and 2nd of July 2020. This period was chosen because of the stability composition in bird community breeding in this area (Alaya-Ltifi and Selmi 2014; Hamza and Hanane 2021). In each oasis, bird species were recorded using the point count method with a fixed radius (50 m) (Bibby et al. 2000). Using the QGIS random selection tool (Quantum GIS Development Team 2018), a total of 264 point counts were selected randomly in the 11 oases.

In a second step, these coordinates were entered into a handheld GPS to determine their location in the oases. Bird surveys were conducted during the highest bird activity in

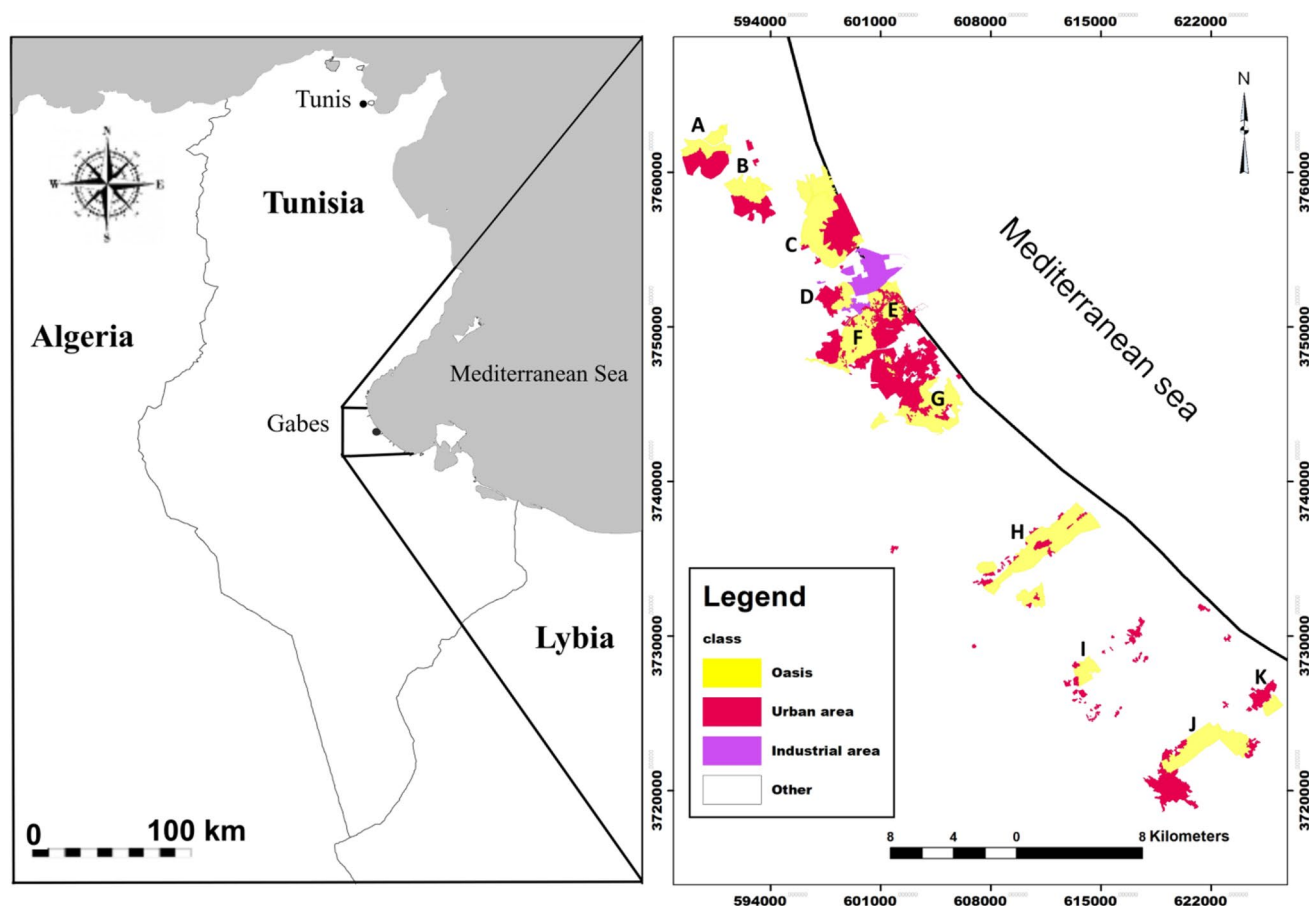


Fig. 1 Distribution of the eleven oases (Ouedhref (A), Matouia (B), Ghannouche (C), Bouchema (D), Chott Essalem (E), Cheneni (F), Teboulbou (G), Kettana (H), Zerkine (I), Mareth (J), Zarate (K)) in the coastal Gabès region

the morning hours (06:00 a.m. to 10:00 a.m.) and only under favorable meteorological conditions. At each point count, all the birds seen and heard within a radius of 50 m were identified and recorded for 10 min (Alaya-Ltifi and Selmi 2014; Hamza and Hanane 2021). Birds flying over the study plot were disregarded to minimize duplication in counts of birds. Counts were carried out by an experienced ornithologist (F. Hamza). Identification of birds was facilitated using 10×50 binoculars. Birds were surveyed at 15 to 40 point counts per oasis, depending on the oasis size. The minimum distance between two points was set to at least 200 m to prevent the risk of counting the same individual twice (Sandström et al. 2006).

