NULL MODEL ANALYSIS OF COMMUNITY STRUCTURE REVEALS THAT PATCH QUALITY INFLUENCES THE CONSERVATION OF COMPLEX BIRD COMMUNITIES IN MEDITERRANEAN HABITATS

Roberto Isotti[1], Luca Luiselli[2] & Alberto Fanfani[1]

Résumé. — *L'analyse de la structure de communauté à l'aide de modèles nuls révèle que la qualité de la parcelle influence la conservation de peuplements aviens complexes dans les habitats méditerranéens*. — Les peuplements aviens de l'État Présidentiel de Castelporziano (Rome, Italie) ont été étudiés afin de déterminer leur structure dans une série de divers habitats naturels. La zone d'étude se présente comme un écosystème complexe, formé par une mosaïque d'habitats différents et de leurs écotones, possédant un haut niveau de biodiversité. Les zones humides hébergent le plus grand nombre d'espèces d'oiseaux, suivies par les forêts de chênes. Les peuplements aviens de Castelporziano sont caractérisés par de hauts degrés de richesse et de complexité. Les analyses par modèles nuls ont montré que la communauté avienne n'est pas organisée au hasard et ceci tant par l'algorithme de randomisation 2 (dénotant ainsi la nature généraliste-spécialiste de la similarité écologique réduite des espèces) que par les algorithmes de randomisation 3 et 4 (dénotant ainsi que les types de ressources utilisées ne réduisent pas la similarité écologique). Sur la base de cette étude nous insistons non seulement sur les niveaux de conservation des habitats isolés pour les oiseaux méditerranéens mais nous modifions également l'approche classique de la "biologie de la fragmentation" en une nouvelle approche où la qualité naturelle des parcelles est évaluée à l'aide d'outils statistiques appropriés.

Summary. — The bird communities of the Presidential Estate of Castelporziano (Rome, Italy) were studied to determine their structure in a set of different natural habitats. This study area presents a complex ecosystem, formed by a mosaic of different habitats and their ecotones, having a high biodiversity level. Wetlands housed the highest number of bird species followed by oak forests. Bird communities of Castelporziano are characterized by high degrees of richness and complexity. Null model analyses revealed that the bird community was not randomly organized by Randomization Algorithm 2 (thus denoting that the generalist-specialist nature of the species reduced ecological similarity) nor by Randomization Algorithm 3 and Randomization Algorithm 4 (thus denoting that the types of resources utilized did not reduce ecological similarity). Based on this study, we will not only focus on conservation levels of single habitats for Mediterranean birds, but also modify the classical approach of 'fragmentation biology' with a new approach where the natural quality of all patches is evaluated with appropriate statistical tools.

Diversity, richness, abundance, dominance and distribution of bird community and target species are used to define community structure, as well as general conclusion on the evaluation of biodiversity level in the area (Bibby, 1999; Uezu *et al.*, 2005; Piratelli *et al.*, 2008; Simberloff, 1994). In this regard, bird community studies may allow improvement of management actions for natural areas due to their easier utilization, compared to other types of organisms,

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[1] Dipartimento di Biologia e Biotecnologie "Charles Darwin", Sapienza University of Rome, Viale dell'Università 32. 00185 Roma, Italy. E-mail: roberto.isotti@uniroma1.it

[2] Eni S.p.A. Environmental Department - Centro di Studi Ambientali Demetra s.r.l.,via Olona 7. 00198 Roma, Italy. E-mail: lucamlu@tin.it

as for the structure and dynamics of their assemblages (Arponen *et al.,* 2008; Benayas & Montaña, 2003; Bibby, 1999; Simberloff, 1994). In the same way the knowledge of bird community needs gives indirect information on the quality level (resource level and habitat diversity) necessary to the area to give refuge to a high level of biodiversity (Haila & Hanski, 1984; Piratelli *et al.*, 2008; Simberloff, 1994).

Local authorities involved in land management are showing an ever-increasing interest in avian community studies and have expressed a need to exploit results, also because the complexity and structuring of bird communities are often positively correlated to the conservation levels of natural areas, and are hence useful indicators of habitat quality (Battisti & Romano, 2007; Bellamy *et al.*, 1996; Bernstein *et al.*, 1991). Studies on bird richness, diversity and abundance are also relatively efficient, compared to analogous studies on other target organisms (e.g., mammals) in terms of cost-benefit analysis because it ensures effective data collection obtained with a relatively low field and money efforts (Balmford *et al.*, 2003; Battisti *et al.*, 2003; Davies *et al.*, 2001; Simberloff, 1994).

