Extreme Landscapes Decrease Taxonomic and Functional Bird Diversity but Promote the Presence of Rare Species

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Abstract. Human activities may generate geometrical landscape (i.e. composed of rectilinear and repetitive landscape units) structures that can significantly influence the spatial distribution of birds. While bird distribution in various landscape types has been extensively studied, the role played by landscape configuration and composition in different facets of bird diversity remains unclear. Here, these two main components of landscape characteristics (i.e. configuration and composition) are disentangled and their relative influence on three different facets of bird assemblages: taxonomic and functional characteristics, and the presence of rare species, is tested. We chose four large coastal salinas of Western France as a relevant model of geometrical and human-dominated landscapes where each landscape unit can be easily identified and mapped. The landscape characteristics of these sites were mapped and quantified. Then, terrestrial breeding birds were sampled in 172 point-counts using a standardized protocol. 69 diurnal terrestrial bird species were detected and considered in analyses (waterbirds and owls excluded). Landscape composition was found to have a higher influence on bird communities than landscape configuration, which fits with the "landscape composition hypothesis". More specifically, the most "extreme" landscapes — those with low terrestrial surface areas, low landscape richness and diversity, low cohesion, and very patchy landscapes with complex geometrical shapes — host the lowest bird taxonomic abundance, richness and diversity and functional richness, but are characterized by the presence of rare species (mainly wetland specialist species, e.g. Reed Bunting *Emberiza schoeniclus* and species with restricted ranges e.g. Bluethroat *Luscinia svecica namnetum*). Our results suggest that conservation plans in such geometrical and human-dominated habitats should not only focus on one aspect of landscape characteristics or one aspect of biological diversity but also consider the adverse effects of landscape characteristics on these different facets.

Key words: fragmentation, landscape, songbirds, passerines, salinas, taxonomic diversity, functional diversity, species rarity, landscape configuration, landscape composition

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INTRODUCTION

The influence of landscape characteristics on birds has been intensively investigated in terrestrial ecosystems, particularly in forests (see Forman et al. 1976 for a seminal article on the subject, or Cushman & McGarigal 2002 for a more recent study in North America) and hedgerow networks (reviewed by Hinsley & Bellamy 1999). However, it is often difficult to compare and synthesize these results, mainly because of the plethora of different landscape indices used, corresponding to different components of landscape characteristics. One of the challenges, therefore, is to distinguish clearly the different components of landscape characteristics in order to test their relative influences.

A first and rather intuitive way of classifying landscape characteristics is to differentiate landscape features related to fragmentation (the subdivision of a habitat into several patches and the size of a patch), connectivity (the number of links — or corridors — between patches) and heterogeneity (the diversity of different habitats and the

complexity of their spatial relationship) (Burel & Baudry 1999).

However, these three different categories have often been interpreted differently according to the authors. For example, fragmentation may correspond to either habitat loss (a decrease in the surface covered by a habitat) or real fragmentation (the breaking up of a habitat) (see Fahrig 2003 for a review).

Beyond this distinction between fragmentation, connectedness and heterogeneity, several authors now propose a less ambiguous classification of landscape features according to two main categories: landscape composition (corresponding to the relative representation of habitats) and landscape configuration (corresponding to the geometry and spatial arrangement of the habitats) (e.g. Fahrig et al. 2011). Although both composition and configuration affect the spatial distribution of organisms (Turner 1989), their relative importance may strongly diverge. For example several authors (e.g. Fahrig 1997, Villard et al. 1999, Wiegand et al. 2005, Ritchie et al. 2009) demonstrated that habitat loss (i.e. spatial composition) has a different influence from habitat fragmentation (i.e. spatial configuration). Recently, Flick et al. (2012) also clearly showed that compositional heterogeneity increases butterfly abundance whereas configurational heterogeneity increases species richness.

