

Article

Responses of Bird Communities to Habitat Structure along an Aridity Gradient in the Steppes North of the Sahara

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Abstract: We explored the influence of habitat structure on bird density and species richness in the poorly known bird communities in the steppes of Eastern Morocco, along a 200 km long N–S gradient of increasing aridity. The birds were surveyed, and habitat structure was measured in 44 transects regularly distributed along the gradient and during the winter and spring seasons in two consecutive years. After applying a principal component analysis (PCA), five axes were identified, including one related to the latitude–altitude–soil-type gradient and another describing the development of herbaceous vegetation. Generalized linear models were used to explore the relations between bird density and species richness with PCA axes in each season, considering both the entire community and groups of granivorous, insectivorous, and mixed-diet species. More than 90% of the birds were year-round residents, with larks dominating the community in both seasons. We conclude that a distinct multifactorial response can be identified for each functional group of species. In the winter, the community is mainly affected by the structure of the habitat, while aridity (and its assumed relation to primary production) is less influential. In the spring, habitat structure continues to have the greatest explanatory power, but location along the aridity gradient becomes more relevant. These findings reveal the interaction of the negative effects of climatic and anthropogenic changes in the habitat available to these bird communities, with a greater impact expected on birds with diets that include seeds, as well as a general shift of optimal breeding conditions toward more northerly latitudes.

Keywords: aridity; bird assemblages; community variability; larks; Mediterranean; Morocco; passerines



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1. Introduction

The structure and composition of bird communities are variable in space and time [1], and the relative importance of the main governing factors continues to be debated among experts. At larger spatial scales, bird communities in arid–semiarid landscapes are thought to be relatively independent of habitat structure, and the role of climatic variables appears to be more influential [2–5]. The role of vegetation (habitat) structure as a determinant of bird abundance and species richness has been supported by approaches focusing on

local to regional geographical scales [6–10], where the relevance of terrain topography has also been invoked [5]. Aridity has been considered the main single structuring factor of steppe bird communities at regional scales, where the uneven distribution of rainfall drives pulses of primary production distributed irregularly both in time and space [11], which may be used by many vagrant and seasonal species [12,13]. In any case, most studies on the factors governing the structure and composition of bird communities in arid–semiarid environments have usually been conducted over a single time period and the variability between seasons (wintering/breeding) or years has rarely been considered (but see [14]).

Both aridity and land cover heterogeneity may have an impact on food resources for birds, ultimately determining the species diversity and richness in a given area (e.g., [15]). This relationship will depend on the use of resources within a community [16], so that the functional relationships manifested in terms of the feeding habits of birds in that particular ecosystem must be taken into account to show how climate and habitat changes influence community dynamics beyond individual species [17].

The steppes of eastern Morocco offer optimal conditions to assess the relative importance of the candidate factors for the explanation of the structure and composition of bird communities in arid and semiarid regions. The “Hauts Plateaux marocaines” expand over a wide area between latitudes of 34°23' N and 32°26' N and longitudes of 1°55' W and 2°33' W, comprising a north–south 200 km expanse free of geographical barriers, which could condition the distribution of species [18–20]. Along that expanse, rainfall decreases and temperature increases toward the south, determining a pronounced aridity gradient that covary with latitude (see the Methods section). Land cover is varied, with perennial bunch grasses, therophytes, chamaephytes, and nanophanerophytes, more or less degraded after pastoralist activities, cereal crops, and fallow land, and also bare soils with sandy, pebbly, or rocky surfaces.

In this study, we use latitude as a surrogate for aridity variation. However, latitude functions as a surrogate for many environmental factors, including vegetation structure, food availability, and altitude [21,22]. Therefore, we aim (a) to assess the relative importance of vegetation structure and latitude (aridity) as explanatory factors of the structure and composition of bird communities in eastern Morocco, which we expect to be different among bird species depending on their main diet; and (b) to explore the seasonal variation in the influence of the factors considered, which we expect to be different between the winter and the spring.

2. Materials and Methods

2.1. Study Area

The study area was located in the region of the Haut Plateaux in eastern Morocco, along a N–S strip of 200 km length, between the Col of Jerada and the south of Bouarfa (Figure 1).

Detailed meteorological data are not available for the entire area due to lack of meteorological stations, but climate data provided by the European Centre for Medium-Range Weather Forecasts (ECMWF; www.ecmwf.int/, accessed on 25 May 2023) have been used to produce monthly rainfall and average temperature series for four locations in the area, from north to south: Jerada, Ain Bni Mathar, Tendrara, and Bouarfa (available at www.climate-data.org, accessed on 25 May 2023).

The climate is characteristically continental Mediterranean (altitude between 930 and 1400 m.a.s.l.), with cool winters and hot summers (average minimum and maximum temperatures of the coldest and warmest months, respectively, 1.6 °C and 35.1 °C in Jerada, and 1.1 °C and 36.6 °C in Bouarfa), and rainfall concentrated in autumn and spring (averages of 311 mm/yr in Jerada and 135 mm/yr in Bouarfa). The Martonne aridity index [23] varies in the study area from 14 in the northern fringe of the gradient (semiarid) to 6 in the southern extreme (arid), while the Global Aridity Index [24] ranges from arid values in the north (0.03) to hyper-arid in the south (0.008), showing a clear relationship with latitude.

