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Breeding bird communities in southern Tunisian oases: the importance of traditional agricultural practices for bird diversity in a semi-natural system

Slaheddine Selmi[a,b,*], Thierry Boulinier[b]

[a]*Département des Sciences de la Vie & de la Terre, Faculté des Sciences de Gabès. Route de Médenine, 6029 Gabès, Tunisia*
[b]*Laboratoire d'Ecologie, CNRS- UMR 7625, Université Pierre and Marie Curie. 7 Quai St Bernard, F-75005 Paris, France*

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Abstract

We investigated the diversity of breeding bird communities in 53 oases in southern Tunisia. In particular, we examined the similarity of bird communities among oases in relation to vegetation structure and geographic location. We found that oases close to each other supported similar bird communities, suggesting that the spatial distribution of oases has played an important role in shaping local communities. Accounting for oasis location, bird richness was related to oasis size and to vegetation traits, namely to the diversity of trees and herbaceous plants. Oases within which traditional practices are used to diversify the agricultural products were found to provide more suitable habitat conditions for birds than modern plantations created to maximize the production of dates. Traditional oases represent semi-natural habitats within which traditional human activities may be essential for maintaining their biodiversity, and we think that more attention to the conservation of these systems is to be paid.
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Keywords: Breeding birds; Community diversity; Oases; Semi-natural systems; Tunisia

1. Introduction

Changes in natural habitats and animal communities due to human land use practices are a major interest in conservation biology. Indeed, dramatic declines in biological diversity during the 20th century have been directly attributed to the growing human activities (Wilson and Peter, 1988; Heywood and Watson, 1995). For instance, changes in agricultural practices and the increasing use of modern intensive agriculture techniques have had a direct negative impact on biodiversity at all levels: ecosystem, species and genes (McNeely et al., 1995).

In traditional agroecosystems, however, people have adapted farming techniques to their environment, which has had, in many cases, positive effects on wildlife richness and abundance (Nabhan et al., 1982; Posey, 1982; Janzen, 1987; Chandran and Gadgil, 1993). By diversifying microhabitats, providing new resources or opening up new niches, traditional farming activities tend to increase local and landscape diversity (McNeely et al., 1995). As ''refuges of biodiversity'' (Oostermeijer et al., 1994), these traditional agroecosystems are receiving increasing attention in studies dealing with the conservation of biodiversity (Pimentel et al., 1992; Greenberg et al., 1997; Thiollay, 1998).

Among traditional agroecosystems, ''semi-natural'' systems, such as European lowland and grasslands, are well known for their important conservation value (McNeely et al., 1995). In these semi-natural areas, the development and maintenance of plant and animal communities require direct or indirect human intervention through a variety of traditional agricultural practices. The long-term persistence of these activities is potentially important for maintaining the biodiversity of these systems. Although rarely considered, desert oases represent an example of such systems where traditional practice may largely be responsible for local level of biodiversity.

* Corresponding author. Present address: Département des Sciences de la Vie & de la Terre, Faculté des Sciences de Gabès, Route de Médenine, 6029 Gabès, Tunisia. Tel.: +216-75-392-600; fax: +216 75 392 421.

E-mail address: slaheddine.selmi@fsg.rnu.tn (S. Selmi).

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In southern Tunisia, oases represent an important component of the landscape and play a major economic role for indigenous people (Sghaier, 1995; Kassah, 1996). In order to maximize the production of dates (*Phoenix dactylifera*), there has been a tendency to modernize agricultural techniques within oases and to create modern palm plantations since the beginning of the 20th century. The economic returns of this agricultural policy have been well studied. However, little consideration has been given to its ecological implications (Kassah, 1996).

It has been repeatedly noticed that diversity of animal species may be dependent on the oasis habitat in southern Tunisia (Heim de Balsac and Mayaud, 1962; Etchécopar and Hüe, 1964; Selmi, 2000). However, detailed studies of local biodiversity are lacking. Such studies are essential if we are to understand the ecological factors accounting for the survival and dynamics of oasis-dependent species. In this context, investigating the relationship between the diversity of oasis breeding bird communities and vegetation structure, itself dependent on the agricultural practices adopted within oases, may represent an important conservation issue.