In addition to different components of landscape characteristics, studies investigating the relationship between landscapes and birds have also often explored single components of biodiversity or a mixture of them, without clearly defining them. Most studies have been conducted on single species (e.g. Clergeau & Burel 1997 on the Short-toed Treecreeper *Certhia brachydactyla* in a hedgerow landscape), while community approaches have mainly focused on abundance, richness or diversity patterns (e.g. Dominik et al. 2012). Although several earlier studies tried to identify which species may benefit or suffer from landscape modification (e.g. Terborgh 1974, Laurance 1991), the impact of landscape characteristics on functional diversity is still unclear. Moreover, in terms of conservation planning, a consideration of the conservation status of different species, or at least their degree of rarity, is often missing in such studies. Recent metrics reflecting several aspects of biodiversity have been proposed to cover the complementary aspects of functional diversity (e.g. Villéger et al. 2008). Other metrics have also focused on the

relative abundance of species with specific traits (community weighted means). In this approach, a specific trait is attributed to each species. A community weighted mean is then calculated for a given assemblage as the average trait value of each species occurring in this assemblage weighted by species' abundances in this assemblage. A change in this index reflects the relative change in species abundance or presence having the specific trait of interest (Webb et al. 2010). These approaches have been used mainly in large-scale studies, to compute for example a community thermal index applied to birds (Devictor et al. 2008b, Godet et al. 2011) and butterflies (Devictor et al. 2012), community weighted latitude (Dulvy et al. 2008); altitude (Clavero et al. 2011) or specialization (Clavel et al. 2010).

Thus, one of the key issues in the investigation of relationships between birds and landscapes is to explore (i) the relative influence of the different characteristics of landscapes (i.e. composition and configuration) on (ii) the different facets of bird biodiversity at community scales.

In this study, we deliberately chose study sites characterized by highly geometrical landscape structures (i.e. composed of rectilinear and repetitive landscape units): traditional coastal salinas. These habitats are good candidates for any study in landscape ecology for at least two reasons. First, their landscape structures are easy to identify and to map by a photo-interpretation process. Second, their landscape structures remained unchanged for centuries, and testing the relationship between landscape features and biodiversity patterns in this habitat cannot be biased by the influence of recent landscape changes. Some of these landscape structures date back to the 9th century (Thompson 1999) and even the 6th century in le Marais breton (Hocquet & Sarrazin 2006). They are traditionally dominated by a hostile aquatic matrix (small to large ponds and a dense hydrographic network) and small terrestrial patches and corridors (mainly constituted by clay banks). Most of the studies working on birds in salinas have focused on aquatic birds (Velasquez 1992, Alcorn & Alcorn 2000, Masero et al. 2000, Warnock et al. 2002, Round 2006, Dias 2009, Sripanomyom et al. 2011) and, to our knowledge, Dominik et al. (2012) were the first to work on the relationship between salina landscape characteristics and terrestrial bird assemblages. However, these authors only explored the influence of landscape characteristics at one single study site, and only on bird abundance, richness and diversity. Moreover, the

relative influence of landscape composition and configuration was not investigated in their study.

The aim of this study is therefore to assess the relative influence of landscape composition and configuration on three facets of bird communities: taxonomic abundance, species richness, and diversity; functional richness, evenness and divergence; and the occurrence of rare species. More precisely, we hypothesize that there may have some adverse effects of each facet of landscape characteristics on each facet of biodiversity.

METHODS

Study sites
Four of the largest salinas of France were selected: Guérande, Marais Breton, Ré Island, Oléron Island (see Fig. 1 for their location, Table 1 for their detailed characteristics and Appendix 1 for their cartography). The areas of these study sites range from 835 ha (Marais breton) to 3668 ha (Guérande). All these salinas, except the Marais breton, are active (i.e. salt extraction is ongoing) and their landscape features (size, shape and distribution of the bank networks and salt-pans) have remained almost unchanged since the Middle Ages (Lemonnier 1975, 1984, Poisbeau-Hémery 1980, Thompson 1999). Their landscapes are constituted by highly geometrical habitats dominated by an aquatic landscape matrix for all sites, except the Marais breton where the matrix is mostly constituted by terrestrial areas (former salt-pans are now terrestrial areas).
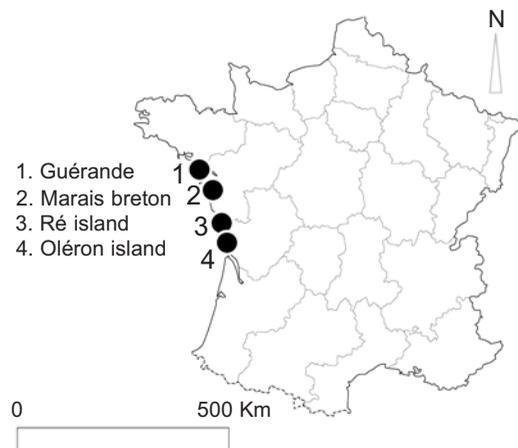

Fig. 1. Location of the study sites.