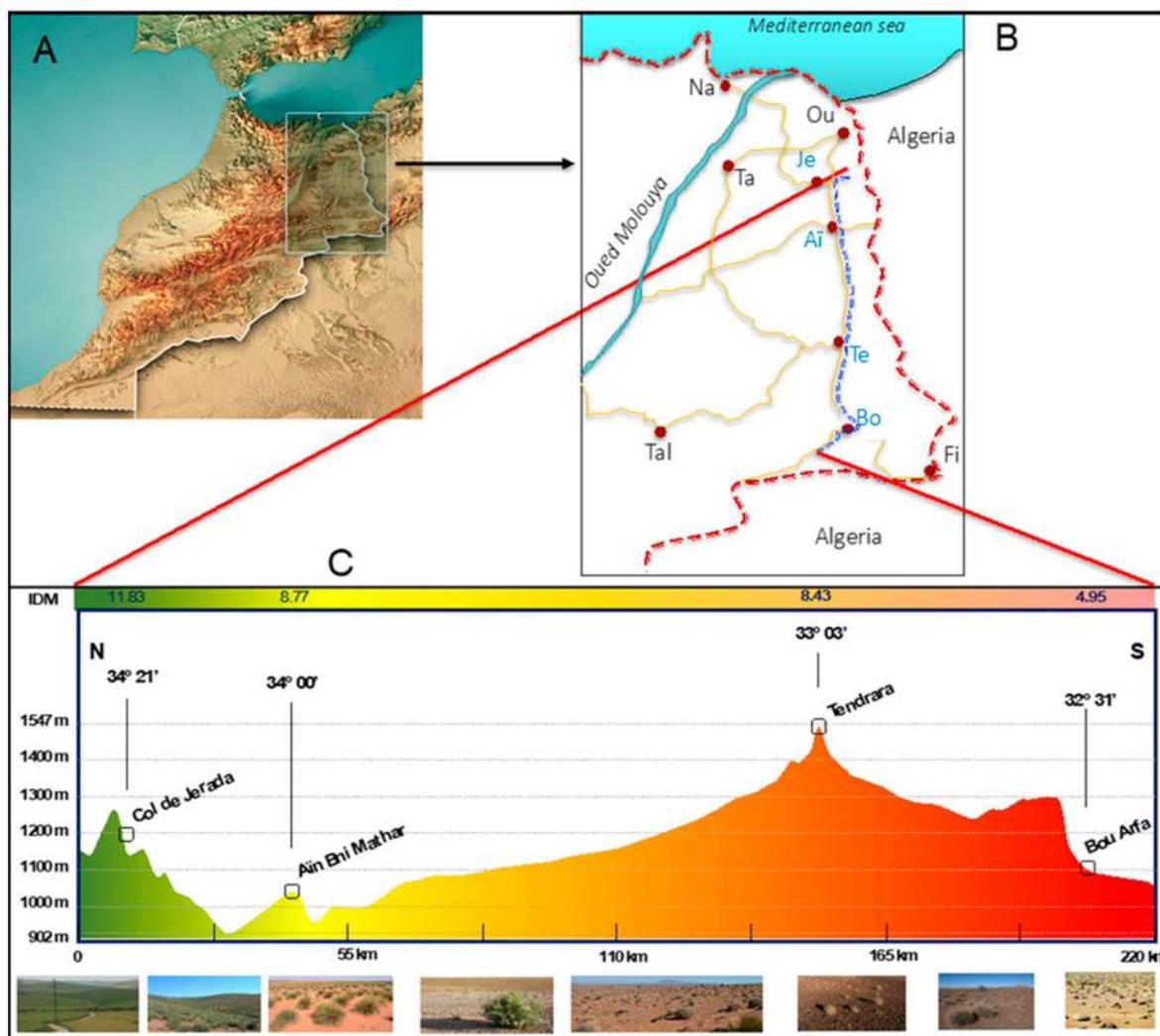


Figure 1. (A) Geographic location of the study area in Morocco (shaded area). (B) Details of the explored area, showing the Morocco–Algeria border (dashed red line), and the main villages (red circles) and routes (yellow lines). (Na: Nador, Ta: Taourirt, Ou: Oujda, Je: Jerada, Ai: Ain Bni Mathar, Te: Tendrara, Bo: Bouarfa, Fi: Figuig, Tal: Talsint). (C) Elevation profile (derived from Google earth) of the latitudinal gradient along which the bird surveys were carried out. IDM: De Martone aridity index (see text).

Clay and silty loam soils tend to predominate toward the north of the area, although they are shallow, poor in organic matter, and have frequent capping crusts, thereby reducing water infiltration and increasing run-off and evaporation. Sandy loam soils are more frequent toward the south, where sand, pebbles, and bare rocky covers are predominant due to increasing erosion toward the transitional Saharan zones [25]. Water resources are limited even in the north, where run-off is harvested for livestock use into *dayas* (natural ponds) and *rdirs* (earth dikes) across the *oueds* (watercourses), and for human use into *jboubbs* (underground cisterns). Underground water is available only in two communes (Bouarfa and Tendrara) from a few shallow aquifers (50 m deep) with low yields [26].

Vegetation varies considerably along the latitudinal gradient. Cereal crops and fallow land are dominant in the north (Jerada), subject to very large annual fluctuations, depending on autumn and early winter rains. Crops are progressively substituted toward the south by alfa grass *Stipa tenacissima* and white wormwood *Artemisia herba-alba* steppes around Ain Bni Mathar; shrublands with *Noaea mucronata*, *Peganum harmala*, *Atractylis serratuloides*, and *Anabasis aphylla* around Tendrara, and *Fredolia aretoides* and *Haloxylon scoparium* in the most

meridional limit south of Bouarfa. Occasional plantations of *Atriplex nummularia* and *Pinus halepensis* [27] reflect efforts to combat land degradation as a result of the combined effects of climate deterioration and overgrazing [28].

2.2. Sampling Methods

We established 1000 m long transects that were regularly distributed along the latitudinal gradient, separated by about six km from each other as long as flat or undulating relief was predominant and there were no human settlements in the immediate vicinity. The central point of each transect was located with a hand-held GPS (error ± 10 m) in order to be able to return to it in the different surveys. Surveys were conducted during four consecutive periods: first week of January 2005 (Winter1, $n = 44$ transects), first week of April 2005 (Spring1, $n = 43$ transects), first week of January 2006 (Winter2, $n = 40$ transects), and first week of May 2006 (Spring2, $n = 40$ transects).

Bird abundance and habitat structure were measured in each transect by experienced observers (researchers) trained on the local avifauna and vegetation and in distance estimation and vegetation data collection. Abundance of birds was estimated by the number of auditive and/or visual contacts registered along each transect with a 25 m band at either side of the observer [29]. Since we were primarily interested in studying the total diversity of the bird community, all present bird species were counted, including resident, migrant, and nomadic ones. During spring, surveys took place between one hour after dawn and until noon, avoiding the hottest central hours of the day. Winter surveys were carried out throughout the day, since patterns of detectability do not significantly vary with time in desert habitats [30]. In all cases, surveys were conducted only in good weather conditions, without precipitation, excessive wind, or sand storms. To avoid bias between seasons or sites due to potential differences in bird detection ability between survey participants, site visits were rotated between observers.

Habitat structure was measured in six circles of five-meter radius (sampling points), separated by 200 m along each 1000 m transect. We recorded the following variables at each sampling point: geographical location (UTM coordinates latitude and longitude); elevation (in meters above sea level); estimation of average slope of the terrain (three levels: 0 = flat; 1 = low slope; 2 = moderate slope); total cover of bare ground; total extent of rocks (>10 cm), pebbles (<10 cm), sand, and lime cover; cover of dry cereal crops; and total cover of vegetation. The latter distinguished cover of herbaceous species (including *Peganum harmala*), shrubs, and alfa grass was measured at three different heights (1, 20, and 40 cm). Vegetation cover was estimated after [31], using the classes <1%; 1–3%; 3–5%; 5–10%; 10–20%; 20–30%; 30–40%; 40–50%; and >50%. Alfa clumps that lacked shoots were also included in vegetation cover and estimated at the same heights. Maximum and modal vegetation heights were also measured.

2.3. Data Analyses

The basic sample units were 1000 m-length transects. For birds, we used the number of different species and density of each species, calculated as the sum of contacts (within the 50 m band) of each species multiplied by the sampled area (5 ha per transect) and multiplied by 2 to obtain the number of individuals per 10 ha. Data on habitat structure from the six sampling points in each transect were averaged and used as representative for the transect.