Explanatory variables

Vegetation structure was characterized using a set of variables reflecting oasis features (Table 1). In each point count (50 m radius), we visually estimated six vegetation variables, including the covers (%) of the date palm trees, fruit trees, and natural and cultivated herbaceous layer, as well as the

number of date palm trees and fruit trees (Table 1) (Alaya-Ltifi and Selmi 2014; Hamza and Hanane 2021). Within each point count, three circular plots with a radius of 11.3 m (0.04 ha) (Haggerty 1998; D'Amato et al. 2009; Hamza and Hanane 2021) were randomly selected to characterize the vegetation. Around each sample point, date palm tree cover, fruit tree cover, number of date palm trees, number of fruit trees, natural herbaceous layer cover, and cultivated herbaceous layer cover were thus measured (Table 1). The mean values, resulting from the three repetitions (plots of 11.3 m radius) within each of the circular plots, were included in the statistical analyses. All vegetation parameter estimations were conducted by the same observer (F. Hamza) to avoid observer-related biases in the vegetation description (Prodon and Lebreton 1981).

Radius selection for the landscape-scale

To assess the effect of habitat at the landscape-scale, we used the spatial analyst tool in QGIS to calculate land-cover (i.e., covers of industrial and urban area and density of road)

Table 1 Values (mean, minimum, and maximum per point count) of structure of oasis habitats, industrialization, and urbanization variables in southern Tunisia

Variables	Code	Mean \pm SE	Min	Max
Structure of oasis habitats				
Date palm tree cover	DPC	5.86 \pm 0.60	0.00	50.00
Fruit tree cover	FTC	42.81 \pm 1.69	0.00	92.00
Number of date palm trees	NDP	38.18 \pm 3.01	0.00	260.00
Number of fruit trees	NFT	110.78 \pm 4.37	0.00	300.00
Natural herbaceous layer cover	NHC	51.30 \pm 1.65	10.00	94.00
Cultivated herbaceous layer cover	CHC	17.23 \pm 1.41	0.00	91.00
Industrial landscape				
Distance to industrial complex (m)	DID	14,543.09 \pm 813.27	73.49	37,329.64
Industrial area cover (%)*	IDC	0.09 \pm 0.06	0.00	16.19
Urban landscape				
Distance to the nearest urban area (m)	DUR	416.50 \pm 25.26	18.95	2,040.81
Distance to the nearest road (m)	DRD	261.42 \pm 12.05	1.16	1,085.24
Density of road (m/ha)*	DSR	14.02 \pm 1.04	0.00	49.64
Urban area cover (%)*	URC	6.02 \pm 0.69	0.00	68.63

around each point within eight radii, namely, 100, 200, 300, 400, 500, 600, 800, and 1000 m. To select the optimal radius for landscape variable measurements, we treated the sets of variables belonging to the eight different radii as competing sets of landscape variables and selected the radius leading to the most parsimonious models. The lowest value of Akaike information criterion corrected for small sample sizes (AICc) was obtained for the 200 m radius (Suppl. Figure 1), followed by those of 300, 400, 500, 600, 100, 800, and 1000 m (Suppl. Figure 1). Based on these statistical analyses, the 200 m radius was selected for the landscape-scale analyses.

Urban and industrial landscapes

To explore the impact of urban and industrial landscapes on the number of breeding bird species, we collected a set of variables related to urban industrial landscapes within a 200 m radius (see the previous section) from the center of each point count (Table 1). Specifically, we used a GIS analysis with QGIS desktop 3.2 (Quantum GIS Development Team 2018) to calculate (i) the distance to industrial complex (DID, m), (ii) the distance to the nearest urban area (DUR, m), (iii) the distance to the nearest road (DRD, m), (iv) the density of roads (DSR, m/ha), as well as (v) the covers of industrial (IDC, %) and urban areas (URC, %).

We classified the landscape using land-use and land-cover data from OS Mastermap (OSM) (Map data copyrighted Open Street Map OSM contributors available from <https://www.openstreetmap.org>). OSM polygon data were displayed in a GIS, and three land classes were identified (namely, the oases, i.e., polygons dominated by the orchards in the OSM land-use feature class; industrial areas, i.e., polygons of the industrial land-use in the OSM feature class; and urban

areas, i.e., polygons dominated by the residential areas in the OSM land-use feature class). We also used a road dataset derived from the OSM to calculate the DRD and the DSR (road length divided by the surface of the buffer). We chose Universal Transverse Mercator (UTM) zone 32 N based on UTM grid zones on a projected world map using the World Geodetic System WGS84 ellipsoid. All spatial analyses were performed using QGIS 3.2 (Quantum GIS Development Team 2018).