In this paper, we report a study of breeding bird communities in a sample of 53 oases from southern Tunisia. We investigated the relationship between the structure of oasian vegetation and the composition and richness of breeding bird communities. In doing so, we used statistical approaches that explicitly incorporated the spatial configuration of the oasis system in the analyses as we showed in an earlier study the importance of accounting for spatial dependence in data when dealing with such a system of suitable patches in unsuitable matrix (Selmi et al., 2002). We use the results to discuss the role of oasis characteristics and geographic position in shaping local communities, and to evaluate the ''biodiversity value'' of traditional oases versus modern oases.

2. History of study area

Situated at the margin of the Western Sahara, southern Tunisia is characterized by harsh climatic conditions. The mean annual rainfall does not exceed 200 mm, while the summer temperature exceeds 40 °C (Henia, 1993; Kassah, 1996). In this part of the country, trees are mostly absent and the vegetation is dominated by sparse steppe shrubs, mainly concentrated in dry watercourses or in the margin of depressions and dry lakes (e.g. *Aristida pungens, Artemisia herba-alba, Atriplex halimus, Calicotome villosa, Lygeum spartum, Nitraria retusa, Ranterium suaveolens, Retama retam, Ziziphus lotus*). Nevertheless, the emergence of groundwater as springs and the use of this water for irrigation have allowed the creation of oases that provide a marked contrast with the desert environment. These oases can be described as intensive and permanent agroecosystems, mainly characterized by palm trees, and which are directly dependent on the availability of water and on human activities for irrigation and maintenance (Kassah, 1996).

Over the last centuries, oases have played an important socio-economic role in southern Tunisia in that they satisfied the needs of a subsistence economy for indigenous semi-nomad people (Sghaier, 1995; Kassah, 1996). Traditional farming methods have been used to exploit in many different ways the available water and arable land, and to diversify the agricultural products (dates, other fruits, cereals and different vegetables). This production system has led to a thick vegetation composed of three distinct layers (palm trees, fruit trees and herbaceous plants), which has induced a local ''micro-climate'' that strongly contrasts with the arid climate of the surroundings (El-Amami and Laberche, 1973; Riou, 1990). As the geographic location of an oasis is primarily constrained by the existence of a water spring, oases are concentrated in some zones where the geological conditions have permitted the emergence of groundwater, such that there exist different regional oasis groups distant from one another.

Since the beginning of the 20th century, the agricultural policies in Tunisia have favored an intensive modern agriculture in the southern part of the country, in order to maximize the production and the exportation of dates and to promote economic development (Sghaier, 1995; Kassah, 1996). As a consequence, oases of a new type were created in the southwestern part of the country, which is the most important oasis zone in Tunisia. Within these modern oases, less importance was given to fruit trees and herbaceous plants, while modern agricultural methods and techniques (namely modern irrigation techniques and infrastructures) are used. Thus, traditional and modern oases in southern Tunisia represent the result of two different agricultural policies, which are the response to two distinct economic constraints. This intensive development has been suggested to contribute to the degradation of traditional oases by competing for limited water resources (Kassah, 1996).

3. Methods

3.1. Vegetation surveys

Our work was carried out in a sample of 40 traditional oases from the different regional oasis groups and 13 modern oases, which are less numerous (Fig. 1). The vegetation structure of each of these oases was characterized by measuring seven variables in 10 20×20-m square sample units which were uniformly spaced along