A matrix of counts of each species in each season (winter and spring) was created, pooling the counts of the two replicates (surveys) of each season. We pooled counts because there were no significant differences in richness or density between the surveys of each season (ANOVA; period (nested in season): $p > 0.18$ and $p > 0.41$ for richness and density, respectively) and because the year effect was not the focus of our study. Based on this matrix, different diversity measures were calculated for each season, considering counts of all the species detected. We calculated richness (S) as the total number of species within the community; Shannon's diversity index ($H' = -\sum pi \ln(pi)$), where pi is the proportion

of individuals belonging to species i ; and Simpson's diversity ($D_1 = 1 - \sum pi^2$), Simpson's dominance ($D_2 = 1/\sum pi^2$), and Simpson's evenness index ($E = D_2/S$) (formulas from [32–34]). We also calculated species turnover between the two seasons following the framework proposed by [35], where the turnover and nestedness components of beta diversity are decomposed. The spatial turnover component used here is calculated as a Simpson-based dissimilarity index (β_{SIM}) [36]: $\min(b,c)/a + \min(b,c)$, where a is the number of species common to both seasons, b is the number of species exclusive to the focal season, and c is the number of species exclusive to the other season.

Since the habitat variables measured in the transects were highly correlated to one another, we used a Principal Components Analysis (PCA) to derive a set of uncorrelated, synthetic components. In addition to the variables on soil and vegetation cover, we included other variables in the PCA that can covary with them along the gradient, such as latitude, average slope, and elevation, to obtain a reduced number of (uncorrelated) factors that summarize soil, habitat, topography, and latitude. We then used the synthetic components derived from the PCA as independent variables in subsequent analyses to eliminate multicollinearity while retaining the variation of the environmental variables for the models.

Besides the whole bird community, we also considered functional groups of species (Table 1) that could be influenced differently by environmental features. While we recognize that bird species are rarely exclusive in their use of resources and that their food requirements vary seasonally, we categorized all bird species registered during surveys on the basis of their primary food (diet and feeding habits) as granivores, insectivores, or mixed diet. Allocation of species to functional groups (Table 1) was based on published studies [37] and the authors' own observations in the study area. For each functional group, bird density (individuals/10 ha) and species richness were derived considering counts of all species in the group.

We used a general linear model (GLM) with a nested design to test whether each of the principal components (PCs) varied between seasons (spring and winter) and between the two surveys within each season (nested effect of survey within season). Generalized linear models (GLZ) were used to test the effect of season (factor) on richness and density of the entire community and of each of the functional groups (dependent variables). We also used GLZ to explore, separately for each season, the relationships between richness and density (dependent variables) and the components derived from the PCA (predictors). Since we have two replicates of each season, we included survey as fixed factor (two levels) in analyses. We used a Poisson error distribution and a log link function (richness) or quasi-Poisson distribution (density) to correct overdispersion [38].

Data were analyzed using Statistica 8.0 [39] and the package lme4 [40] in the statistical environment R version (4.2.1) [41].

Average values and their variations along the text have been quoted as average \pm standard error.

Table 1. List of species and their residency status in the study area following [42] (R = resident; S = spring visitor; W = winter visitor; N = nomadic), number of birds (n_i) and proportion of the total (p_i) recorded in the spring and winter surveys. The functional groups (I = insectivores; G = granivores; M = mixed diet) and the diversity metrics used in this study are also indicated.

Species	Status	Diet	Spring		Winter	
			n_i	p_i	n_i	p_i
<i>Cursorius cursor</i>	N	I	3	0.00	0	0.00
<i>Pterocles orientalis</i>	R	G	6	0.01	0	0.00
<i>Alaemon alaudipes</i>	N	I	3	0.00	12	0.01
<i>Chersophilus duponti</i>	R	I	2	0.00	1	0.00
<i>Ammomanes cinctura</i>	R	G	36	0.05	68	0.05
<i>Ammomanes deserti</i>	R	M	1	0.00	0	0.00

Table 1. Cont.

Species	Status	Diet	Spring		Winter	
			<i>ni</i>	<i>pi</i>	<i>ni</i>	<i>pi</i>
<i>Ramphocoris clotbey</i>	N	G	14	0.02	57	0.04
<i>Melanocorypha calandra</i>	R	G	108	0.16	181	0.14
<i>Calandrella brachydactyla</i>	S	M	106	0.16	0	0.00
<i>Calandrella rufescens</i>	R	M	135	0.20	185	0.14
<i>Eremophila bilopha</i>	R	G	107	0.16	258	0.20
<i>Galerida cristata</i>	R	M	35	0.05	57	0.04
<i>Galerida theklae</i>	R	M	13	0.02	39	0.03
<i>Alauda arvensis</i>	R	M	12	0.02	27	0.02
<i>Anthus pratensis</i>	W	I	0	0.00	3	0.00
<i>Motacilla alba</i>	S	I	2	0.00	0	0.00
<i>Oenanthe deserti</i>	S	I	5	0.01	0	0.00
<i>Oenanthe hispanica</i>	S	I	3	0.00	0	0.00
<i>Oenanthe leucura</i>	R	I	1	0.00	0	0.00
<i>Oenanthe moesta</i>	R	I	18	0.03	8	0.01
<i>Oenanthe oenanthe</i>	S	I	2	0.00	0	0.00
<i>Saxicola rubetra</i>	W	I	2	0.00	0	0.00
<i>Lanius excubitor</i>	W	I	0	0.00	1	0.00
<i>Lanius senator</i>	S	I	1	0.00	0	0.00
<i>Passer domesticus</i>	W	G	0	0.00	5	0.00
<i>Passer hispaniolensis</i>	R	M	40	0.06	0	0.00
<i>Bucanetes githagineus</i>	N	G	2	0.00	410	0.31
<i>Emberiza calandra</i>	R	G	2	0.00	2	0.00
N° birds			659		1314	
N° transects			83		84	
Mean density/transect ± s.d.			7.67 ± 11.3		31.28 ± 46.4	
Richness (S)			25		16	
Mean richness/transect ± s.d.			1.92 ± 1.61		1.78 ± 1.45	
Shannon's diversity (H')			1.00		0.85	
Simpson's diversity (D ₁)			0.86		0.81	
Simpson's dominance (D ₂)			7.53		5.47	
Simpson's evenness (E)			7.49		6.39	
Simpson-based dissimilarity (β _{SIM})				0.19		

3. Results

A total of 1973 contacts of 28 different species were registered during all the surveys (Table 1). Some species were very scarcely detected, but we preferred to consider all of them for the subsequent analyses given our primary interest in studying the total diversity of the bird community.

The whole community was dominated by larks in both seasons, accounting for 87% of all contacts in the spring (48% of all species) and 67% in the winter (62.5% of all species). The numerical importance of winter migrant species in the wintering community was low (0.7% of the winter birds; 19% of the species), being somewhat higher than that of spring migrants in the breeding community (18% and 24% of spring birds and species, respectively). Nomadic birds were more abundant in the winter (36%; 19% of all species) than in the spring (3%; 16% of all species). More than half (56%) of the contacted species in the spring were year-round residents (78% of detected birds), while residents accounted for 62.5% of the species in the winter (63% of detected birds). While the mean bird density per transect was clearly larger in the winter, the mean richness remained much more stable between the seasons.

All diversity metrics consistently indicated greater richness, average diversity, and evenness in the spring compared to the winter (Table 1), and the temporal dynamic in the community structure showed a moderate species turnover rate between the two seasons.

