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Richness and Composition of Oasis Bird Communities: Spatial Issues and Species–Area Relationships

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ABSTRACT.—We used data on breeding bird communities of the oases of southern Tunisia to investigate variation in species richness and composition among local communities in relation to spatial configuration of the oasis system and to assess significance of the relationship between oasis size and local richness. Oases could be grouped into three regional systems, namely littoral, saharan, and mountainous oases. We found that at the scale of the entire oasis system, species richness and species composition exhibited significant spatial autocorrelation. That result was consistent with our prediction that the particular spatial organization of oases may have led to regional differences in availability of potential colonizers and that higher species exchange within oasis zones than among oasis zones may have played an important role in shaping local communities. With regard to the species–area relationship, we thus found that a model accounting for spatial covariance was more parsimonious than a standard regression model not incorporating information on the spatial location of oases. Overall, oasis size was a good predictor of species richness, but results were sensitive to spatial scale at which the relationship was examined. Aside from oceanic islands and forest patches, oases may constitute interesting systems to study how regional processes affect local diversity.

RESUMÉ.—Dans ce travail nous présentons une analyse de données sur la richesse et la composition spécifiques des peuplements d'oiseaux nicheurs d'un échantillon d'oasis des trois principales régions oasiennes de Tunisie (oasis littorales, oasis de piémont et oasis sahariennes). L'objectif est d'examiner le rôle de la configuration spatiale du système d'oasis dans la détermination de la diversité locale et de tester la relation entre la richesse spécifique locale et la superficie de l'oasis. Nous trouvons qu'à l'échelle de tout le système oasien, la richesse et la composition spécifiques montrent une autocorrélation spatiale significative. Ceci suggère que la configuration spatiale particulière du système d'oasis ait conditionné des différences entre les pools régionaux de colonisateurs potentiels, et que la plus grande probabilité d'échange d'espèces entre peuplements locaux au sein d'un même groupe régional d'oasis qu'entre oasis de groupes régionaux différents ait joué un rôle important dans le façonnement des peuplements locaux. Nos résultats montrent également qu'un modèle de régression admettant que les résidus sont dépendants et que leur covariance est fonction de la distance séparant les oasis est un meilleur candidat pour l'estimation de la relation entre la richesse spécifique et la superficie de l'oasis qu'un modèle de régression standard admettant l'indépendance des résidus. Quoique le résultat du test de la relation superficie-richesse spécifique varie avec l'échelle spatiale au niveau de laquelle la relation a été testée, la superficie de l'oasis s'avère globalement un bon indicateur de la richesse spécifique locale.

Understanding ecological processes determining species richness and composition of isolated habitat patches is one of the most important issues in community ecology and conservation (Ricklefs and Schluter 1993). In many previous studies, ecologists have used the island biogeography approach (MacArthur and Wilson 1967) to infer from patterns of diversity something about processes that generated them (e.g. Riebesell 1982, Schieck et al. 1995). Those studies have proved clearly the importance of patch physical characteristics for determining local species richness and composition. However, spatial distribution pattern of patches over the studied area has rarely been explicitly considered. The relative geographic location of patches is to be taken into account when investigating effect of patch physical characteristics on local diversity, because two patches may share very similar species richness and composition not because they are similar in size or in habitat conditions, but because they are geographically close.

This spatial covariance in local diversity could be the result of autocorrelation in environmental factors, but it could also be related to the relatively higher possibility for individuals (and species) to move from one patch to neighboring ones than to reach more distant patches (Morand 2000, Selmi and Boulinier 2001). That seems to be more likely to occur in a system with many levels of patchiness (i.e. when patches are organized into distinct geographic sys-

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TABLE 1. Detailed number and sizes of the sampled oases.

Oases	<100 ha	100–300 ha	>400 ha	Total	Mean oasis size (ha)	SD
Littoral	5	5	5	15	278	223
Mountainous	5	—	5	10	335	300
Saharan	5	5	5	15	344	322

tems of clustered patches). We find a possible example of such a system in traditional Tunisian oases. Indeed, those oases are isolated man-made woodlots created within a desert matrix and aggregated in three distinct oasis zones. Several bird species were found to be related to the oases for both foraging and nesting, and because most oases seem suitable for all those species, metapopulation processes have been suggested to shape occupancy patterns (Selmi 2000). In that system, one could expect that species with moderate to low dispersal capability will exchange within oasis zones more readily than among oasis zones, and that differences in long-distance ability among species may lead to differences in availability of colonizers for local communities. For that reason at least, oases from the same zone are expected to support more similar communities when compared to oases of similar characteristics (e.g. size) but situated in other oasis zones. Thus, we predicted a spatial autocorrelation in species richness and composition.