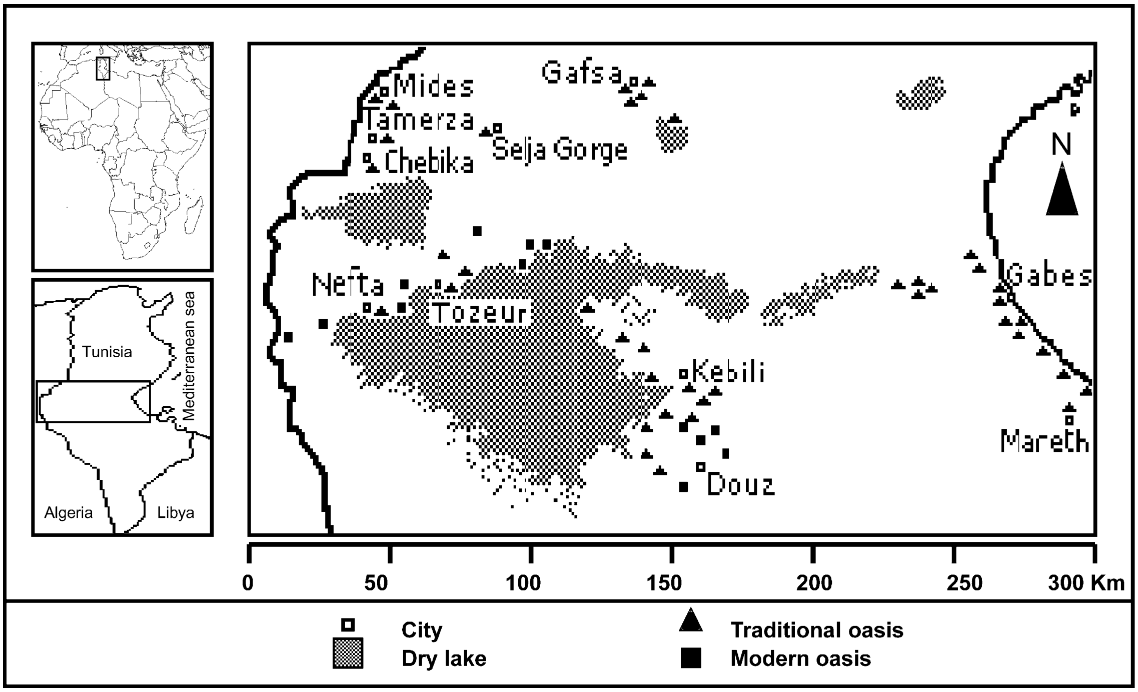

Fig. 1. Distribution of the 53 sampled oases in southern Tunisia. Triangle: traditional oasis; Square: modern oasis.

a line transect. Between-sample units distance varied according to oasis area: 100 m in large oases (> 100 ha) and 50 m in small ones (< 100 ha). Selection of vegetation variables was based on Morisson et al. (1992) modified to suit the needs of this study. The following attributes were quantified in each sample unit: density of palm trees (plants/400 m^2), cover of palm trees (%), total number of tree species, density of trees (plants/400 m^2), cover of trees (%), total number of herbaceous plant species and cover of herbaceous plants (%). The cover of palm trees and the cover of trees were directly measured in each sample unit. However, the cover of herbaceous plants was estimated visually. All estimations were conducted by the same observer in order to avoid sampling errors associated with different observers (Prodon and Lebreton, 1981).

3.2. Bird surveys

Breeding bird communities in each of the 53 sampled oases were surveyed during the breeding season of 1999 (February–June) using the "IPA" point count method (Blondel et al., 1970, 1981; IBCC, 1977). This method was particularly suitable for our study because of time constraints and the frequency, in southern Tunisia, of windy days in which counts could not be conducted. It corresponded to performing two counts of 20 min each per oasis at the same point but at two different times of the breeding season. This allowed the same observer to sample a large number of localities during the same breeding season. The first count was carried out at the beginning of the breeding season to sample early-nesting resident bird species (mid-February), while the second count was carried out two months later, after the settlement of migratory breeding species.

In order to avoid a possible observer effect (Sauer et al., 1994), all counts were conducted by the same observer (S. Selmi). Counts were carried out early in the morning under appropriate meteorological conditions. No count was conducted on rainy or windy mornings, as birds are less detectable under those conditions (O'Connor and Hicks, 1980; Robbins, 1981). During each count, the observer recorded all birds heard or seen in the surroundings at unlimited distances. Within each oasis surveyed, the point at which both counts were conducted was surrounded by representative vegetation of the oasis and located at least 250 m from the oasis edge.

For each oasis, the total number of bird species recorded during both counts (one IPA) was used as an estimation of species richness of the corresponding community (see Blondel et al., 1970, 1981). We are aware of the potential bias in our species richness estimation because of the use of only one IPA per oasis. However, in a related work conducted within a subsample of 28 oases (26 traditional oases and two modern oases), it was possible to carry out IPA counts in five different points per oasis, which gave five lists of records of species per oasis. These lists were used to estimate species detection probability in the corresponding communities by using a capture–recapture approach (Burnham and Overton, 1979; Nichols and Conroy, 1996; Boulinier et al., 1998). Overall, the probability of detecting all species using only one IPA survey was very high ($P > 0.9$ in all sampled oases), suggesting that the use of one IPA survey per oasis provided reliable information on local species richness (unpublished data). This might be related to the low number of species and to the good fieldwork conditions within oases. For instance, the high visibility within oases, compared to temperate or tropical forest habitats, permitted more easily to detect bird visually, which may have increased the chance of detecting the more inconspicuous species.