The PCA considering soil, habitat, topography, and latitude variables yielded five components with eigenvalues greater than 1, accounting for 73.5% of the total variance (Table 2). The first component (PC1) alone explained 22.2% of the total variance, and the correlation coefficient values show that it has a strong positive correlation with alfa grass cover and vegetation height. PC1 may thus be regarded as a gradient of development of alfa grass, given that this species reaches the maximum height measured among all plants detected in the surveys when fully grown and well preserved. The second component (PC2; 17% of variation) was positively correlated with latitude, silty loam soils, and cereal crops, and negatively correlated with elevation and sand cover. Therefore, this component may be regarded as a geographic (elevation–latitude) gradient in soil texture that determines land suitability for agriculture, from silty loam arable lands at low elevations in the north, to the southern sandy soils in the highest plateau that are less suitable for cultivation.

Table 2. Results of the principal component analysis (PCA), showing the score values obtained for each variable for each factor (PCs). Vegetation cover was measured at three different heights (1, 20, and 40 cm). Values with the highest positive (>0.65) and negative (<−0.65) significant correlations with each PC are highlighted in bold.

Variable	PC1	PC2	PC3	PC4	PC5
Latitude	0.13	0.78	−0.01	−0.11	−0.26
Elevation	0.05	−0.66	0.11	−0.02	0.24
Slope	0.12	0.00	0.15	0.15	0.67
Rocks cover	−0.10	−0.06	0.00	0.04	0.79
Pebble cover	−0.07	−0.30	0.10	−0.21	0.65
Sand cover	−0.05	−0.77	0.08	−0.14	−0.30
Silty loam cover	−0.08	0.80	−0.03	0.00	−0.20
Herb cover ₁	−0.17	0.19	0.00	0.71	0.18
Herb cover ₂₀	0.01	0.04	0.03	0.94	−0.03
Herb cover ₄₀	0.05	−0.05	−0.01	0.90	−0.07
Shrub cover ₀	−0.04	0.10	−0.92	−0.06	−0.04
Shrub cover ₂₀	0.00	0.08	−0.94	−0.05	−0.10
Shrub cover ₄₀	0.01	−0.03	−0.74	0.05	−0.08
Alfa cover ₀	0.93	−0.01	0.14	−0.12	0.09
Alfa cover ₂₀	0.95	0.03	0.12	−0.12	0.07
Alfa cover ₄₀	0.92	0.16	0.11	−0.10	0.04
Vegetation height _{max}	0.80	−0.21	−0.24	0.14	−0.11
Vegetation height _{mode}	0.87	−0.08	−0.15	0.08	−0.17
Crops cover	−0.19	0.66	0.12	0.38	0.17
Eigenvalue	4.22	3.26	2.71	2.21	1.57
Total variance (%)	22.20	17.17	14.25	11.64	8.26
Cumulative variance	22.20	39.37	53.62	65.25	73.52

The third and fourth components (14.2% and 11.6% of variation, respectively) were strongly correlated with lower coverage of shrubs and larger development of herbaceous cover, respectively. The fifth component was mainly positively correlated with the slope, and the cover of rocks and pebbles, in such a way that its highest values correspond to places with stony soils on sloping terrains.

We found a “season” effect for PC4, with significantly higher values in the spring than in the winter, and a “season” (spring > winter) and “survey” effect for PC5 (larger values in the second spring survey as compared to the first one). No significant variations between seasons or between surveys within each season were found for PC1, PC2, or PC3 (Table 3).

Table 3. Nested ANOVA table, testing for the effect of season (winter vs. spring) and survey (nested within each season) on each component resulting from the PCA (see Table 2).

Component	Effects	df	MS	F	<i>p</i> -Value
PC1	Season	1	0.0003	0.000	0.98
	Survey (Season)	2	0.6813	0.674	0.51
	Standard error	163	1.0100		
PC2	Season	1	1.5078	1.517	0.21
	Survey (Season)	2	1.2878	1.295	0.27
	Standard error	163	0.9939		
PC3	Season	1	0.1474	0.146	0.70
	Survey (Season)	2	0.7412	0.734	0.48
	Standard error	163	1.0086		
PC4	Season	1	5.0300	5.176	0.02
	Survey (Season)	2	1.3615	1.401	0.25
	Standard error	163	0.9716		
PC5	Season	1	5.7674	7.323	0.007
	Survey (Season)	2	16.147	20.50	<0.001
	Standard error	163	0.7874		

The seasonal variation of total species richness was not statistically significant (GLZ: Estimate = 0.044, Wald = 0.62, $p = 0.43$). Insectivores and mixed-diet groups showed higher richness in the spring than in the winter, although neither reached the significance level (p -values of 0.07 and 0.089, respectively). In contrast, granivores showed the opposite trend, with greater (non-significant, p -value = 0.09) richness in the winter than in the spring. The total bird density per transect was significantly higher in the winter than in the spring (GLZ: Estimate = -0.338 , Wald = 7.81, $p = 0.0052$). The effect of season on bird density was mainly conditioned by the group of granivorous species (GLZ: Estimate = -0.629 , Wald = 13.94, $p = 0.0001$), since the density of the mixed-diet group remained stable between seasons ($p = 0.73$) and the density of insectivores was almost significantly higher in the spring than in the winter (GLZ: Estimate = 0.265, Wald = 3.51, $p = 0.060$).

Generalized linear models revealed no significant influence of the principal component 1 (alfa grass cover and vegetation height) on species richness or bird density in any of the two seasons (Tables 4 and 5). PC5 (stony soils on sloping terrain) only favored granivores density in the spring, and PC3 (low coverage of shrubs) negatively influenced the bird density of the mixed-diet group in the winter. The most consistent influences were identified for PC2 and PC4. In the spring, species richness and bird density, both for all species as a whole and for the mixed-diet group, significantly increased towards northern loam clay arable lands at lower altitude (PC2) and in patches of higher herbaceous cover (PC4). Herbaceous cover also favored species richness and bird density of the granivorous group and bird density of the insectivorous one. In the winter, the extent of herbaceous cover significantly favored species richness and bird density of all species as a whole and of those of the mixed-diet group, as well as bird density of the granivores group. The influence of PC2 was more limited, favoring species richness and bird density of the mixed-diet group and negatively influencing the bird density of the granivorous group. Significant differences were detected between spring surveys for total and mixed-diet species richness (Table 4) and for total, granivorous, and mixed-diet bird densities (Table 5).

Table 4. Results of the generalized linear model (GLZ) for the effect of the five components derived from the PCA (Table 2) and the survey factor (two levels) on species richness of the different functional groups and total species richness in spring and winter. The reference levels for *Survey* factor are “spring 2” and “winter 2”.