Our aim in this paper is to test whether habitat heterogeneity (i) has any effect on the richness and abundance of bird communities in mosaic landscapes of Mediterranean central Italy, and (ii) does influence community structure. For community structure, we accept the definition of Gotelli & Graves (1996), where a structured (non-random) community of organisms is that assemblage of species where the co-occurrence and abundance of each species are not independent on those of the coexisting species. The hypothesis behind issue (ii) is that, the more complex is the species' assemblage, the more likely is the presence of a non-random structure, given that in species-rich communities from pristine habitats the non-random organization of the community is more likely to occur than in species-poor assemblages from altered habitats (Luiselli, 2006, 2007; Luiselli *et al.*, 2006).

In other words, we are working to define whether the number of species and their assemblages are influenced by the presence of patches from natural origin mosaics that are produced by natural processes developing in mature and well-preserved habitats - and not by altered habitat patches, where the signs of human activities are heavily present (Haila & Hanski, 1984; Lauga & Joachim, 1989; Shaffe, 1981). Hence, we investigate whether the use of habitat types by the various species is non-randomly organized, under the null hypothesis that the communities are expected to be neutral, i.e. they show stochastic habitat occupancy with random abundance distributions. We quantified the niche of species in terms of individual counts for each species in each habitat type.

In more detail, we will answer the following key questions: (i) are the bird assemblages different by habitat type in a mosaic landscape? (ii) are these bird assemblages assembled randomly? (iii) if not, is the non-random structure of the community (sensu Gotelli & Graves, 1996; Luiselli *et al*., 2007; Vignoli & Luiselli, 2012) driven by quantitative niche separation of the available resources or qualitative separation of a single habitat resource by sympatric species?

In order to find an answer to these questions, we selected the Presidential Estate of Castelporziano as the study area. This area was selected because of its specific characteristics, being similar to a wilderness of natural patches, interspersed within a "matrix" of human-altered landscape (Della Rocca *et al.,* 2001; Grignetti *et al*., 1997; Fanfani *et al*., 2001, 2006; Isotti & Fanfani, 2006; Isotti *et al*., 2006).

MATERIAL AND METHODS

STUDY AREA

The Presidential Estate of Castelporziano is one of the better-preserved natural areas in Italy and the Mediterranean Basin. This area (geographic coordinates: 41°69' N; 12°39' E) (Fig. 1) covers approximately 6000 hectares, and is characterized mainly by chaparral vegetation (which ranges from the coastal dune vegetation to the garrigue and the Mediterranean and sub-Mediterranean forest types) (Focardi *et al.*, 1991). In the study area there are several small-sized temporary pools and permanent pounds (160 total). The climate is characterized by mild and rainy winters and dry summers (Focardi *et al.,* 1991).

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- Coastal dunes
- Grassland
- Agricoltural areas
- Maquis
- Wetland
- Pine forest
- Oak forest

Figure 1. — Map of the study area, showing the habitat types.

Protocol

Two methods were applied in the study area from 1997 to 2008 to study bird communities: the transect method (TRM) and the point count method (PCM) with index of abundance (IPA) (Bernoni, 1984; Blondel, 1969; Blondel & Frochot, 1981; Bibby *et al*., 2000). Transects and points are truncated to the distance of 200 mt.

TRM was carried out on a monthly basis. Records were collected by identifying species both through direct sightings and through acoustic identification. PCM was carried out during the breeding season (from April to the end of June) in different monitoring stations. Each station was assumed to be separated in data collection from the others because they were spaced at least 1.0 km apart.

Seven main vegetation types were classified and investigated for this study: Maquis and Mediterranean forest (M), Pine forest (P), Oak forest (Q), Grassland (A), Agricultural areas (C), Wetland (L), Coastal dunes vegetation (D) (Fig. 1).

The mentioned vegetation types are represented by the following associations (Pignatti *et al.*, 2001): Maquis and Mediterranean forest (M): *Viburno/Quercetum ilicis*; Pine forest (P): Pine forest, ancient reforestation; Oak forest (Q): *Echinopo/Quercetum*; Grassland (A): Dry prairie vegetation; Agricultural areas (C): Crop vegetation; Wetland (L): Wet prairie vegetation. Wet wood. *Rubo/Ulmion*; Coastal dunes vegetation (D): Garrigue. Coastal dune vegetation.