3.3. Data analysis

Given that the original vegetation variables were correlated, a principal component analysis (PCA) was used to summarize the vegetation data into a few independent factors. The analysis was carried out on the average value of each variable for each oasis. With regard to bird species, we excluded open-country specialist species from the analyses. The criterion used was that these species occurred commonly in the desert steppes surrounding the oases, and that they were found to avoid densely vegetated palm groves.

3.3.1. Association between vegetation structure and bird community composition

The association between bird community composition and vegetation structure in the oasis system was investigated using Mantel and partial Mantel approaches (see Legendre and Fortin, 1989; Legendre, 1993). This approach has proved useful in among-site comparisons of similarity matrices in several previous ecology studies (Legendre and Troussellier, 1988; Leduc et al., 1992; Kadmon and Pulliam, 1993; Holl, 1996; Shankar Raman et al., 1998). A Mantel's test (1967) was first computed to measure the correlation between a matrix of vegetation similarity and a matrix of similarity in bird species composition among the 53 sampled oases. The Mantel's r-value was tested for significance by 999 permutations according to the Hope (1968) method (see also Manly, 1997).

In order to integrate the spatial structure of the oasis system in the analysis, a matrix of geographic distance among oases was computed and was used to perform a partial Mantel test (Smouse et al., 1986). This statistic has the same formula as a partial product–moment correlation coefficient and allowed us to measure the correlation between vegetation and bird composition similarity matrices when the effect of "space" was controlled for. This permitted us to investigate the link between vegetation structure and bird composition by testing whether similarities between local bird communities were related to similarities in vegetation structure within the corresponding oases or simply to the geographic distance from one another. As with the simple Mantel approach, the significance of each partial Mantel's test was assessed by 999 permutations. Results of partial Mantel's tests were used to propose scenarios of links between oasis location, vegetation structure and composition of bird communities according to Legendre (1993).

Among the several possible measures of between-communities similarity in species composition, we used the Jaccard index. For vegetation structure, the similarity matrix was computed using the distribution of oases in the PC1-PC2 space. This distribution was first used to compute a matrix of between-oasis Euclidean distance in vegetation structure. The distance matrix was then converted to a vegetation similarity matrix according to Legendre and Vaudor (1991).

Analyses were first conducted on data from the entire oasis sample (traditional and modern oases), then on data from the traditional oases only, and finally using data from modern oases only. Calculations and conversion of matrices, as well as computations of Mantel and partial Mantel tests were performed using the "R 3.0″ package (Legendre and Vaudor, 1991).

3.3.2. Relationship between species richness and vegetation descriptors

The association between breeding bird species number (log-transformed) and vegetation descriptors (PC1 and PC2) was investigated by means of multiple regression, in which oasis size (log-transformed) was entered as a covariate. The analysis was performed using the MIXED procedure (Littell et al., 1996) of the SAS statistical package (SAS Institute, 1996). This procedure has proved useful to account for the possible lack of statistical independence among observations when investigating the relationships between patch/island characteristics and species richness in a system of islands/patches organized into different regional groups (Selmi and Boulinier, 2001). The MIXED procedure uses the coordinates of the locations in which the associated variables are measured and allowed us to compare a standard regression model, that assumes independence among the errors, with a mixed model which assumes that the errors are spatially dependent and their covariance is a function of distance. In the latter case, we gave initial values of the spatial covariance parameters (sill, range and nugget in geostatistics notation) to the program in order to improve convergence and the likelihood of obtaining reasonable estimates of these parameters. These initial values were first obtained by plotting variograms of the residuals of the standard regression (see Littell et al., 1996). The parsimony of the tried models (standard and mixed regression models) was then compared using the Akaike's Information Criterion: $\mathrm{AIC} = -2$ Log likelihood $+ 2k$, where k is the number of model parameters (Burnham and Anderson, 1998). The lower the value of the AIC, the most parsimonious the model is (Burnham and Anderson, 1998).

An ANCOVA for species richness with "oasis type" (traditional or modern) as a factor and oasis size as a covariate was also conducted to test for the significance of the differences in species richness between similar sized traditional and modern oases. As in the regression analysis, a spatial covariance model was incorporated in the ANCOVA by means of the MIXED procedure in order to account for the spatial dependence in data.