Group	Spring			Winter			Z-Value
	Estimate	SE	Z-Value	Estimate	SE	Z-Value	
<i>Granivores</i>							
Intercept	−0.207	0.180	−1.15	0.146	0.153	0.95	
Survey	−0.385	0.323	−1.19	−0.284	0.240	−1.18	
PC1	−0.234	0.220	1.06	−0.289	0.171	−1.68	^
PC2	−0.038	0.131	−0.29	−0.175	0.120	−1.46	
PC3	0.001	0.177	0.00	−0.045	0.093	−0.48	
PC4	0.183	0.072	2.53	0.342	0.187	1.83	^
PC5	0.075	0.140	0.54	0.194	0.103	1.89	^
<i>Mixed diet</i>							
Intercept	−0.117	0.177	−0.66	−1.036	0.282	−3.66	***
Survey	−0.703	0.337	−2.08	0.302	0.314	0.96	*
PC1	−0.127	0.177	−0.71	0.168	0.096	1.74	^
PC2	0.510	0.133	3.82	0.693	0.188	3.68	***
PC3	−0.237	0.154	−1.54	−0.167	0.088	−1.89	^
PC4	0.254	0.071	3.59	0.497	0.204	2.44	*
PC5	0.049	0.155	0.32	0.213	0.151	1.40	
<i>Insectivores</i>							
Intercept	−1.022	0.270	−3.78	−1.634	0.388	−4.21	***
Survey	0.009	0.451	0.02	−0.037	0.463	−0.08	
PC1	−0.251	0.318	−0.78	−0.033	0.211	−0.15	
PC2	0.109	0.178	0.61	0.136	0.228	0.59	
PC3	−0.325	0.207	−1.56	−0.008	0.185	−0.04	
PC4	0.173	0.094	1.83	−0.476	0.655	−0.72	^
PC5	−0.316	0.244	−1.29	−0.320	0.359	−0.89	
<i>Total richness</i>							
Intercept	0.775	0.111	6.97	0.676	0.115	5.86	***
Survey	−0.444	0.205	−2.16	−0.143	0.171	−0.83	*
PC1	−0.196	0.127	−1.53	−0.021	0.076	−0.27	
PC2	0.212	0.080	2.63	0.118	0.086	1.37	**
PC3	−0.158	0.101	−1.57	−0.075	0.059	−1.26	
PC4	0.209	0.044	4.76	0.313	0.133	2.35	*
PC5	−0.012	0.095	−0.13	0.154	0.084	1.84	^

^ $p < 0.10$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Table 5. Results of the generalized linear model (GLZ) presenting the effect of the five components derived from the PCA (Table 2) and the survey factor (two levels) on bird density of the different functional groups and total bird density in spring and winter. The reference levels for *survey* factor are “spring 2” and “winter 2”.

Group	Spring			Winter			Z-Value
	Estimate	SE	Z-Value	Estimate	SE	Z-Value	
<i>Granivores</i>							
Intercept	1.996	0.207	9.64	3.094	0.285	10.85	***
Survey	−0.823	0.379	−2.17	0.082	0.398	0.20	*
PC1	−0.342	0.278	−1.22	−0.079	0.223	−0.35	
PC2	0.285	0.154	1.84	−0.448	0.210	−2.13	*
PC3	0.027	0.224	0.12	0.338	0.280	1.20	
PC4	0.309	0.078	3.95	0.625	0.271	2.30	*
PC5	0.352	0.143	2.46	0.217	0.159	1.36	

Table 5. Cont.

Group	Spring			Winter				
	Estimate	SE	Z-Value	Estimate	SE	Z-Value		
<i>Mixed diet</i>								
Intercept	2.114	0.265	7.96	***	1.439	0.395	3.64	***
Survey	−1.479	0.536	−2.76	**	0.140	0.418	0.33	
PC1	−0.363	0.340	−1.06		0.262	0.136	1.91	^
PC2	0.837	0.196	4.26	***	0.752	0.260	2.89	**
PC3	−0.396	0.206	−1.91	^	−0.244	0.113	−2.15	*
PC4	0.364	0.100	3.62	***	0.760	0.280	2.71	**
PC5	−0.101	0.269	−0.37		−0.345	0.361	−0.95	
<i>Insectivores</i>								
Intercept	−0.267	0.283	−0.94		−0.585	0.368	−1.58	
Survey	0.314	0.437	0.72		−0.150	0.475	−0.31	
PC1	−0.351	0.353	−0.99		−0.049	0.218	−0.22	
PC2	0.094	0.177	0.53		0.114	0.234	0.49	
PC3	−0.374	0.211	−1.77	^	−0.105	0.157	−0.66	
PC4	0.183	0.089	2.05	*	−0.397	0.618	−0.64	
PC5	−0.427	0.248	−1.72	^	−0.102	0.319	−0.32	
<i>Total density</i>								
Intercept	2.923	0.159	18.33	***	3.523	0.222	15.83	***
Survey	−1.101	0.318	−3.46	***	−0.029	0.333	−0.09	
PC1	−0.388	0.229	−1.69	^	0.042	0.148	0.28	
PC2	0.545	0.122	4.43	***	−0.138	0.168	−0.82	
PC3	−0.234	0.151	−1.55		0.035	0.148	0.24	
PC4	0.324	0.064	5.06	***	0.582	0.228	2.55	*
PC5	0.142	0.138	1.02		0.146	0.156	0.93	

^ $p < 0.10$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

4. Discussion

A total of 28 species were counted in the transects. Residents comprised the greatest proportion of detected species (50%) and of individuals counted (68%). Despite the higher detectability due to courtship and breeding behavior [43], the number of individuals counted was higher in the winter than in the spring, which is a reflection of the gregarious nature in the winter of part of the species with the largest bird numbers. Four of the recorded species were nomadic (14%, including *Alaemon alaudipes*, *Bucanetes githagineus*, and *Cursorius cursor*). Spring (24% of the species) and wintering migrants (19%) had a reduced importance in comparison to other Mediterranean environments with greater structural complexity, in particular those forests and shrubs with abundant fruits [44], but it was similar to what happens in the desert areas of Tunisia [45] or in semiarid Spain [14]. Our results corroborate previous knowledge regarding the dominance of larks in the composition of breeding bird communities in the Northern Maghreb, both in species and bird numbers [45–47]. The community species turnover was moderate (Simpson-based dissimilarity index, $\beta_{SIM} = 0.19$), and there was a high coincidence between seasons in the species with larger quantitative importance, in particular lark species, such as *Melanocorypha calandra*, *Calandrella rufescens*, and *Eremophila bilopha*. Higher numbers of species found during the spring may reflect the passage or arrival of migrants, although the bird count was higher in the winter, mainly due to the detected flocks and nomadic species.

PCA allowed a comprehensive interpretation of the main factors structuring the bird community, with PC1 capturing the potential influence of alfa grass coverage and development; PC2 integrating the combined role of increasing latitude (less aridity), silty loam soils, and cover of cereal crops in opposition to lower latitude (greater aridity), larger sandy soil cover, and higher elevation; PC3 and PC4 reflecting lower and larger coverage, respectively, of shrub and herbaceous vegetation; and PC5 capturing the dominance of stony soils (rocks and pebbles) on sloping terrains.

The consistency of this interpretation between surveys is large, with no significant variation for the first three PCs, and expected higher values of herbaceous cover development in the spring (PC4). The interpretation of the seasonal variation of PC5 is more doubtful, given that slopes or pebble cover should not vary appreciably between seasons or years. Most probably, the observed variation is an artifact derived from location errors (despite the use of GPS) of the transects between surveys, linked to the inaccurate selection of the exact point and the orientation of the line of progression from that point. However, it could not be discarded that pebble cover could vary between years in relation to seasonal/interannual effects of high, hot, and dry winds, giving rise to significant sandstorms, particularly frequent in the dry summer season in the area [48].