Landscape mapping
Geographical Information System (GIS) (Quantum Gis 1.8®) software was used to map the salinas and orthorectified aerial photographs (to a spatial resolution of 50 cm) were used for photo-interpretation. Twelve different landscape units (listed in Table 1) were detected, identified and mapped using a zoom of 1: 1000 (Appendix 1).

Calculation of landscape metrics from the maps
Around each bird sampling point (see below), landscape metrics were calculated in square buffers. Because the calculation of metrics may lead to different conclusions depending on the scale of the study (Wu 2004), we calculated all landscape metrics at three different spatial extents (9, 16 and 25 ha). These extents were chosen to

Table 1. Site-by-site characteristics and bird sampling work.

	Site			
	Guérande	Marais breton	Ré Island	Oléron Island
Area mapped (in ha)	3668	835	2736	1575
Area of each landscape unit (in %)				
Terrestrial patches and corridors				
Clay banks	14.5	0.0	23.0	38.6
Buildings	2.6	0.6	1.2	2.8
Artificial areas	2.6	1.4	1.0	2.2
Parks and gardens	7.5	5.1	4.9	2.6
Farmlands	10.4	76.3	10.5	12.9
Wastelands	5.8	0.4	2.2	3.5
Woodlands	6.5	2.1	4.7	4.1
Reed beds	0.8	0.0	0.0	0.0
Salt-marshes	1.4	0.0	2.1	5.9
Beaches and sand dunes	1.8	0.0	1.6	1.1
Aquatic (hostile) matrix				
Water ponds / hydrographic network	36.2	14.1	36.2	17.1
Marine / fluvial domain	10.0	0.0	12.5	9.3
Number of bird sampling points	60.0	29.0	53.0	30.0

both encompass the areas where birds where sampled in each point, and to not overlap each other. Around each bird sampling and for each landscape metric, we used mean values of the metrics at the three spatial scales (i.e. for a given point and a given landscape index xi, the mean values of the index xi calculated at the three spatial extents around the point were used). Six different landscape metrics were used (Table 2) corresponding to either the composition or the configuration of the landscapes. For consistency among all these metrics, traditional landscape metrics were selected or transformed so that their lowest values corresponded to the *a priori* most extreme (hostile) landscapes for terrestrial birds while their highest values corresponded to the *a priori* more favorable landscapes for terrestrial birds. Hereafter, "extreme landscapes" are thus considered those with the lowest values of any of these six different landscape metrics and "favorable landscapes" those with the highest values.

Three landscape indices of landscape composition were used: the total area (TA) of all the terrestrial units (i.e. all landscape units excluding water ponds/hydrographic networks and the marine/fluvial domain), landscape richness (LR) (corresponding to the number of all landscape units), and landscape diversity (LD) (estimated by Shannon's index of all landscape units and their respective areas).

Three landscape indices of landscape configuration were also used: patch unity (PU) (which corresponds to the opposite values of the patch density of all the terrestrial units pooled), patch shape simplicity (PS) (which corresponds to the opposite values of the fractal dimension of all the terrestrial units pooled), and patch cohesion (CO) (which corresponds to the physical connectedness of all the landscape units pooled).

All landscape metrics were calculated with FRAGSTATS 3.3 ® (McGarigal et al. 2002) and are detailed in Table 2.