One important possible repercussion of this is that it could be inappropriate to view local communities from the entire system as independent realizations of the same stochastic process when investigating relationship between local diversity and oasis characteristics, for example, the species–area relationship. Because of this possible lack of independence among data points, use of a standard regression model, which assumes independence among errors, is questionable (Caroll and Pearson 2000, Lennon 2000). In such a case, use of a model that accounts for spatial covariance of errors (whatever the source of such a covariance) would be more parsimonious than the standard model and should permit better inferences.

In this article, we use data on breeding birds in the traditional oases of southern Tunisia to investigate such issues. We first performed spatial autocorrelation analyses to explore spatial structure of the data and to test for predicted patterns of spatial autocorrelation in species richness and composition. Second, we investigated the relationship between oasis size and species richness at different scales using a standard regression model and then a regression model that accounts for the spatial covariance in species richness.

Methods.—Data analyzed in this work come from a sample of 40 traditional oases of different sizes and from the three different oasis zones in southern Tunisia, namely the littoral, mountainous, and saharan oasis zones (Table 1). Breeding bird communities were surveyed during the breeding season of 1998 by the *Indices Ponctuels d'Abondance* (IPA) method (Blondel et al. 1970, International Bird Census Committee 1977). Application of that method consisted in doing two counts of 20 min each at the same site but at two different times of the breeding season to sample (1) early nesting resident birds (February), and (2) migratory birds, which begin to breed much later (May). We used only one IPA survey (two partial

TABLE 2. Breeding bird species recorded in the traditional oases from the different zones of oases in southern Tunisia. Asterisk indicates a species was found in that zone.

Common name	Scientific name	Littoral oases	Mountainous oases	Saharan oases
European Turtle Dove	*Streptopelia turtur*	*	*	*
Palm Dove	*Streptopelia senegalensis*	*	*	*
Eurasian Hoopoe	*Upupa epops*	*	*	*
Rufous Bushchat	*Cercotrichas galactotes*	*	*	*
Eurasian Blackbird	*Turdus merula*	*	*	
Fan-tailed Warbler	*Cisticola juncidis*	*		*
Olivaceous Warbler	*Hippolais pallida*	*	*	*
Orphean Warbler	*Sylvia hortensis*	*	*	*
Spotted Flycatcher	*Muscicapa striata*	*	*	
Blue Tit	*Parus caeruleus*		*	*
Great Grey Shrike	*Lanius senator*	*	*	
House Sparrow	*Passer domesticus*	*	*	*
Common Chaffinch	*Fringilla coelebs*	*	*	
Serin	*Serinus serinus*	*	*	*
House Bunting	*Emberiza striolata*	*	*	*
Regional Species richness		14	14	11
Range of variation in local richness		10–14	8–14	7–10

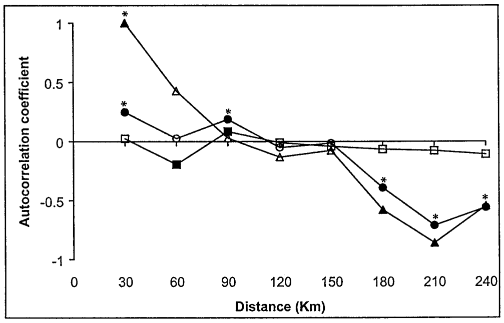

FIG. 1. Correlograms of oasis area (squares), species richness (circles), and species composition (triangles) among local breeding bird communities for the 40 sampled traditional oases. Spatial autocorrelation is measured by Moran's I for oasis area and species richness, and standardized Mantel's r for species composition. Black symbols represent significant values at the 0.05 level whereas white symbols represent nonsignificant values. Starred black symbols represent significant values at the corrected Bonferroni level ($\alpha' = 0.05/8 = 0.00625$).

counts) per oasis, but the ability of our IPA survey to accurately estimate species richness was preliminarily assessed by using patterns of detection and nondetection of species obtained on 15 different sites within one oasis (see Boulinier et al. 1998, Nichols et al. 1998). Using the computer program SPECRICH2 (Hines et al. 1999), we found that the jackknife estimator associated to model M_h (Burnham and Overton 1979), which makes the assumption of a heterogeneous detection probability among species, provided a good model for species-richness estimation (goodness of fit test, $\chi^2 = 14.60$, $P = 0.406$). Overall, average probability of detecting all species per IPA count was very high ($p_i = 0.9333$), suggesting that the use of one IPA survey per oasis provided reliable information on local species richness. That high detection probability was also found using data collected in 1999 at 5 locations within each oasis of a sample of 26 traditional oases (S. Selmi unpubl. data). That might be due to the low vegetation density and high visibility within the oasis habitat.