Statistical analyses

Statistical analyses were performed in R software, version R-4.0.3 (R Core Development Team 2020). For all of our models, the dependent variable was the number of bird species observed per plot of 7850 m² during the breeding period. To ensure normality, two explanatory variables were log-transformed and square root-transformed (DUR and URC, respectively). To avoid multicollinearity, the predictive variables were tested with the variance inflation factor (VIF) analysis (Quinn, 2002), using the “car” package (Fox and Weisberg 2011). The assessment of the multicollinearity between the eight explanatory variables (i.e., DID, IDC, DUR, URC, DRD, DSR, PC1, PC2) (Table 1) using the VIF allowed maintaining them for the subsequent analyses (VIF values ranged from 1.13 to 1.93).

Given that the six oasis habitat structure variables were intercorrelated, we performed a principal component analysis (PCA). A varimax normalized rotation was applied to the set of principal components with eigenvalues > 1.0 to obtain interpretable gradients (Legendre and Legendre 1998). Next we performed Kaiser–Meyer–Olkin test (KMO) to measure data adequacy for the PCA. After this stage of analysis, the generalized linear mixed models (GLMM) with Poisson

error distribution and log link function was performed (using the lme4 package in R, Bates et al., 2014) to test the effect of industrialization, urbanization, the structure of oasis habitats, and space on breeding bird richness. Study plots and point identities were included as random factors in the model to account for the potential non-independence of multiple observations at the same plot.

An all-inclusive design (all possible combination models) was developed using information-theoretic approach (Burnham and Anderson 2002). The models were then ordered by increasing Akaike information criterion corrected for small sample sizes using AICc (Burnham and Anderson 2002) and using the package “MuMIn” (Bartoń 2015). All models with ΔAICc lower than 2 were considered equally good (Burnham and Anderson 2002). We used model averaging over the set of competitive models (i.e., $\Delta\text{AICc} \leq 2$) to estimate the coefficients, SE, and p values for each predictor, included in the best AICc models with the “full average” output from the “model.avg” function (Guyot et al. 2017). The variance explained was calculated using the methods of Nakagawa and Schielzeth (2013). The marginal R^2 , which describes the variance explained by fixed effects, and the conditional R^2 , which describes the variance explained by the full model, were calculated using the package “MuMIn” and the function “rsquared.glm.”

To ensure that observations were independent of each other and to be able to address spatial autocorrelation in data before analyzing them, we implemented Moran’s index of the residuals of the best models based on AICc using the package “spdep” (Paradis et al. 2004). We assessed the significance of the values for each lag (900 m) with a Monte Carlo test of 999 permutations. A correlogram is significant if at least one lag results in $p < 0.005$ ($0.05/10 = 0.005$, a value at the corrected Bonferroni level). When spatial autocorrelation was encountered, we used spatial generalized linear mixed models fitted via penalized quasi-likelihood (glmmPQL), which enables the construction of spatial models with dependent data not normally distributed and is among the best techniques for this kind of data (Dormann 2007). We adopted an exponential spatial correlation structure; however, tests with Gaussian and spherical structures led to the same results. We also created spatial variables (Suppl. Tables 3 and 4) using Moran’s eigenvector maps method (MEMs) (Dray et al. 2006) that produces flexible spatial predictors through principal coordinate analysis of a truncated geographic distance matrix among different points while capturing spatial effects at multiple spatial scales. Because of the presence of spatial autocorrelation (Table 3; Suppl. Figure 2a, b), we created 11 spatial variables by means of Moran’s eigenvector maps (MEM47, MEM6, MEM76, MEM2, MEM16, MEM3, MEM12, MEM1, MEM11, MEM29, MEM28) to perform the variation partitioning (VP) analyses.

For subsequent VP analyses, we retained only the variables composing the final best AICc model with confidence intervals of parameter estimates not encompassing zero. VP was applied (package “vegan”) (Oksanen et al. 2013) to assess the specific contribution of industrialization, urbanization, oasis habitat structure, and space and their joint fractions to explaining the breeding bird species richness. We tested the significance of the unique fractions using the function “rda” from the vegan package (Oksanen et al. 2013). However, it was not possible to test the significance of the shared variation (Truchy et al. 2019).

To map the predictions of the spatial model (considering the estimates of glmmPQL) of breeding bird species richness, we used the ordinary kriging, a widely used interpolation technique (Sarker et al. 2016), thanks to its ability to provide estimates of unobserved locations of the studied variable (Setianto and Triandini, 2015) and to take into account the local variations in the mean (Tapia-Silva et al. 2015).

We used the package “visreg” (Breheny and Burchett 2012) to plot the relationship between the predicted bird species richness and the covariates included in the best AICc models. Means are shown \pm SE.