Three transects and points were drawn within each of the main vegetation typologies: The 1-km transects were covered within the first seven days of each month, totalling about 882 km. All birds heard and seen while displaying territorial behaviours along the transects and the points were recorded inside a 250 m main belt (Jàrvinen & Vàisànnen, 1973). For each species, we indicated the number of individuals. Data were recorded by the same observer (RI) to control bias due to observer effect. Bird species were listed using Brichetti & Massa's (1984) systematic order. For each species, we indicated the number of individuals, the habitat type in which they were sighted, and the status within the area of study: (M = Migrant; B = Breeding; W = Wintering; S = Stantial) (Fig. 2, Tab. I).

Statistical analyses

In order to calculate overlap indices and generate Monte Carlo simulations we used Ecosim software (Acquired Intelligence Corp., Kesey-Bear; http://www.garyentsminger.com/ecosim/index.htm" or http://www.uvm.edu/~ngotelli/

EcoSim/ EcoSim.html). We calculated Pianka's (1973) niche overlap index using counts data of birds, for all communities and randomized the original species habitat type utilization matrices from which Pianka's overlap was calculated by distributing the original values among resource states. Pianka's (1973) index is as follows:

$$O_{xy} = \frac{\sum_{i=1}^{n} p_{xi} p_{yi}}{\left(\sum_{i=1}^{n} p_{xi^2} \sum_{i=1}^{n} p_{yi^2} \right)^{1/2}}$$

where p_{xi} is the proportional utilization of habitat type i by species x and p_{yi} the proportional utilization of habitat type i by species y. This index ranges from 0 (no prey in common in the diet spectrum) to 1 (same diet spectrum).

We used three randomization algorithms (RA2, RA3, RA4) from Lawlor (1980), as they are particularly robust for niche overlap studies (Gotelli & Graves, 1996). RA2 tests for structure in the generalist–specialist nature of the resource utilization matrix by conserving guild structure (i.e., keeping the zero states of the observed matrix) but destroying observed niche breadth. RA3 tests for guild structure by conserving the niche breadth for each species but destroying the guild structure manifested by the resource utilization matrix's zero structure (Vignoli & Luiselli, 2012); RA4 tests for the occurrence of character displacement patterns within the studied assemblages (Gotelli and Graves 1996). For each pair of species, 30,000 random Monte Carlo permutations were generated. This amount ensures that algorithm bias is minimized (Lehsten & Harmand, 2006). Pianka's niche overlap values were calculated for each of these randomly generated matrices, and species-pair and community-summary statistics were computed (i.e. observed versus expected niche overlap values and variances and relative P-values; Friggens & Brown, 2005). In our data matrix, 0 values are assumed to be structural zeroes and not stochastic zeroes. Actual overlap values were then compared to the distributions of expected values. Structure was assumed when $p_{(observed \leq expected)} \leq 0.05$ (Gotelli & Graves, 1996; but see also Yoccoz, 1991 for the limits of this type of assumptions). Hence, we interpreted the P-value significance as the strength of the evidence against the null hypothesis H_0 (no non-random structure), conditionally to the available data, with the P-value being the probability, calculated under H_0, of obtaining a value of Pianka's index as extreme as that observed in the data. In all cases, equiprobable resource use was assumed *a priori* in the analyses.

Relationships between number of species and habitat availability were assessed by Pearson's correlation coefficient, under the assumption of a linear association between these variables.

RESULTS

The whole bird community totalled 98 species, out of which 51 were nesting species (Tab. I). Availability of each habitat type did not influence species richness ($r = 0.025$; $P = 0.957$). The numbers of bird species found in each habitat type are shown in figure 2. The frequency of species did differ significantly by habitat type, with wetland species richness being higher than species richness in the other habitat types ($\chi^2 = 29.81$, df = 6, P < 0.00001).
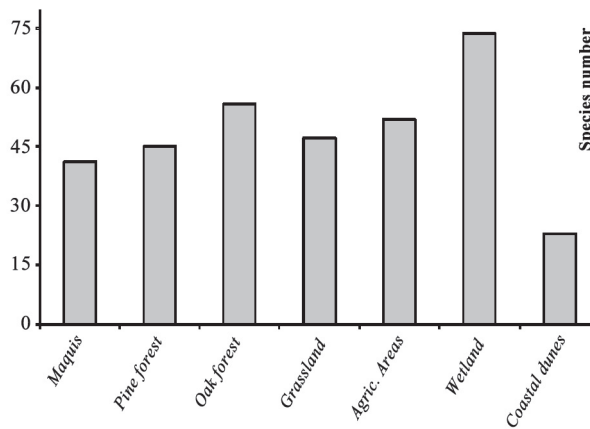

Figure 2. — Numbers of bird species found in each habitat type at the study area.