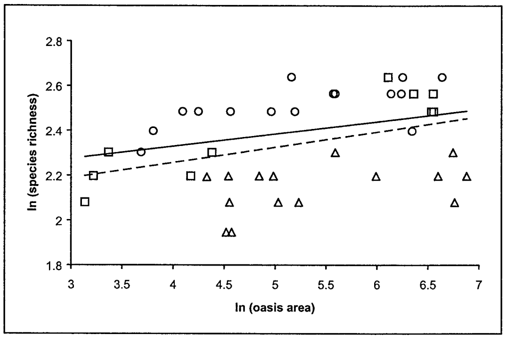

FIG. 2. Plot of ln(species richness) on ln(oasis area) for the entire oasis sample. Circles represent littoral oases; squares represent mountainous oases; triangles represent saharan oases. Dotted line represents the regression estimated by the standard regression model, whereas solid line represents the regression estimated by the regression incorporating a Gaussian covariance model.

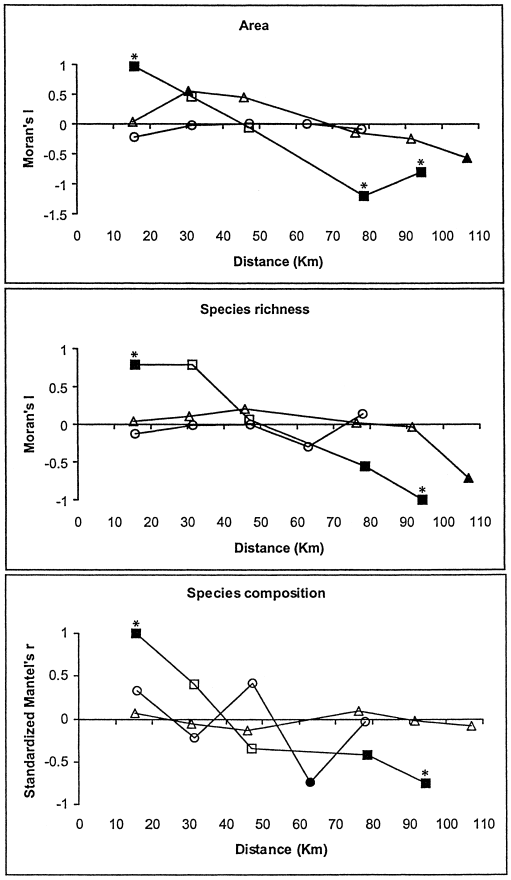

FIG. 3. Correlograms of oasis area, species richness and species composition among local breeding bird communities for the different regional oasis groups. Circles represent littoral oases; squares represent mountainous oases; triangles represent Saharan oases. Black symbols represent significant values at the 0.05 level, whereas white symbols represent nonsignificant values. Starred black symbols are significant at the corrected Bonferroni level (0.01 for littoral and mountainous oases; 0.0083 for saharan oases).

Spatial autocorrelation in our variables was investigated by drawing correlograms (Oden and Sokal 1986, Legendre and Fortin 1989) in which spatial au-

TABLE 3. Results of regression analyses of ln(species richness) on ln(oasis size) at the scale of the entire oasis system and at the scale of each oasis zone using an error-independent model (standard regression model) and a spatially dependent error model (mixed model assuming that the covariance of the errors follows a Gaussian covariance function). Note: AIC_c = Akaike's Information Criterion with correction for small sample size: $AIC_c = -2 \log \text{likelihood} + 2k + [2k(k+1)/(n-k-1)]$ where k is number of model parameters and n is sample size.