Although the seasonal variation of total richness was not statistically significant, the total density per transect was significantly higher in the winter than in the spring. These larger densities were not observed by [45], who reported larger densities in the spring. However, the communities they studied were dominated by insectivorous species, while in our case, the seasonal differences were mainly due to the higher bird density of granivorous species in the winter. Furthermore, the study in Tunisia focused on a single southern study area at the edge of the desert (e.g., ecologically equivalent to the southern tip of our latitudinal gradient, see Figure 1), while we sampled a considerable latitudinal range in eastern Morocco. In fact, we found a positive effect of PC2 on the overall bird density in the spring (Table 5); that is, bird density increased toward northern areas. Our community seems to be relatively stable in its specific composition (as expected, given the harsh conditions in both periods of the year), but with increasing numbers of wintering bird populations coming from more northerly latitudes.

Habitat (vegetation) structure has a significant influence on the composition and structure of bird communities along the 200 km extension studied in the Moroccan High Plateaux. This general result coincides with other studies at local or regional scales [6–10,43]. Aridity (an inverse correlate of latitude in our study, PC2) was less influential [1,3–5].

The extent and development of herbaceous vegetation (PC 4, Table 2) resulted in our study to the main single factor related to higher total species richness and bird density, particularly in the spring, but also in the winter for some functional groups (Tables 4 and 5). Species richness and bird density of the three functional groups considered were all positively related to this factor in the spring, and also richness and density of the mixed-diet group and density of the granivorous group showed this relation in the winter. In contrast, neither the richness nor density of the insectivorous group showed a relationship to this factor in the winter. Furthermore, bird density of the mixed-diet group appeared to be positively related to shrub cover in the winter.

Two possible explanations may be considered for the role of habitat structure as a factor shaping the studied bird communities. First, although our study expanded along a 200 km N–S strip, it did not reach the desertic areas beyond Bouarfa to the south (<100 mm/yr of highly irregular precipitation) [49]. Therefore, primary productivity pulses in the studied area (with precipitation of 130–319 mm/yr) are more predictable than if we had considered a broader climate gradient, which could favor resident species at the expense of vagrant ones. This fact seems to be reflected in the percentage of nomadic species, which in our case, is less than half that of the Australian deserts (14% in our case; 46% in Australians [13]). In addition, the importance of spring or winter species is also low in our communities, with a quite moderate species turnover between seasons.

A second explanation may be related to the higher spatial variability of habitat structures in the studied area in comparison to the relatively homogeneous environments in which the prevalence of climate-related variables was stated. Although the study area was only 200 km in length, it encompassed a marked diversity of soil types (from silty loam in the north to sandy, pebbly, and rocky soils in the south). Further, human activities linked to pastoralism and cultivation have altered the original alfa grass and white wormwood formations into a variety of degradation facies [25], with heterogeneous composition and coverage. These influences are reflected in a high habitat patchiness at different spatial

scales (plot and landscape, mainly), originating a set of environments with contrasting structural characteristics (pers. Obs). This means that the species can use a wide range of structural conditions of the habitat in the study area, producing a clearer differentiation between them than if it were a more homogeneous landscape. Our results are, therefore, consistent with previous findings in suggesting the importance of scale and environmental heterogeneity in the relative importance of resident vs. vagrant species in ecological communities. The larger the scale, the greater the chance of including a suitable habitat in sufficient quantity to support persistent or resident populations (e.g., [50]). In addition, landscapes showing low environmental heterogeneity tend to support communities with low temporal turnover and a higher proportion of resident species—probably because more heterogeneous landscapes are more spatially segmented, effectively reducing the area and resources available per habitat type to support viable resident populations [51,52].

PC2 was the second-most important factor, significantly explaining bird density and species richness in these communities. As mentioned above, this factor reflects the different linked geographical gradients existing in the area, from less arid northern arable lands to arid and sandy lowlands in the south. Total species richness and bird density were related in the spring to the less arid northern croplands, and the mixed-diet group showed higher richness and density in these areas also in the winter, coinciding with lower densities of the granivorous group. The influence of soil type was also reflected in the inverse relation shown by the bird density of the mixed-diet group to the dominance of pebbly and rocky covers and sloping terrains. The importance of soil type in the composition of bird communities or the selection of habitats in semi-desert environments has been frequently highlighted (for North Africa, see [37,42]; see also [53,54]. However, in our case, the typology of soil types also varies in an accentuated way with the same north–south geographic gradient, potentially confounding its effects with those of aridity (latitude) or the abundance of crops. In North American shrub steppes, it has been suggested that the overlap between species of the factors affecting their distribution and density is very high, making it difficult to differentiate their habitat selection [55,56]. Our results suggest a multiple and differential response between species to the different parameters that determine habitat structure, including the type of soil, as expected, considering the existence of interspecific differences in their biology.

Our results offer a valuable first insight on the primary factors influencing the poorly studied bird communities in the High Plateaux of eastern Morocco, especially considering the accelerated process of degradation suffered by their natural environments. The combined effect of climatic change and land use intensification is driving widespread desertification in the arid and semi-arid environments of North Africa [57]. In the High Plateaux of eastern Morocco, continued overgrazing and the substitution of grassland by itinerant cropland have reduced the alfa grass and white wormwood formations from 2 million hectares in the 1970s to less than 420,000 hectares in less than 50 years [28]. Consequently, moderately to severely degraded and very severely degraded vegetation classes have become dominant (1,800,000 ha and 650,000 ha, respectively) [28]. In the inventories of [58], one of the most abundant species was the shrub warbler *Scotocerca inquieta*, which was not contacted in our transects and was only observed once throughout the study. We could not establish an historical comparison with the work of these authors since they only sampled alfa grass stands. However, these formations have suffered severe degradation, particularly around Aïn Bni Mathar [59], resulting in the disappearance of one of the bird species more strongly associated with this specific vegetation, the Dupont's lark [60], also conditioning corvids' and raptors' abundance [61]. However, other passerines must also have been affected. In the face of these accelerated changes, detailed monitoring of bird communities in these areas is urgently needed, especially considering that quantitative records are almost non-existent.

Four essential conclusions are derived from our study. First, the explanatory variables considered affect the species richness and density of individuals in the studied bird communities in a differential way, making it possible to establish multifactorial behavior for each

functional group of species that includes geographical, soil, and vegetation structure factors. Second, the total density of the bird community is strongly affected by the development of herbaceous vegetation, independently of the prevailing aridity gradient N–S, probably reflecting the erratic rainfall in these semi-desert areas, as well as the vagrant behavior of many bird species in these communities. Third, species richness along the studied N–S 2000 km gradient was affected in the winter by factors related to habitat structure and not by variables related to the aridity gradient. Fourthly, the rapid changes in habitat structure that seem to be occurring in the area, associated with anthropic activities and climate degradation, suggest that they could have important effects on these singular bird communities. Our data reveal that ongoing climate change may exert negative impacts on the community, especially on birds with mixed or granivorous diets and during the breeding season. Further northward shifts in environmental favorability are predicted for the study species due to the interaction between climate change and human-induced changes in the habitat. However, to better understand the combined effects of habitat and climate changes as well as determine gains and losses in favorability across the range, more long-term studies are necessary.