4. Results

4.1. Vegetation structure

The first two factors derived from the principal component analysis of the seven vegetation variables accounted for 79.76% of the variance in the original data set. PC1 (50.02% of the variance of the original data set) was positively correlated with the density, the cover and the number of species of trees, and with the cover and the number of species of herbaceous plants, but was negatively correlated with the cover of palm trees. The second factor (PC2; 29,74% of variance) was strongly positively correlated with the density and cover of palm trees. It was also positively correlated with the number of tree species, but negatively correlated with the number of herbaceous plant species (Table 1). PC1 can be interpreted as an axis of increasing diversity and abundance of trees and herbaceous plant. It separated traditional oases from modern ones, as the ordination of study oases in PC1-PC2 space suggests (Fig. 2). PC2 summarized mainly the abundance of the palm tree layer.

4.2. Vegetation structure and composition of breeding bird communities

A total of 19 bird species were found to use the oasis habitat for breeding. Four species were classified as "open-country specialist" species, and were also found to occur commonly in the desert surrounding the oases in all parts of southern Tunisia (Table 2).

At the scale of the entire oasis system, a significant positive Mantel correlation was found between bird composition similarity matrix and vegetation similarity matrix, and significant negative correlations were found between bird composition similarity matrix and geographic distance matrix and between vegetation similarity matrix and geographic distance matrix (Table 3). Given that all modern oases were situated in the same region (southwestern Tunisia), the negative correlation between vegetation structure and geographic distance was not surprising. The results of the partial Mantel

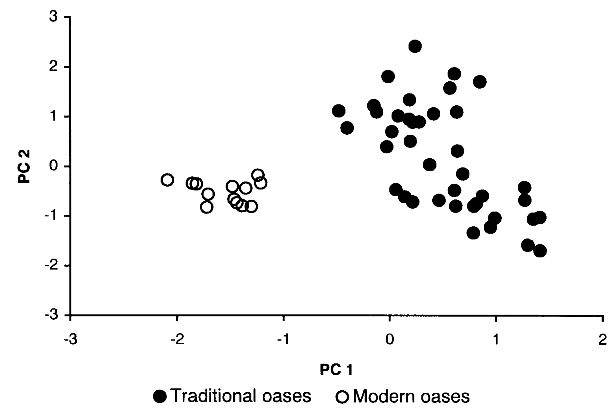

Fig. 2. Distribution of the 53 sampled oases in the PC1-PC2 space derived from the principal components analysis of the seven measured vegetation variables.

Table 1
Variables describing the vegetation structure in studied oases and their correlations with the components extracted by the principal components analysis ($n=53$)

Variable	PC1	PC2
Density of palm trees (plants/400 m^2)	−0.04118	0.95252**
Cover of palm trees (%)	−0.35496*	0.88439**
Number of tree species	0.82076**	0.45664**
Density of trees (plants/400 m^2)	0.91935**	0.07143
Cover of trees (%)	0.89181**	0.13203
Number of herbaceous plant species	0.74333**	−0.38541*
Cover of herbaceous plants (%)	0.71197**	0.11437
Eigenvalue	3.5013	2.0821
Variance explained (%)	50.02	29.74
Cumulative variance (%)	50.02	79.76

*$P<0.01$. **$P<0.001$.

Table 2
List of breeding bird species recorded in southern Tunisian oases and their occupancies (%) in the oasis samples

Species	Traditional oases ($n=40$)	Modern oases ($n=13$)	Entire oasis system ($n=53$)
Alectoris barbara[a]	–	23.08	5.66
Streptopelia turtur	100	100	100
Streptopelia senegalensis	100	100	100
Upupa epops	100	100	100
Galerida cristata[a]	–	100	24.53
Cercotrichas galactotes	100	100	100
Turdus merula	45	–	39.62
Cisticola juncidis	42.50	38.46	41.51
Hippolais pallida	100	100	100
Sylvia hortensis	60	–	45.28
Muscicapa striata	22.50	–	16.98
Turdoides fulvus[a]	–	100	24.53
Parus caeruleus	30	–	22.64
Lanius meridionalis[a]	–	100	24.53
Lanius senator	15	–	13.21
Passer domesticus	100	100	100
Fringilla coelebs	50	–	28.30
Serinus serinus	100	–	67.92
Emberiza striolata	100	–	75.47

[a] Marked species are classified as open-country specialist species and are excluded from the analyses.