	Entire oasis sample ($n = 40$)		Littoral oases ($n = 15$)	
	Standard model	Mixed model	Standard model	Mixed model
	Fitting criterion			
AIC_c	−7.0483	−55.5153	−22.3362	−20.2288
	Solution for fixed effects (estimate ± SE):			
Intercept	1.984 ± 0.151	2.110 ± 0.155	2.173 ± 0.110	2.178 ± 0.010
Oasis size	0.068 ± 0.028	0.055 ± 0.016	0.065 ± 0.021	0.063 ± 0.018
	Test of fixed effects:			
Type III *F*	5.87	11.73	9.79	11.62
P	0.0202	0.0015	0.0080	0.0047

tocorrelation coefficients were plotted on the ordinate against equidistant classes among the 40 sampled oases on the abscissa. We used Moran's I (1950) to measure spatial autocorrelation in oasis size and species richness (see Legendre and Fortin 1989), and Mantel's r (1967) to measure correlation between a matrix of geographic distances among oases and a matrix of similarity in species composition for each distance class (see Oden and Sokal 1986, Legendre and Fortin 1989). The latter matrix was calculated using the Jaccard index. Computations were performed using programs AUTOCORRELATION and MANTEL available in the ''R'' package (Legendre and Vaudor 1991), and which also give a test of significance for each Moran's I and Mantel's r-value in the correlograms. Bonferroni method of correcting for multiple tests was used to assess the significance of the correlograms (see Oden 1984).

Regression analyses of log–log transformed species–area plots were used to characterize relationships between oasis size and species richness. Those analyses were performed using the ''Mixed'' procedure (Littell et al. 1996) in SAS (SAS Institute 1996). The ''Mixed'' procedure uses 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 that 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 to improve convergence and the likelihood of obtaining reasonable estimates of those parameters. Those 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 models) was then compared using Akaike's Information Criterion (AIC). In order to correct for small sample size, we used the corrected AIC: $AIC_c = -2 \log \text{likelihood} + 2k + [2k(k+1)/(n-k-1)]$, where k is number of model parameters and n is sample size (Burnham and Anderson 1998). The log likelihood value was taken from SAS (see Littell et al. 1996). The lower the value of the AIC_c, the more parsimonious the model is (Burnham and Anderson 1998). The *F*-value for the test of the null hypothesis of no oasis size effect (and its associated *P*-value) given by both models were then compared to assess how the significance of the effect of oasis size on species richness could be affected by accounting for relative geographic location of oases.

Results.—Fifteen nesting bird species were recorded in the entire traditional oasis system, with local richness varying between 7 and 14 (Table 2). As predicted, the correlograms show evidence of spatial autocorrelation in species richness and species composition at the scale of the entire oasis system (Fig. 1). Conversely, oasis size did not show evidence of spatial autocorrelation (oases of different sizes exist in each of the three oasis zones; Table 1). Small-scale positive autocorrelation in richness and composition (30 km class in the correlogram) suggests that species assemblages from pairs of oases close to each other are more similar than expected for randomly associated pairs of observations. That could be interpreted as a within-oasis-zone effect because distances between pairs of oases from different zones are much higher (>60 km). Seemingly, large-scale negative autocorrelation suggests that observations from pairs of oases distant from each other (>180 km, i.e. from different zones) are less similar than expected for randomly associated pairs of observations. Thus,

TABLE 3. Extended.

Mountainous oases (n = 10)		Saharan oases (n = 15)	
Standard model	Mixed model	Standard model	Mixed model
Fitting criterion			
−9.0897	−10.9338	−14.8679	−14.7027
Solution for fixed effects (estimate ± SE):			
1.805 ± 0.097	1.852 ± 0.112	1.883 ± 0.159	1.965 ± 0.158
0.114 ± 0.018	0.106 ± 0.023	0.049 ± 0.029	0.032 ± 0.028
Test of fixed effects:			
38.24	21.85	2.80	1.34
0.0003	0.0016	0.1179	0.2679

when viewed at a large geographic scale, local communities from the same oasis zone appear nonindependent from one another, in that they are more similar to one another than to local communities from other zones. Under the hypothesis that all traditional oases are suitable for all recorded species, that is consistent with our prediction that the possibly higher probability of exchange of species within oasis zones than among oasis zones may have played an important role in shaping local communities.

With regard to the species–area relationship (Fig. 2), results of the regression analyses at the scale of the entire oasis system showed that a mixed model, assuming that the covariance of the errors follows a Gaussian covariance function, was more parsimonious than the standard regression model (AIC_c of the mixed model $<$ AIC_c of the standard model; Table 3). Even though estimates of the oasis size effect given by both models were not very different (Table 3, Fig. 2), the F-value given by the mixed model was twice as large as that given by the standard model (and the P-value over 10× lower). Species richness was thus strongly associated to oasis size (Table 3).