Summary of the number of individuals observed for each bird species at the study area, and divided by status, season and habitat type

Specie	Status	Habitat				
		Spring	*Nestling*	*Summer*	*Autumn*	*Winter*
Tachybaptus ruficollis	**MB**	L	L		L	L
Phalacrocorax carbo	**M**	L				
Egretta garzetta	**MW**			L	CL	CL
Ardea cinerea	**SM**	C	L	L	CL	CL
Anas strepera	**M**				L	
Anas crecca	**MW**				L	L
Anas platyrhynchos	**MWB**	L	L		L	L
Anas querquedula	**M**	L				
Milvus migrans	**MB**	AC	C	C		
Circus aeruginosus	**M**	L				
Accipiter nisus	**M**	P				
Buteo buteo	**SB**	AC	C		C	ACL
Falco tinnunculus	**SB**	C			AC	C
Phasianus colchicus	**SB**	PQAL	A			L
Gallinula chloropus	**SB**	L		L	L	L
Fulica atra	**MW**				L	L
Haematopus ostralegus	**M**	D				
Recurvirostra avosetta	**M**				L	
Charadrius dubius	**MB**		D	D		D
Charadrius alexandrinus	**MB**		D	D		D
Lymnocryptes minimus	**M**					L
Gallinago gallinago	**MW**				L	L
Scolopax rusticola	**MW**				L	L
Tringa totanus	**M**				L	
Tringa stagnatilis	**M**				L	
Tringa ochropus	**M**	L				
Actitis hypoleucos	**M**	L				
Larus ridibundus	**M**	D				
Larus argentatus	**SMW**	LD	D	D	D	D
Sterna caspia	**M**	D				
Sterna sandvicensis	**M**	D				
Columba palumbus	**MW**	MPQC			MPQACL	MPQACL
Streptopelia turtur	**MB**	MPL	MACL	MPQACL		
Cuculus canorus	**MB**	MPQACL	PQAC		L	
Tyto alba	**SB**	AC	PAC	AC	C	C
Athena noctua	**SB**	PQ	QC	PQ	Q	Q
Strix aluco	**SB**	M	PQAC	PQ	P	PQ
Apus apus	**MB**	QAC	PQACL	CL		
Alcedo atthis	**SM**	L		L		L
Upupa epops	**MB**	PC	C	CL		
Jynx torquilla	**SB**	CL	AL	QACL	PQ	
Picus viridis	**SB**	MPQACL	P	PAL	PQA	PQA
Dendrocopos major	**SB**	MPQAL	MP	PQ	MPQA	MPQACL
Dendrocopos minor	**SB**	MPQAL				MPQACL
Galerida cristata	**SB**	A	A			
Riparia riparia	**M**	L				
Hirundo rustica	**MB**	QACL	AC	ACL	CL	
Delicon urbica	**MB**	CLD				
Anthus trivialis	**M**	C				