Table 3
Mantel (above diagonal) and partial Mantel (below diagonal) correlations between matrices of bird similarity, vegetation similarity and geographic distance among oases

	Bird similarity	Vegetation similarity	Geographic distance
Entire oasis system (n=53)			
Bird similarity	–	0.4821**	−0.4831**
Vegetation similarity	0.4548**	–	−0.1885**
Geographic distance	−0.4559**	0.0579	–
Traditional oases (n=40)			
Bird similarity	–	0.1706*	−0.1712**
Vegetation similarity	0.1778*	–	0.02673
Geographic distance	−0.1784**	0.0576	–
Modern oases (n=13)			
Bird similarity	–	0.0081	−0.1597
Vegetation similarity	0.0139	–	0.0352
Geographic distance	−0.1601	0.0369	–

*P <0.01. **P <0.001.

tests showed a significant relationship between bird composition and vegetation structure when the effect of space was controlled for. Similarly, they showed a significant relationship between bird composition and space when the effect of vegetation was controlled for (Table 3). Thus, when data from traditional and modern oases were considered together, variation in bird species composition among oases appeared partly related to variation in vegetation structure but also to the geographic location of oases. Independently of similarity in vegetation structure, oases close to each other support more similar bird communities than oases from far apart. The scenario supported by these results is presented in Fig. 3A.

Using only data from traditional oases, Mantel and partial Mantel statistics suggest significant positive relationships between similarity in bird composition and similarity in vegetation structure, and significant negative relationships between similarity in bird composition and geographic distance. However, no correlation was found between similarity in vegetation structure and geographic distance (Table 3). The latter result would suggest that, variation in vegetation structure among traditional oases could not be explained by the effect of geographic location. This also would mean that traditional oases from all parts of the study area are not separated into different homogeneous subsets. The scenario supported by data from traditional oases (Fig. 3B) suggests that, even though composition of bird communities was related to vegetation structure, the spatial structure of the oasis system is likely to have, by itself, played an important role in shaping local bird communities.

With regard to modern oases, Mantel and partial Mantel tests were not significant (Table 3). This result was predictable as all 13 modern oases are situated almost in the same region (Fig. 1), their vegetation is very similar (Fig. 2) and they support similar bird communities (Table 2).

4.3. Vegetation structure and bird species richness

It is first interesting to mention that based on AIC, we found that, in both the regression analysis and the ANCOVA, the models accounting for spatial dependence in data were better candidates to estimating the relationships between species richness and the explanatory variables than the standard models (see AIC values in Tables 4 and 5). Oases close to each other support more similar numbers of species than expected by chance and should not be considered as independent data points. This could be interpreted as an effect of the spatial configuration of the oasis system and is consistent with the hypothesis that the higher probability of exchange of species within subsets of oases close to each other than among oasis subsets may have played an important role in shaping local communities.

The results of the mixed regression model, which is more parsimonious than the standard model, suggest that both vegetation descriptors as well as oasis size were significantly relevant for species richness of breeding bird communities (Table 4). Species richness was primarily associated with PC1, suggesting that the diversity and abundance of trees and herbaceous plants

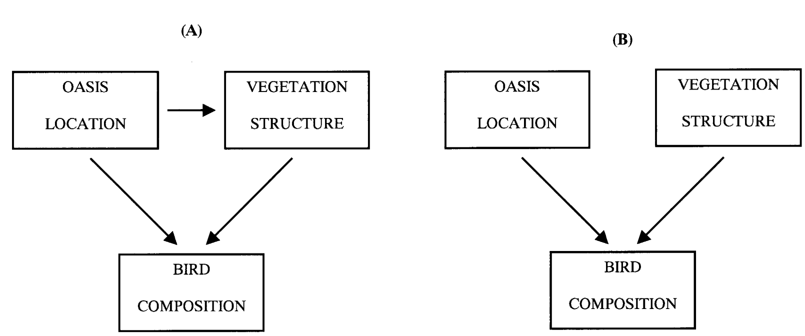

Fig. 3. Representation of scenarios linking species composition of local breeding bird communities to vegetation structure and geographic location of the corresponding oases. (A): scenario proposed for the entire oasis system (traditional and modern oases); (B): scenario proposed for traditional oases.