Results

A total number of 20 bird species belonging to 14 families were recorded across the 11 studied oases (Table S2). The families with the highest numbers of species were Columbidae (16% of species), Sylviidae (11%), Laniidae (11%), and Fringillidae (11%). The mean number of bird species recorded per plot was $5.25 (\pm 0.16)$, while the maximum and minimum were 13 and 1 species, respectively.

The PCA summarized the oasis habitat structure variables into two independent factors (PC1 and PC2) that accounted for 77.6% of the variance of the original data set and whose eigenvalues exceeded 1 (respectively, 2.60 and 2.05). PC1 (48.7% of the original variance) was positively correlated with fruit tree cover ($r = 0.821$, $p < 0.0001$), number of fruit tree species ($r = 0.818$, $p < 0.0001$), and natural ground cover ($r = 0.857$, $p < 0.0001$) but negatively with cultivated herbaceous layer ($r = 0.711$, $p < 0.0001$). High PC1 scores characterize oases dominated by fruit trees and a natural ground cover. However, PC2 (28.9% of the original variance) characterizes oases dominated by date palm trees with less presence of fruit trees, as it was positively correlated with date palm tree cover ($r = 0.968$, $p < 0.0001$) and number of date palm trees ($r = 0.977$, $p < 0.0001$) but negatively associated with fruit tree cover ($r = -0.307$, $p = 0.003$) and number of fruit trees ($r = -0.241$, $p < 0.006$). The Kaiser–Meyer–Olkin measure of sampling adequacy (KMO) indicated that our

data were suitable for the PCA (PCA, KMO=0.612; Bartlett test for sphericity, $\chi^2 = 1292.82, p < 0.0001$).

The models that best explained variations in breeding bird species richness are summarized in Tables 2 and 3. As can be seen in the two tables, the GLMM analyses indicate a positive effect of PC1 (Table 3; Fig. 2c), a negative effect of the URC (Table 3; Fig. 2b), and a quadratic effect of DID (Table 3; Fig. 2a). Breeding bird richness increased with increasing distance from the industrial complex, reaching an optimum of 6.41 (± 0.89) bird species at around 24 km and then decreased (Fig. 2a).

The significant spatial pattern in the residuals of our best AICc models was recorded (Table 3; Fig. 3a, b). When explicitly considering the spatial autocorrelation in the modeling through the glmmPQL models, the effect of all the aforementioned variables was maintained, in addition to that of PC2 (Table 3; Fig. 2d), which became very significant (Table 3). Oases with a higher richness of breeding birds are mainly localized in the southern part

of the study zone, namely, the oases of Kettana, Zerkine, Mereth, and Zarate (Fig. 4).

For the studied Mediterranean oases, the shared fraction of industrial landscape, structure of oasis habitats, and space was the most robust to explain breeding bird species richness (Adj. $R^2 = 0.21$) (Fig. 3). The unique fraction of space (Adj. $R^2 = 0.13, F = 5.065, p = 0.001$) and the joint effect of space and oasis habitat structure (Adj. $R^2 = 0.09$) were also important in explaining this richness. The joint effect of industrial and urban landscapes, structure of oasis habitats, and space (Adj. $R^2 = 0.06$) was also considered. Despite the weak contribution, the unique fractions of structure of oasis habitats (Adj. $R^2 = 0.04, F = 14.602, p = 0.001$), industrial landscape (Adj. $R^2 = 0.02, F = 6.185, p = 0.003$), and urban landscape (Adj. $R^2 = 0.01, F = 10.544, p = 0.001$) were statistically significant, highlighting a maximization of their contribution in explaining bird species richness when they are in association with space.

Table 2 The most supported models for the effect of structure of oasis habitats, industrialization, and urbanization on breeding bird species richness in southern Tunisia. Models are ranked according to Akaike’s information criterion corrected for small sample size (AICc). The degree of freedom (Df), difference in AICc from the

best-supported model ($\Delta AICc$), Akaike’s weights (w_i), -2 log-likelihood values (Loglik), and Moran’s index and p value of Moran test are shown. See Methods for details. The best model for each habitat and group of predictor variables is given in bold

Models	Df	Loglik	AICc	$\Delta AICc$	W_i	Moran’s I (p value)
DID + DID ² + URC + PC1 + PC2	8	− 532.137	1080.8	0.00	0.518	0.109 (0.0004)
DID + DID ² + URC + PC1	7	− 533.731	1081.9	1.06	0.305	0.106 (0.0005)
DSR + PC1 + PC2 + URC	7	− 535.542	1085.5	4.68	0.050	
PC1 + PC2 + URC	6	− 536.634	1085.6	4.76	0.048	
DID + DID ² + log (DUR) + PC1 + PC2	8	− 535.448	1087.5	6.62	0.019	
DSR + PC1 + URC	6	− 537.823	1088.0	7.13	0.015	
DR + PC1 + URC	6	− 537.884	1088.1	7.26	0.014	
PC1 + URC	5	− 538.944	1088.1	7.28	0.014	
DID + DID ² + log (DUR) + PC1	7	− 537.019	1088.5	7.64	0.011	
DID + DID ² + DSR + PC1 + PC2	8	− 537.477	1091.5	10.68	0.002	
Null	3	− 580.336	1166.8	85.93	0.000	