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References

1. Wiens, J.A. *The Ecology of Bird Communities*; Cambridge University Press: Cambridge, UK, 1989.
2. Wiens, J.A. Habitat heterogeneity and avian community structure in North American Grasslands. *Am. Midl. Nat.* **1974**, *91*, 195–213. [[CrossRef](#)]
3. Rotenberry, J.T. Components of avian diversity along a multifactorial climatic gradient. *Ecology* **1978**, *59*, 693–699. [[CrossRef](#)]
4. Naranjo, L.G.; Raitt, R.J. Breeding bird distribution in Chihuahuan desert habitats. *Southwest. Nat.* **1993**, *38*, 43–51. [[CrossRef](#)]
5. Kaboli, M.; Guillaumet, A.; Prodon, R. Avifaunal gradients in two arid zones of central Iran in relation to vegetation, climate and topography. *J. Biogeogr.* **2006**, *33*, 133–144. [[CrossRef](#)]
6. Cody, M.L. Mulga bird communities. I. Species composition and predictability across Australia. *Aust. J. Ecol.* **1974**, *19*, 206–219. [[CrossRef](#)]
7. Tomoff, C.S. Avian species diversity in desert scrub. *Ecology* **1974**, *55*, 396–403. [[CrossRef](#)]
8. Rotenberry, J.T. The role of habitat in avian community composition: Physiognomy or floristics? *Oecologia* **1985**, *67*, 213–217. [[CrossRef](#)]
9. Recher, H.F.; Davis, W.E., Jr. Foraging ecology of a mulga bird community. *Wildl. Res.* **1997**, *24*, 27–43. [[CrossRef](#)]
10. Pavel, C.R.; Nano, C.E.M. Bird assemblages of arid Australia: Vegetation patterns have a greater effect than disturbance and resource pulses. *J. Arid. Environ.* **2009**, *73*, 634–642. [[CrossRef](#)]
11. Le Houérou, H.N.; Bingham, R.L.; Skerbek, W. Relationship between the variability of primary production and the variability of annual precipitation in world arid lands. *J. Arid. Environ.* **1988**, *15*, 1–18. [[CrossRef](#)]

12. Dean, W.R.J.; Hockey, P.A.R. An ecological perspective of lark (*Alaudidae*) distribution and diversity in the southwest-arid zone of Africa. *Ostrich* **1989**, *60*, 27–34. [[CrossRef](#)]
13. Dean, W.R.J. *Nomadic Desert Birds*; Springer: Berlin/Heidelberg, Germany, 2004.
14. Tellería, J.L.; Santos, T.; Suárez, F. Bird communities of the Iberian shrubsteppes: Seasonality and structure along a climatic gradient. *Holarctic Ecol.* **1988**, *11*, 171–177.
15. Lorenzón, R.E.; Beltzer, A.H.; Olguin, P.F.; Ronchi-Virgolini, A.L. Habitat heterogeneity drives bird species richness, nestedness and habitat selection by individual species in fluvial wetlands of the Paraná River, Argentina. *Austral Ecol.* **2016**, *41*, 829–841. [[CrossRef](#)]
16. Ricklefs, R.E. Evolutionary diversification, coevolution between populations and their antagonists, and the filling of niche space. *Proc. Natl. Acad. Sci. USA* **2010**, *4*, 1265–1272. [[CrossRef](#)] [[PubMed](#)]
17. González-Salazar, C.; Martínez-Meyer, E.; López-Santiago, G. A hierarchical classification of trophic guilds for North American birds and mammals. *Rev. Mex. Biodivers.* **2014**, *85*, 931–941. [[CrossRef](#)]
18. García, J.T.; Suárez, F.; Garza, V.; Calero-Riestra, M.; Hernández, J.; Pérez-Tris, J. Genetic and phenotypic variation among geographically isolated populations of the globally threatened Dupont's lark *Chersophilus duponti*. *Mol. Phylogenet. Evol.* **2008**, *46*, 237–251. [[CrossRef](#)] [[PubMed](#)]
19. Guillaumet, A.; Crochet, P.A.; Godelle, B. Phenotypic variation in *Galerida* larks in Morocco: The role of history and natural selection. *Mol. Ecol.* **2004**, *14*, 3809–3821. [[CrossRef](#)]
20. Guillaumet, A.; Pons, J.M.; Godelle, B.; Crochet, P.A. History of the Crested Lark in the Mediterranean region as revealed by mtDNA sequences and morphology. *Mol. Phylogenet. Evol.* **2006**, *39*, 645–656. [[CrossRef](#)]
21. Meiri, S.; Dayan, T. On the validity of Bergmann's rule. *J. Biogeogr.* **2003**, *30*, 331–351. [[CrossRef](#)]
22. Rahbek, C. The role of spatial scale and the perception of large-scale species-richness patterns. *Ecol. Lett.* **2005**, *8*, 224–239. [[CrossRef](#)]
23. De Martonne, E. Une nouvelle fonction climatologique: L'indice d'aridité. *Météorologie* **1926**, *2*, 449–458.
24. Zomer, R.J.; Xu, J.; Trabucco, A. Version 3 of the Global Aridity Index and Potential Evapotranspiration Database. *Sci. Data* **2002**, *9*, 409. [[CrossRef](#)]
25. Bechchari, A.; El Aich, A.; Mahyou, H.; Baghdad, B.; Bendaou, M. Analyse de l'évolution du système pastoral du Maroc oriental. *Rev. Elev. Méd. Vét. Pays Trop.* **2015**, *67*, 151–162. [[CrossRef](#)]
26. El Harradji, A. Aménagement, érosion et désertification sur les Hauts-Plateaux du Maroc oriental. *Méditerranée* **1997**, *86*, 15–23. [[CrossRef](#)]
27. Ben El Mostafa, S.; Haloui, B.; Berrichi, A. Contribution à l'étude de la végétation steppique du Maroc oriental: Transect Jerrada—Figuig. *Acta Bot. Malacit.* **2001**, *6*, 295–301. [[CrossRef](#)]
28. INRA-ONUDI. *Etude sur la Situation de Référence au Niveau des Hauts Plateaux du Maroc Oriental. Rapport Final. Projet de Lutte Participative Contre la Désertification et de Réduction de la Pauvreté dans les Écosystèmes Arides et Semi Arides des Hauts Plateaux du Maroc Oriental*; Centre Régional de La Recherche Agronomique d'Oujda: Oujda, Morocco, 2012.
29. Bibby, C.J.; Burgess, N.D.; Hill, D. *A Bird Census Techniques*; Academic Press: London, UK, 1992.
30. Weathers, W.W.; Mayhew, W.W. Time of day and desert bird censuses. *West. Birds* **1981**, *12*, 157–172.
31. Prodon, R.; Lebreton, J.D. Breeding avifauna of a Mediterranean succession: The holm oak and cork oak series in eastern Pyrenees. 1. Analysis and modelling of the structure gradient. *Oikos* **1981**, *37*, 21–38. [[CrossRef](#)]
32. Morris, E.K.; Caruso, T.; Buscot, F.; Fischer, M.; Hancock, C.; Maier, T.S.; Meiners, T.; Müller, C.; Obermaier, E.; Prati, D.; et al. Choosing and using diversity indices: Insights for ecological applications from the German Biodiversity Exploratories. *Ecol. Evol.* **2014**, *4*, 3514–3524. [[CrossRef](#)]
33. Shannon, C. A mathematical theory of communication. *Bell Syst. Technol. J.* **1948**, *27*, 379–423. [[CrossRef](#)]
34. Simpson, E.H. Measurement of diversity. *Nature* **1949**, *163*, 688. [[CrossRef](#)]
35. Baselga, A. Partitioning the turnover and nestedness components of beta diversity. *Global Ecol. Biogeogr. Lett.* **2010**, *19*, 134–143. [[CrossRef](#)]
36. Lennon, J.J.; Koleff, P.; Greenwood, J.J.D.; Gaston, K.J. The geographical structure of British bird distributions: Diversity, spatial turnover and scale. *J. Anim. Ecol.* **2001**, *70*, 966–979. [[CrossRef](#)]
37. De Juana, E.; Suárez, F.; Ryan, P. Family *Alaudidae* (Larks). In *Handbook of the Birds of the World, Cotingas to Pipits and Wagtails*; Del Hoyo, J., Elliott, A., Christie, D., Eds.; Lynx Edicions: Barcelona, Spain, 2005; Volume 9, pp. 496–601.
38. Crawley, M.J. *The R Book*; John Wiley & Sons: Chichester, UK, 2012. [[CrossRef](#)]
39. StatSoft, Inc. STATISTICA (Data Analysis Software System), Version 8.0. 2007. Available online: www.statsoft.com (accessed on 25 May 2023).
40. Bates, D.; Mächler, M.; Bolker, B.; Walker, S. Fitting linear mixed-effects models Using lme4. *J. Stat. Softw.* **2015**, *67*, 1–48. [[CrossRef](#)]
41. R Core Team. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2022; Available online: <https://www.R-project.org/> (accessed on 25 May 2023).
42. Thévenot, M.; Vernon, R.; Bergier, P. *The Birds of Morocco*; BOU Checklist n° 20; British Ornithologists' Union-British Ornithologists' Club: Tring, UK, 2003.
43. Heezik, Y.V.; Seddon, P.J. Effects of season and habitat on bird abundance and diversity in a steppe desert, northern Saudi Arabia. *J. Arid. Environ.* **1999**, *43*, 310–317. [[CrossRef](#)]