Motacilla alba	**SB**	LD		QC	CLD	MACD
Troglodytes troglodytes	**SBM**	MPQC	MQA	PQC	PC	MPCL
Prunella modularis	**MW**					L
Erithacus rubecula	**SBMW**	MQAL			MPQACL	MMPQACLD
Luscinia megarhyncha	**SBM**	MPCL	MPQACL	PC	P	PA
Phoenicurus ochruros	**M**					C
Phoenicurus phoenicurus	**M**	A				
Saxicola rubetra	**MW**	AC			A	AC
Saxicola torquata	**SB**	AC	A	C	A	ACL
Oenanthe oenanthe	**M**				C	
Monticola solitarius	M					Q
Turdus merula	**SB**	MPQACL	MPQACL	MPQCL	MPQACL	MPQCL
Turdus philomelos	**M**				C	
Cettia cetti	**SB**	L	L	L	CL	CL
Cisticola juncidis	**B**		CL			
Acrocephalus schoenobaenus	**M**	CL				CL
Acrocephalus scirpaceus	**M**					L
Acrocephalus arundinaceus	**MB**	L	L			
Hippolais polyglotta	**M**	L				
Sylvia melanocephala	**SB**	MLD	L		L	MP
Sylvia communis	**M**	M		M		M
Sylvia borin	**M**	C				
Sylvia atricapilla	**SBM**	MPQAC	MPQL	MPQ	MPC	PQL
Phylloscopus sibilatrix	**MW**	C				CL
Phylloscopus collybita	**SBM**	MPQCL	P		MP	PL
Phylloscopus trochilus	**M**	P	M			
Regulus regulus	**W**					PQ
Regulus ignicapillus	**MB**	MP	PQ		MPQ	
Muscicapa striata	**M**	C				
Ficedula albicollis	**M**	C				
Ficedula hypoleuca	**M**	Q				
Aegithalos caudatus	**SB**	P	PQ		Q	Q
Parus caeruleus	**SB**	MPQL	MPQ	PQ	MPQC	MPQA
Parus major	**SB**	MPAC	P	P	MPQC	MPQA
Sitta europaea	**SB**	MPQA	P	M	PQ	PQA
Certhia brachydactyla	**W**					Q
Oriolus oriolus	**MB**	PQ	QAC	M		
Lanius collurio	**M**	C				
Lanius senator	**MB**	AD				
Garrulus glandarius	**SB**	MPQACL	PQA	MPQACL	PQACL	MPQL
Corvus corone cornix	**SB**	MPACLD	MPQACL	MACL	MPACDL	PACDL
Sturnus vulgaris	**SBMW**	QAC	MACL	QC	QAC	PQACL
Passer italiae	**SB**	ACLD	ACLD	ACLD	ACL	A
Passer montanus	**B**		A	L		
Fringilla coelebs	**SBM**	MQC	MPP	QC	PC	
Serinus serinus	**SBM**	MPQACL	PAL	L	Q	
Chloris chloris	**SBM**	CL			PQCL	L
Carduelis carduelis	**SBM**	MPQC	MPQCL	MPQL	MPC	C
Emberiza cirlus	**M**					C

HABITAT: Maquis (M); Pine forest (P); Oak forest (Q); Grassland (A); Agricultural areas (C); Wetland (L); Coastal dune (D)
STATUS: Migratory(M); Breeding (B); Wintering (W); Stazionario (S)

Null model analyses revealed a non-random niche habitat use in the bird assemblages under study as far as the RA2 algorithm is concerned (Observed mean = 0.14547; Mean of simulated indices = 0.16397; Variance of simulated indices = 0.00001; $p_{(observed \leq expected)}$ = 0.00001).

On the other hand, RA3 algorithm did not uncover any non-random structure in the communities under study (Observed mean = 0.14547; Mean of simulated indices = 0.11612; Variance of simulated indices = 0.00042; $p_{(observed \leq expected)}$ = 1.00000). RA4 algorithm did not find any non-random pattern (Observed mean = 0.14547; Mean of simulated indices = 0.14126; Variance of simulated indices = 0.00001; $p_{(observed \leq expected)}$ = 0.93600), thus producing no evidence for a character displacement structure within the studied bird assemblages. The results of these algorithms are presented in figure 3.
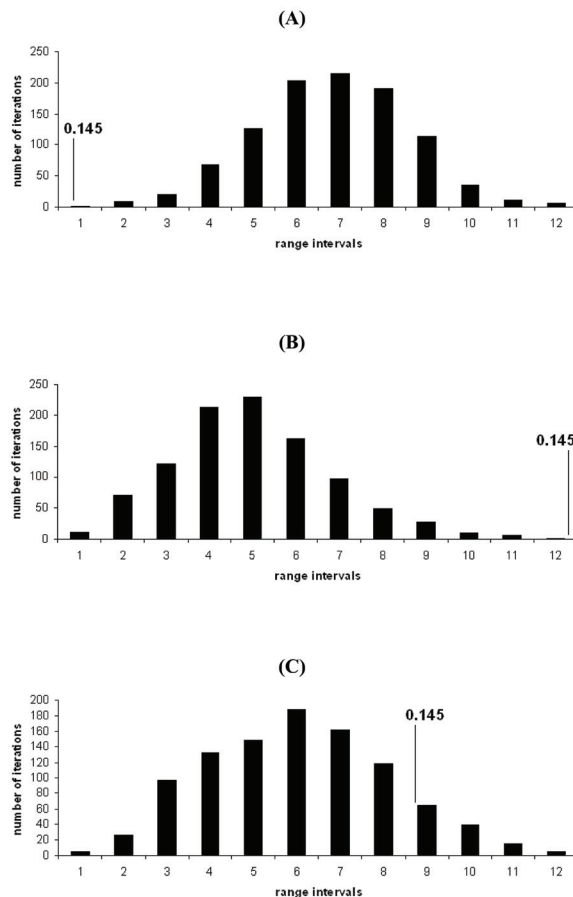
Figure 3. — Distribution of the simulated niche overlap matrices (30,000 Monte Carlo iterations) for the bird species at the study area, and relative position of the observed mean overlap value. Graphic A: RA2 algorithm; B: RA3 algorithm; C: RA4 algorithm.