Table 3 Non-spatial and spatial model parameters (estimate; based on models with $\Delta AICc < 2$) and standard error (SE) from the best-supported oasis structure of oasis habitats and urban industrial land-

scape models on breeding bird species richness in southern Tunisia. See Methods for details

Non-spatial model (GLMM)						Spatial model (glmmPQL)				
Variable	Coeff	SE	z value	Pr ($> z $)	R^2	Coeff	SE	t value	Pr ($> t $)	R^2
Intercept	1.394	0.084	16.469	0.0000	$R^2_m = 0.462$	1.399	0.056	25.124	0.0000	$R^2_m = 0.481$
DID	4.423E-05	1.226E-05	3.591	0.0003	$R^2_c = 0.479$	4.060E-05	1.084E-05	4.159	0.0000	$R^2_c = 0.568$
DID ²	− 1.003E-09	3.130E-010	− 3.190	0.0014		− 0.0000000	0.0000000	− 4.700	0.0000	
URC	− 0.012	0.003	− 3.661	0.0003		− 0.011	0.003	− 4.354	0.0000	
PC1	0.246	0.039	6.759	0.0000		0.243	0.029	8.323	0.0000	
PC2	− 0.038	0.039	− 0.950	0.3419		− 0.062	0.026	− 2.404	0.0169	

Fig. 2 Predicted species richness of breeding birds (solid lines) as a function of distance to industrial complex (a), structure of oasis habitats (PC1) (b), urban area cover (c), and structure of oasis habitats (PC2) (d)

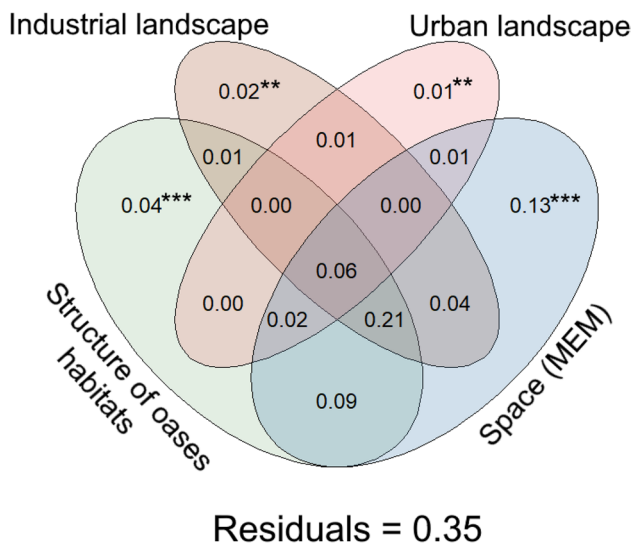
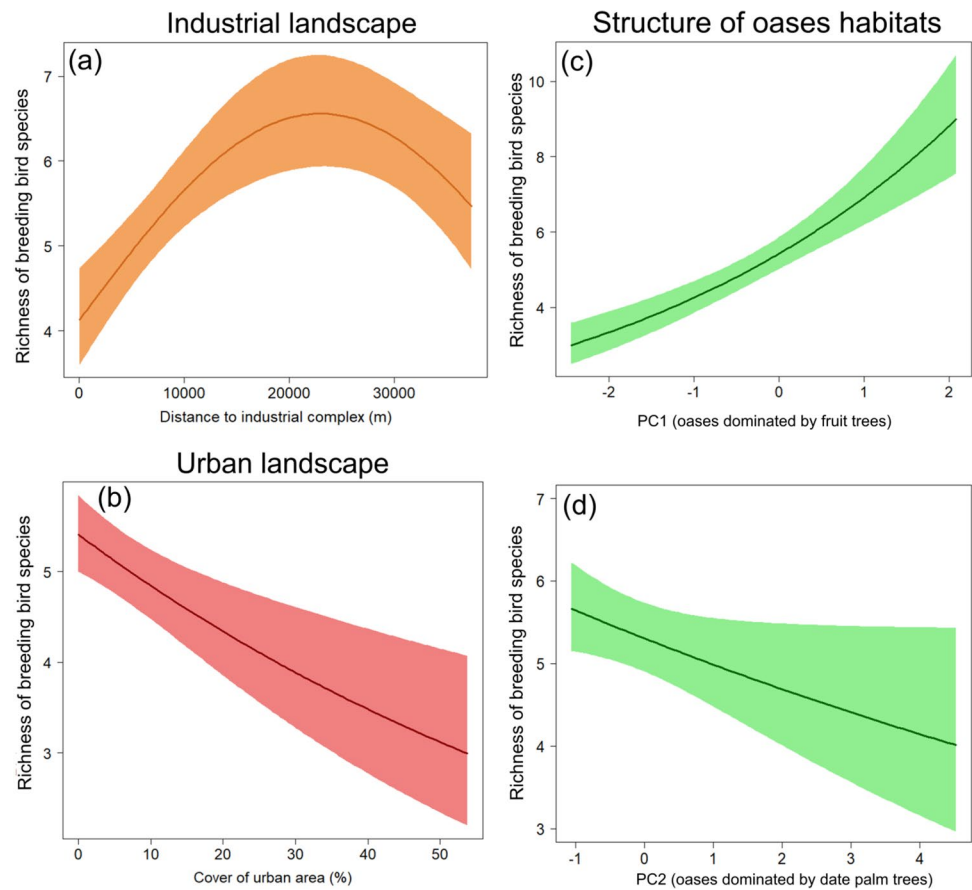