Table 4
Results of multiple regression analysis of log-transformed species richness on vegetation descriptors and oasis size (log-transformed) using a standard regression model and a mixed model accounting for spatial dependency in the data[a]

	Standard model (AIC = −18.4877)			Mixed model (AIC = −70.0348)		
	Estimate (±SE)	Type III F	P	Estimate (±SE)	Type III F	P
Intercept	2.0250±0.1183			2.2453±0.7997		
PC1	0.2141±0.0239	80.51	0.0001	0.1100±0.0154	50.64	0.0001
PC2	0.0066±0.0232	0.08	0.7766	0.0392±0.0124	9.95	0.0027
Oasis size	0.0385±0.0224	2.96	0.0915	0.0477±0.0124	14.82	0.0003

[a] AIC = Akaike's Information Criterion.

Table 5
Results of ANCOVA of species richness (log-transformed) with "oasis type" as a factor and oasis size (log-transformed) as a covariate using a standard model and a mixed model accounting for spatial dependence in the data[a]

	Standard model (AIC = −24.6463)		Mixed model (AIC = −56.1373)	
	Type III F	P	Type III F	P
Oasis type	79.32	0.0001	32.01	0.0001
Oasis size	9.21	0.0038	6.35	0.0150

[a] AIC = Akaike's Information Criterion.

are more relevant for the richness of breeding bird communities than the palm tree layer. Oases in which the agricultural practices have led to a high diversity of trees and herbaceous plants were likely more suitable for a greater number of bird species than oases in which the agricultural system was concentrated on cultivating palm trees.

This result is supported by that of the ANCOVA of species richness with oasis type as a factor and oasis size as a covariate (Table 5). For an equivalent oasis size, traditional oases were found to support higher numbers of bird species than do modern oases (Fig. 4).

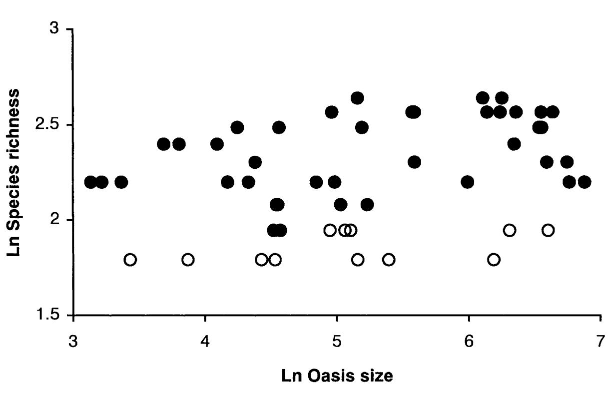

Fig. 4. Plot of Ln (bird species richness) on Ln (oasis size) for traditional and modern sampled oases.

5. Discussion

5.1. Agricultural practices and geographic location are important determinants of bird diversity in Tunisian oases

Breeding bird communities in southern Tunisian oases were found to be affected by oasis characteristics, but also by factors related to the spatial distribution pattern of the oasis system. Among-oases variation in species composition was related to variation in vegetation structure and to the geographic distance separating oases. When the effect of spatial dependence in the data was accounted for, vegetation structure as well as oasis size were found to be significant predictors of species richness of bird communities. Species richness was mainly related to the diversity and abundance of trees and herbaceous plants summarized in our analyses by the first component derived from the PCA of the original vegetation variables.

This vegetation descriptor was found to make a clear distinction between traditional and modern oases. This is likely a direct consequence of the difference in agricultural practices adopted within these oases, themselves dependent on the priorities of the production systems. Within traditional oases, the production system is aimed at diversifying the agricultural products, which explains the relatively high diversity of trees and herbaceous plants. However, modern agricultural techniques employed within modern oases, in order to maximize the production of dates, have been less favorable to the development of trees and herbaceous plants, thus producing a vegetation with a low structural complexity. This factor appears to be of major importance in determining the composition and richness of local bird communities.

Habitat conditions within modern oases were more similar to those of the desert environment, which may explain the presence in these oases of open-country specialist bird species that avoided densely vegetated traditional oases: *Alectoris barbara, Galerida cristata, Turdoides fulvus* and*Lanius meridionalis*. For the remaining bird species, oases represent isolated habitat patches within an inhospitable desert matrix. For these species, the composition and richness of local assemblages were determined by local habitat conditions, oasis area and also by the effect of isolation, conditioned by the particular spatial distribution pattern of the oasis system.