At the scale of each oasis zone, the correlograms of species richness and species composition show no evidence of spatial autocorrelation in the case of littoral and saharan oases, whereas significant spatial autocorrelation was found in the case of the mountainous ones (Fig. 3). That latter pattern is to be related to the significant autocorrelation in oasis size observed within that oasis zone (Fig. 3). Indeed, unlike for the littoral and saharan oasis zones, similar-sized oases were close to each other within the mountainous one. Given these results, we predict that in the case of littoral and saharan oases, a model accounting for relative location of oases will not be more parsimonious than the standard regression model. However, within the mountainous oasis zone, communities from similar-sized oases are not independent from each other and could not be accounted for a full observation each in the regression. For that reason, we predict that a model accounting for spatial covariance in species richness could be more parsimonious than the standard model.

These predictions were supported by the results of the regional-scale analyses (Table 3). Indeed, in the case of littoral and saharan oasis zones, a model accounting for relative location of oases was not more parsimonious than the standard model. Oasis size was a good predictor of species richness within the former zone, whereas no significant relationship was found within the latter. In the case of mountainous oases, the regression model accounting for relative location of oases was slightly more parsimonious than the standard model. Within that zone, effect of oasis size on species richness could have been partly amplified by the effect of isolation, in that small oases support fewer species than large ones because they are smaller, but also because they are distant from large oases, assuming that large oases may be the source of colonizers for small ones. Nonetheless, oasis size was found to account significantly for species richness even when relative location of oases was accounted for.

Discussion.—The results of spatial autocorrelation analyses were consistent with species long-distance dispersal capability and colonization events from nearby oases having played important role in shaping local communities. That was predicted because oases are not the result of the fragmentation of a forest, but they are artificial woodlots created at the margin of the geographic range of several palearctic species (Cramp 1977–1994). Thus, oasis zones may have received colonists from populations of northern Tunisian or Algerian forests or from those established in other oasis zones. Within each oasis zone, local communities are the result of some constraints imposed by the oasis properties such as oasis size, but also correspond to subsets of species sampled from the pool of colonists that have reached the corresponding oasis zone.

Among the recorded bird species in the traditional oasis system, nine species have reached the three oasis zones whereas six species were restricted to only two oasis zones (Table 2). We think that pattern can not be attributed to differences in habitat conditions among oasis zones. Indeed, there is a great similarity in vegetation structure among traditional oases from the three zones, which is the result of similar agricultural production systems adopted by people within those traditional oases (Kassah 1996). Second, there are no important differences in climatic conditions among the three Tunisian oasis zones; all of them receiving a rainfall <200 mm per year, with an average annual temperature that ranges between 19.2 and 20.9°C (Kassah 1996). Furthermore, there is evidence of the occurrence of ''empty but suitable habitat patches'' (Hanski 1999) in the oasis system, because at least three invasion events of bird species have happened within the oasis system in the course of the twentieth century (Selmi 2000). That point of view is supported by the comparison of the distributions of *Parus caeruleus* and *Turdus merula* in the oasis system. Those species are among the most generalist palearctic birds, and they are often found to coexist over their geographic ranges (Cramp and Simmons 1977–1994). Both species inhabit the mountainous oases. *Parus caeruleus* is absent from the littoral oasis zone but inhabit the saharan one, whereas *Turdus merula* has the opposite pattern (Table 2). It is unlikely that those patterns could be related to differences in habitat conditions among those oasis zones.

The relationship between oasis size and number of breeding bird species was investigated under an island biogeography approach. The results obtained were sensitive to the spatial scale at which the relationship was investigated. Indeed, even though species richness was not related to oasis size within the saharan zone, a significant relationship was found at the scale of the entire oasis system. That provides an example of a case where ecological patterns are not independent of the spatial scale at which they are examined, and it illustrates the consequences of changing the scale on which a system is viewed (Wiens 1989). The problem of scale is fundamental in ecological studies because it has become clear that ecological communities are organized by a variety of processes operating at different spatial scales and that a multiscale approach is necessary to investigate ecological patterns and processes (Wiens 1989, Ricklefs and Schluter 1993). In this context, initially checking for spatial autocorrelation in the data may prove to be a useful method as it provides a way to describe the spatial structure of the data (Legendre 1993). Our results also suggest that the degree of isolation of a given patch or island can not be measured by the simple geographic distance to the nearest large patch or to the mainland (for a mainland–island system), and that there is a need for a measure that takes into account the global spatial configuration of the patch system. A possible convenient measure can be a distance matrix among the studied patches. Recent works have proved the utility of such an approach in island biogeography studies (Kadmon and Pulliam 1993, Morand 2000).

Our work stresses the need to more explicitly consider the spatial configuration of patch systems when investigating relationships between patch characteristics and local diversity. Taking that finding into account is important not only for studies of community ecology, but also for applied problems associated with conservation of biodiversity in patchy landscapes.

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