44. Santos, T.; Tellería, J.L. Patrones generales de la distribución invernal de passeriformes en la Península Ibérica. *Ardeola* **1985**, *32*, 17–30.
45. Heatwole, H.; Muir, R. Population densities, biomass and trophic relations of birds in the pre Saharan steppe of Tunisia. *J. Arid. Environ.* **1982**, *5*, 145–167. [[CrossRef](#)]
46. Blondel, J. Données écologiques sur l’avifaune des Monts des Ksour (Sahara septentrional). *Terre Vie* **1962**, *16*, 209–251.
47. Suárez, F. Introducción al estudio de las comunidades de aves reproductoras de los espartales norteafricanos. *Bol. Estac. Cent. Ecol.* **1985**, *28*, 29–34.
48. Mahyou, H.; Tychon, B.; Balaghi, R.; Louhaichi, M.; Mimouni, J. A knowledge-based approach for mapping land degradation in the arid rangelands of North Africa. *Land Degrad. Dev.* **2016**, *27*, 1574–1585. [[CrossRef](#)]
49. Le Houérou, H.N. Classification éoclimatique des zones arides (s.l.) de l’Afrique du Nord. *Ecol. Mediterr.* **1989**, *15*, 95–146. [[CrossRef](#)]
50. Jenkins, M.F.; White, E.P.; Hurlbert, A.H. The proportion of core species in a community varies with spatial scale and environmental heterogeneity. *PeerJ* **2018**, *6*, e6019. [[CrossRef](#)] [[PubMed](#)]
51. Stegen, J.C.; Freestone, A.L.; Crist, T.O.; Anderson, M.J.; Chase, J.M.; Comita, L.S. Vellend M. Stochastic and deterministic drivers of spatial and temporal turnover in breeding bird communities. *Glob. Ecol. Biogeogr.* **2013**, *22*, 202–212. [[CrossRef](#)]
52. Gaston, K.J.; Davies, R.G.; Orme, C.; David, L.; Olson, V.A.; Thomas, G.H.; Ding, T.S.; Rasmussen, P.C.; Lennon, J.J.; Bennett, P.M.; et al. Spatial turnover in the global avifauna. *Proc. R. Soc. B* **2007**, *274*, 1567–1574. [[CrossRef](#)] [[PubMed](#)]
53. Kantrud, H.A.; Kologiski, R.L. Avian associations of the northern Great plains grasslands. *J. Biogeogr.* **1983**, *10*, 331–350. [[CrossRef](#)]
54. Van der Haegen, W.M.; Dobler, F.C.; Price, D.J. Shrubsteppe bird response to habitat and landscape variables in Eastern Washington, USA. *Conserv. Biol.* **2000**, *14*, 1145–1160. [[CrossRef](#)]
55. Rotenberry, J.T.; Wiens, J.A. Habitat structure, patchiness, and avian communities in North American steppe vegetation: A multivariate analysis. *Ecology* **1980**, *61*, 1228–1250. [[CrossRef](#)]
56. Wiens, J.A.; Rotenberry, J.T. Habitat associations and community structure of birds in shrubsteppe environments. *Ecol. Monogr.* **1981**, *51*, 21–41. [[CrossRef](#)]
57. Le Houérou, H.N. Biogeography of the arid steppeland north of the Sahara. *J. Arid. Environ.* **2001**, *48*, 103–128. [[CrossRef](#)]
58. Suárez, F.; Fernández, A.; de Lope, M.J. Note sur les effets de l’aridité sur la structure et la composition des communautés de Passeriformes des hauts-plateaux à alpha (*Stipa tennacissima*) au Maroc. *Bull. Inst. Sci. Rabat* **1986**, *10*, 185–192.
59. Bechchari, A.; El Aich, A.; Mahyou, H.; Baghdad, B.; Bendaou, M. Study of the degradation of steppic rangelands in Béni Mathar and Maâtarka communes (northeastern of Morocco). *J. Mater. Environ. Sci.* **2014**, *5*, 2572–2583.
60. García, J.T.; Suárez, F.; Garza, V.; Justribó, J.H.; Oñate, J.J.; Hervás, I.; Calero, M.; García de la Morena, E.L. Assessing the Distribution, Habitat, and Population Size of the Threatened Dupont’s Lark *Chersophilus Duponti* in Morocco: Lessons for Conservation. *Oryx* **2008**, *42*, 592–599. [[CrossRef](#)]
61. Brosset, A. L’évolution récente de l’avifaune du nord-est marocain: Perte et gains depuis 35 ans. *Rev. Écol.* **1990**, *45*, 237–245. [[CrossRef](#)]

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