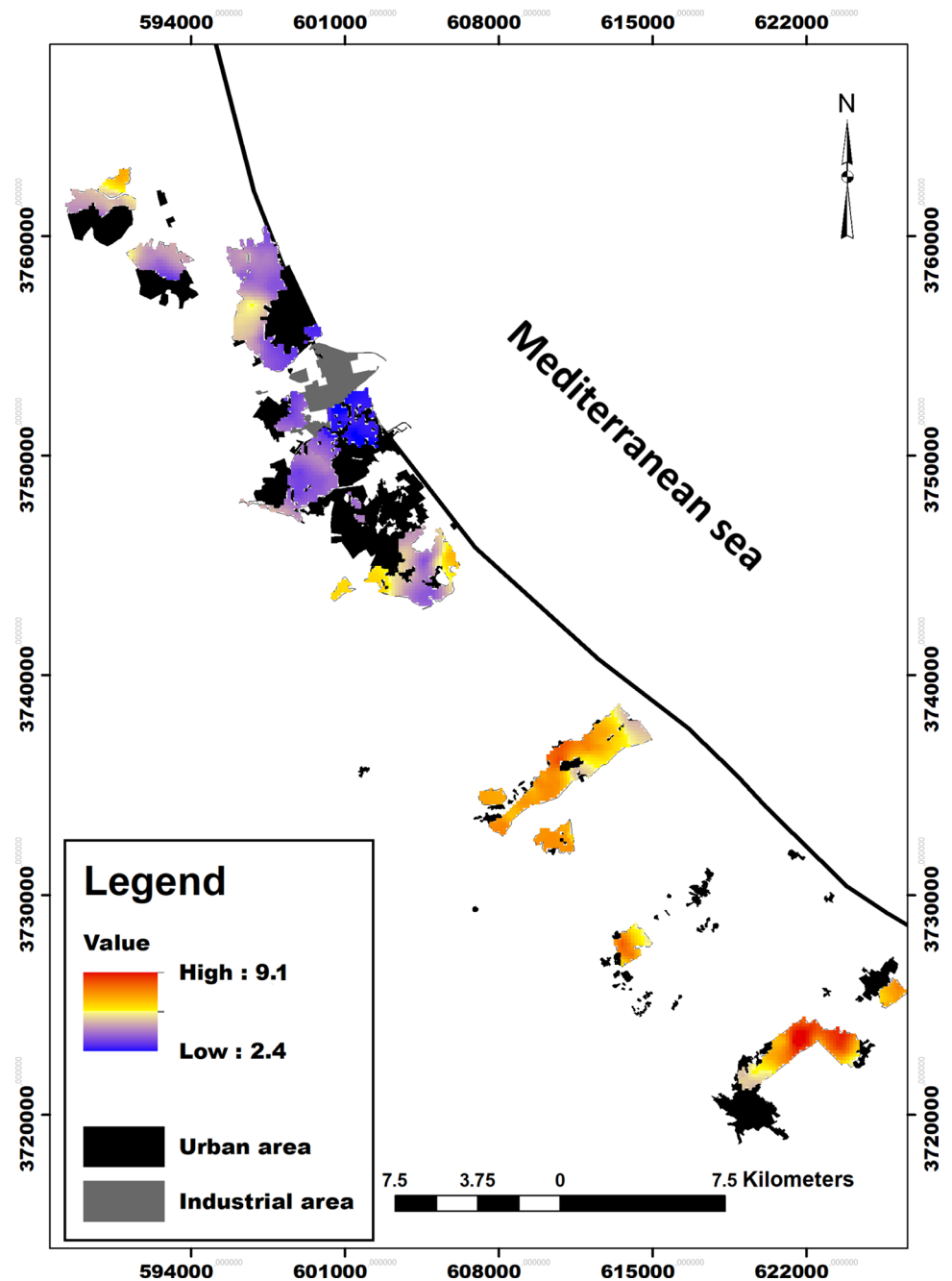
Fig. 3 Venn diagrams for variation partitioning showing the proportional contribution of industrial landscape, urban landscape, structure of oasis habitats, and spatial components (Moran's eigenvector maps [MEM] variables), in explaining breeding bird species richness in the coastal oases of Gabès region. MEM = Moran's eigenvector maps