DISCUSSION

ARE THE BIRD ASSEMBLAGES DIFFERENT BY HABITAT TYPE IN A MOSAIC LANDSCAPE?

We found that the number of species differed significantly by habitat type, with the richest assemblages being linked to wetlands. This pattern of a higher number of wetland birds is

already known in the available literature for the Mediterranean Regions (Benassi *et al.* 2007, 2009; Papi & Capizzi, 1998; Abellan *et al*., 2007). This work showed that habitats differ in number of species and individuals depending on seasons, size of habitat/area and geographical position. We also found that the assemblages were clearly different among habitat types.

ARE THESE BIRD ASSEMBLAGES ASSEMBLED BY CHANCE? AND IF NOT, IS THE NON-RANDOM STRUCTURE OF THE COMMUNITY DRIVEN BY QUANTITATIVE NICHE SEPARATION OF THE AVAILABLE RESOURCES OR QUALITATIVE SEPARATION OF A SINGLE HABITAT RESOURCE BY SYMPATRIC SPECIES?

Our study revealed that the bird community of Castelporziano has a clear structure (composition of species and their relationships) as detected by one of the contrasting null model algorithms used (RA2). The fact that our bird community was not randomly organized by RA2 denotes that the generalist-specialist nature of the species reduces the ecological similarity (Rugiero & Luiselli, 2007). This type of resource partitioning reflected earlier data on other communities (Abellan *et al.*, 2007; Beger *et al*., 2003; Bevers *et al.*, 1995; Bio *et al*., 2002; Burnett *et al*., 2007; Luiselli & Filippi, 2006; Rugiero & Luiselli, 2007). Regarding birds, even if many studies have analysed community organization (Bellamy *et al.*, 1996; Green & Hirons, 1991; Hinsley *et al.*, 1995; Stephens *et al.*, 2004; Wethered & Lawes, 2005; Winter & Faaborg, 1999), few previous researches have explored the randomness in species assemblage and the potential importance of interspecific competition as a shaping force by null models. It is obvious that our study has conservation implications. One of our results is that the entire bird assemblage cannot be supported by a big area of a single habitat, but by the set of mosaic habitats available on the study site. This result has already been pointed out by Moreno Rueda & Pizzaro (2009).

Actually, there is an aggregate community distributed in all the habitats, changing its structure and the relationship among the species on basis of the characteristics of each habitat and its resource availability. In other words an area characterized by high, but not too high, habitat heterogeneity that makes an extremely complex natural mosaic, ensures the development and the maintenance of a rich and complex bird community. Indeed, excessively heterogeneous environment may decrease species richness, as a consequence of reduced population sizes and thus increased risk of stochastic extinction.

Being this heterogeneity similar to the effect of fragmentation caused by humans, it seems not identifiable through existing fragmentation analysis tools, like Fragstat software for instance (Akçakaya, 2004; Araújo *et al*., 2004; Baguette & Mennechez, 2004; Hinsley, 2000; Westphal *et al.*, 2007; Zharikov *et al.*, 2007). Therefore, these results encourage the creation and use in ecological studies of a new kind of analysis that makes tools able to read any single patch and thereby adding a quality evaluation (richness and diversity values) to that of quantitative (number and size of patches). This would be useful to distinguish human fragmentation from natural heterogeneity in the habitats.

Hence, it would be a priority for conservation biologists (i) to focus attention not only on single habitats, but on the whole range of habitats, (ii) to modify the classical approach of 'fragmentation biology' with emphasis on patch quality (Battisti & Romano, 2007; Bellamy *et al.,* 1996; Bernstein *et al.*, 1991; Boulinier *et al.*, 1998; Fahrig 2003) and to work towards a new approach where the natural quality of all patches is evaluated with appropriate statistical tools.

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