The importance of the latter factor is illustrated by data from traditional oases. Indeed, within traditional oases, vegetation similarity among oases was independent of oases' geographic location, suggesting that habitat conditions in traditional oases from all parts of the study area were relatively homogeneous. However, the spatial organization of traditional oases into different regional groups has resulted in high similarities in local bird communities between oases close to one another compared with oases from other regional groups. This suggests that colonization events from nearby oases may have played an important role in shaping local bird communities, and that differences in species composition between local communities from distant oases may be, at least partly, due to differences in the composition of regional pools of colonizers. The absence of certain species from some traditional oases could not simply be attributed to unsuitable habitat conditions, but may be related to the fact that these species have not reached those oases. The occurrence of "suitable but empty" habitat patches (Hanski, 1999) in the oasis system is also supported by historical information on colonization and invasion events that have occurred during the 20th century (Selmi, 2000).

Our findings provide an illustration of the importance of explicitly considering the spatial attributes, for instance the relative geographic location of study localities, when investigating relationships between local habitat conditions and species diversity in habitat patches (Selmi and Boulinier, 2001; Selmi et al., 2002). Spatial attributes can affect the probability of colonization of new habitat patches through their effect on the success of dispersal of individuals between patches, which may affect patterns of occupancy of species and may contribute to determine the richness and composition of local communities. Similar conclusions have been reported in recent ecological studies (Diaz et al., 1998).

When spatial dependence in data was accounted for, species richness of oasis bird communities was found to be strongly associated with vegetation descriptors. This was predictable as vegetation traits have repeatedly been reported to be among the most important correlates of species richness of bird communities in artificial and natural wood lots (Cieslak, 1985; Opdam et al., 1985; Ford, 1987; Farley et al., 1994; Greenberg et al., 1997). As the structural complexity of vegetation increases, the diversity of resources (i.e. food and nest sites) increases, which may be favorable to the establishment and the survival of a higher number of bird species (Wiens, 1989). In the case of oases, vegetation seems to play a more prominent role for birds. Indeed, the "oasis effect", which is responsible of the creation of a "microclimate" highly different from climatic conditions of the desert environment, is directly related to the structural complexity of the vegetation (Riou, 1995). This microclimate is needed for the establishment and survival of populations of at least seven forest and shrub bird species: *Turdus merula, Sylvia hortensis, Muscicapa striata, Parus caeruleus, Lanius senator, Fringilla coelebs* and *Serinus serinus*. For these species southern Tunisia is situated at the margin of their geographic range (see Cramp and Simmons, 1977–1994). The long-term persistence of these populations in oases is likely to be dependent on the persistence of this microclimate and, consequently, on the persistence of traditional agricultural practices on which depends the maintenance of highly diversified vegetation. Due to their low vegetation complexity, modern oases are unsuitable for these species, which may explain the low diversity of their avifaunas.

5.2. Conservation issues

By using water springs for irrigation, indigenous semi-nomad people have created oases, which has increased the landscape diversity in southern Tunisia. Using birds as indicators, we found that the role played by oases in increasing the biological diversity of the entire southern Tunisia landscape was affected by the manner with which people used the resources of oases in response to economic constraints. Traditional oases, which were adapted to a rural subsistence economy, are characterized by a higher species diversity than the recent "technified" oases, created in order to maximize the production and exportation of dates. The long-term persistence of the traditional agricultural practices, as well as the availability of water within oases, seem to be essential for maintaining the biological diversity of these precarious systems.

It has recently been noticed that due to the excessive exploitation of water resources for creating modern palm groves, traditional oases are suffering from a decrease in the availability of water for irrigation (Kassah, 1996). Furthermore, because of a complex set of socio-economic constraints, there has been a tendency of young people to modernize the production system within traditional oases or to leave their lands for other economic activities (mainly tourism and industry) or for emigrating (Sghaier, 1995; Kassah, 1996). This has resulted in an increasing degradation of habitat conditions within some traditional oases (Kassah, 1996), which may constitute a serious menace for biodiversity in these semi-natural systems.

As the transformations of the socio-economic role played by oases seem to be inevitable, realistic conservation plans should be developed in order to minimize the possible resulting loss of diversity. Before doing so, assessing quantitatively the biodiversity role played by traditional human practices in oases, as well as identifying other factors that may account for oasis-dependent plant and animal communities is needed. For example, understanding the importance of the traditional irrigation networks for maintaining the diversity of aquatic oasis communities (i.e. fishes, amphibians and aquatic invertebrates) should be considered in the future water management programs. This may, for instance, provide solutions aiming to minimize the possible resulting loss of diversity and to preserve the ecological integrity of the oasis system.

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