Discussion

Our results highlight the importance of the urban and industrial landscapes and oasis habitat structure as predictors of bird richness in the Gabès region. Breeding bird richness is positively affected by the structure of oases' habitats dominated by fruit trees and natural ground cover. However, it is negatively influenced by the high cover of urban areas and the structure of oases' habitats dominated by date palm trees with a low presence of fruit trees. Bird richness also varies quadratically with distance to the industrial complex.

In agreement with our hypothesis, statistical analyses show that plots with a higher cover of fruit trees and natural herbaceous layer shelter high breeding bird richness. Similar results were recorded in Thailand by Jayathilake et al. (2021) who compared species richness in rubber (*Hevea brasiliensis*) agroforestry plantations and monocultures. A high tree cover is known to positively affect the richness of birds as it provides more food resources, sites for foraging, nesting, and perching (Luck and Daily 2003; Myczko et al. 2013; Jakobsson and Lindborg 2017; Godoi et al. 2018; Hamza and Hanane 2021). According to Hamza and Hanane (2021) and McKechnie and Wolf (2010), such cover also provides microclimatic refuges during periods of environmental stress, such as extreme heatwaves. The high breeding

Fig. 4 Representative map of predicted values of breeding bird species richness according to the best-supported oasis structure of oasis habitats and urban industrial landscape models



bird richness in oases dominated by fruit trees and the natural herbaceous layer is also related to the nesting activity. Indeed, several species use oasis fruit trees as nesting supports (e.g., olive and pomegranate *Punica granatum* trees), such as the European blackbird (*Turdus merula*) Selmi et al., 2003), the laughing dove (*Spilopelia senegalensis*) (Boukhriss and Selmi 2019), the rufous bush robin (*Cercotrichas galactotes*) (Alaya-Ltifi et al. 2015), the Orphean warbler (*Sylvia hortensis*) (Alaya-Ltifi et al. 2012), and the woodchat shrike (*Lanius senator*) (Alaya-Ltifi et al. 2012). These fruit trees are also used by some breeding bird species in other

Mediterranean agroecosystems, such as the European turtle dove (*Streptopelia turtur*) in olive trees (Hanane and Baïmal 2011; Hanane 2012), orange trees (Hanane 2018; Kafi et al. 2015), and apple trees (Mansouri et al. 2020). Orange and olive trees also shelter breeding populations of rufous bush robins (López and Gil-Delgado, 1988) and blackbirds (Taberner et al. 2012), respectively. In addition, fruit trees also provide secure nesting sites. The high cover of their canopies allows attracting breeding birds while allowing the concealment of their nests (Hanane 2012; Boukhriss and Selmi 2019).

In Mediterranean oases, higher breeding bird richness was recorded in plots with high natural ground vegetation cover. Similar results were reported by Díaz, (2006) in Spanish woodlands and forests, Ghadiri Khanaposhtani et al. (2012) in Iranian Kheyroud forest, Dagan and Izhaki (2019) in the pine forests planted in the Eastern Mediterranean, and Jayathilake et al. (2021) in Thailand rubber plantations. Indeed, according to our field observations, natural herbaceous plants constitute a source of seed supply for some granivorous species, such as the European turtle dove, laughing dove, and European serin. If these habitat features (i.e., PC1) are beneficial for breeding bird richness in the studied oases, their decrease or absence remains prejudicial (i.e., PC2). Indeed, oases dominated by a high cover of cultivated grounds are not as attractive for breeding birds as those sheltering high cover of natural ground vegetation. This difference would partly be attributed to human attendance, which is, by its nature, important in oases with the cultivated grounds. Indeed, daily agricultural practices, such as irrigation, mowing (the case of Alfalfa *Medicago sativa*), and weeding, are known to influence bird biodiversity (Gabriel et al. 2010; Jeliakov et al. 2016). Furthermore, the application of chemicals for agricultural needs also contributes to reducing breeding bird richness, as suggested by Jeliakov et al. (2016) in the cropping regions of northern France. By contaminating food sources, pesticides also affect the reproductive success of breeding birds (Kumar Arya et al. 2019). All these agricultural activities are, however, absent (except irrigation) in oases with natural ground vegetation, thus explaining the significant difference in breeding bird richness between the two types of oases (i.e., between PC1 and PC2).

As hypothesized, remoteness from the industrial complex has a positive impact on the richness of breeding birds until an optimum of 24 km and then slightly decreases. This spatial pattern in breeding bird richness may be due to the intolerance to toxic emanations (gases) ejected by the Gabès industrial complex. Indeed, previous studies, in the same study region, have highlighted a negative impact of these gases on some breeding bird species, such as, for instance, the rufous bush robin (Alaya-Ltifi et al. 2015), European blackbird (Alaya-Ltifi et al. 2012), Orphean warbler (Alaya-Ltifi et al. 2012), woodchat shrike (Alaya-Ltifi et al. 2012), spotted flycatcher (*Muscicapa striata*) (Alaya-Ltifi et al. 2012; Alaya-Ltifi and Selmi 2014), and serin (*Serinus serinus*) (Alaya-Ltifi et al. 2012; Alaya-Ltifi and Selmi 2014). A negative correlation between bird species richness and exposure to industrial air pollution has also been highlighted by several previous works (e.g., Belskii and Lyakhov 2003; Eeva et al. 2012; Belskii and Belskaya 2013a, 2013b; Alaya-Ltifi and Selmi 2014; Sanderfoot and Holloway 2017). The gradual increase of breeding bird richness as one moves away from the industrial complex can be due to the toxic

emanations which have negative effect on the number of bird species. However, this relationship is not linear since a decrease is recorded beyond 24 km. Such variation would be related to the quality of habitats in southern oases, especially those located close to urban areas. This is not surprising since urbanization is known to negatively affect the quality of habitats (Xu et al. 2018; Bai et al. 2019). In addition to its prejudicial role on the quality of habitats, and as hypothesized, a great cover of the urban area has a negative impact on the richness of breeding birds in the Gabès region. Although highly context-dependent (Chace and Walsh 2006), biodiversity loss due to urbanization is a relatively known process (Jokimäki and Suhonen, 1993; Aronson et al. 2014; Hensley et al. 2019). The need for shelters, nesting, and feeding places, usually provided by the fruit trees and natural herbaceous layer (context of Gabès region), would explain the decrease of the number of breeding bird species in the presence of an urban-dominated landscape.

Results of the Venn diagram analysis showed that the shared variation between industrial landscape, structure of oasis habitats, and space is robust in explaining the richness in breeding birds. The high richness of breeding birds is recorded far away from the industrial complex and in the oases dominated by fruit trees and natural herbaceous layers. These characteristics are overall met in four oases located in the south, namely Kettana, Zerkine, Mereth, and Zarate. Space is, therefore, relevant to explain the richness of birds, and its unique fraction explains alone 13% of the total variance. Nesting, feeding, and sheltering requirements are almost entirely satisfied at the level of the four southern oases. Although statistically significant, the contribution of the unique fractions of the structure of oasis habitats, industrial landscape, and urban landscape (4%, 2%, and 1%, respectively) is not very relevant in explaining the richness of breeding birds. Their contribution becomes nonetheless essential only when they are associated with space, mainly for the structure of oasis habitats (9%) and to a much lesser extent for industrial landscape (4%) and urban landscape (1%). Consequently, Kettana, Zerkine, Mereth, and Zarate are key oases for breeding birds in this southern part of Tunisia.

Conclusions, implications, and perspectives

Our experimental study suggests that, in the Gabès region, the industrial landscape (distance to industrial complex), oasis habitat structure (PC1 and PC2), and space (MEM) combine to predict the richness of breeding birds.

As the uninstallation of the Gabès industrial complex is very hard (at least currently), we are convinced that management actions should take place in the main oases of the south to improve their attractiveness for breeding birds.

Improving habitat quality close to urban areas in these oases would be beneficial for the breeding bird community of Gabès. To this end, two steps are to be considered: (1) encouraging oasis managers and owners to plant more fruit trees (e.g., apricot, olive, and pear trees) at the edge of urban areas and (2) carrying out awareness campaigns that target oasis owners and citizens living close to oases. Indeed, raising awareness of the planting interest would successfully carry them out in the field. Furthermore, the efficient and rapid growth of young fruit plants will not only depend on water availability but also on plant health (phytosanitary treatments if necessary). The financial contribution (subsidies) of the Tunisian Ministry of Agriculture to these agricultural operations is very desired to improve both fruit production (socioeconomic aspect) and vegetation structure (habitat quality).

We should not lose sight that our combined models explained only 65% of the variance. Therefore, there are still other not yet assessed covariate classes that may also influence the richness of breeding birds, including (i) food resources and (ii) predation. Future research works have to identify sensitive and non-sensitive species to industrialization and urbanization. Detecting and identifying affinities between breeding bird species (vis-à-vis industrialization and urbanization) would help manage them efficiently and effectively. Another research axis that has to be developed is identifying fruit tree species that could support high gas emanations. Knowledge of these species would serve to consider, in the medium term, possible fruit tree planting operations in the oases located close to the industrial complex. By their proximity to the industrial complex, the oases of Gabès remain of outstanding significance as they offer an opportunity to assess and improve knowledge on its detrimental impact on oasis habitats and wildlife diversity.

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Data availability The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

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