Bird counts

Birds were surveyed with a point-count method (Bibby et al. 2000) in spring 2011 in Guérande, le Marais Breton and Oléron island, and spring 2012 in Ré island. Overall, 172 point-counts were carried out, placed at 600-m intervals at all sites (see Table 1 for the number of points per site). At each point, the same observer counted all the individual birds heard or seen during a period of 5 min. Birds were counted within a 100-m radius around each point. Binoculars were only used to identify a previously detected bird. Each point was surveyed within a 1–4 h period after sunrise and was visited twice: first during the first week of April in order to identify early breeders and secondly during the first week of May to detect the others. Bird detectability may vary according to the weather, time-of-day or habitats. All point-counts were carried out in sunny weather, and those carried out in the early morning during the April visit were performed in the late morning during the May visit (and *vice versa*). Moreover, all habitats surveyed were open areas, largely dominated by salinas, and bird detectability was assumed constant over the study area. Observed species richness was therefore used without correction for possible differences in detectability in different habitats. For each species and each point, only the highest abundances were used during the two visits. All waterbirds were excluded from the analyses (herons, waders, rails, ducks, gulls), and only diurnal terrestrial birds were taken into account (thus, the few contacts with Long-eared Owls *Asio otus* and Tawny Owls *Strix aluco* were removed).

Biological metrics

Three different components of bird assemblages were assessed. First, indices related to abundance (log (x+1) transformed, because few species such as Black Swift *Apus apus* had punctually high abundances and may thus disproportionally contribute to the total bird abundance of the assemblage), species richness (raw number of species) and species diversity (estimated by the H' Shannon index (Shannon 1948)) were calculated.

Secondly, we calculated the functional diversity of bird assemblages, defined as a quantification of the value and range of organismal traits that influence their performance (Diaz & Cabido 2001). We calculated three different indices of functional diversity following Villéger et al. (2008): functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv). FRic measures the volume of the functional space occupied by the community by estimating the convex hull volume index (Cornwell et al. 2006). FEve measures the regularity of the distribution of abundance in this volume by estimating the minimum spanning tree that links all the species in the multidimensional functional space. FDiv measures the divergence in the distribution of abundance in this volume, based on an index developed by Villéger et al. (2008), which quantifies how species diverge in their distances (weighted by their abundance) from the center of gravity in the functional space.

Table 2. Landscape metrics used.

Metric	Definition	Formula	Notes (Min-Max)	Correspondence with the landscape indices used in FRAGSTATS®
Landscape composition				
TA	Total Area of terrestrial areas	TA = total area covered by all terrestrial areas.	0 (no terrestrial area) to n (n unit of areas of the terrestrial area)	"CA" (total class area).
LR	Landscape Richness	LR = number of all landscape units	1 (only one landscape unit) to n (n different landscape units)	"PR" (patch richness).
LD	Landscape Diversity	$LD = -\sum_{i=1}^{m}(P_i.\ln P_i)$ With P_i = proportion of area occupied by landscape unit i.	0 (only one landscape unit) to n (n different landscape units and/or the proportional distribution of area among landscape units becomes more equitable)	"SHDI" (Shannon's diversity index).
Landscape configuration				
PU	Patch Unity of terrestrial areas	PU = - the number of terrestrial patches.	-n (n terrestrial patches) to -1 (one single terrestrial patch). Note that there is no 0 value because there is at least one terrestrial patch in every cell	Opposite values of "PD" (patch density).
PS	Patch shape Simplicity of terrestrial areas	$PS = -\dfrac{2\ln(0.25\,p_{ij})}{\ln a_{ij}}$ With p_{ij} = perimeter (m) of terrestrial patch ij. a_{ij} = area (m²) of terrestrial patch ij.	-2 (shapes with convoluted, plane filling perimeters) to 1 (shapes with simple perimeters)	Opposite values of "FRAC" (fractal dimension index).
CO	Patch Cohesion of terrestrial areas	$CO = \left[1-\dfrac{\sum_{j=1}^{n} p_{ij}}{\sum_{j=1}^{n} p_{ij}\sqrt{a_{ij}}}\right]\left[1-\dfrac{1}{\sqrt{A}}\right]^{-1}(100)$ With p_{ij} = perimeter of terrestrial patch ij in terms of number of cell surfaces. a_{ij} = area of terrestrial patch ij in terms of number of cells. A = total number of terrestrial cells in the landscape.	0 (proportion of the landscape subdivided and less physically connected) to 100 (patches are more physically connected)	"COHESION" (patch cohesion index).

To compute these three functional indices, 21 life history traits were used, previously employed by Devictor et al. (2010) and taken from Cramp (1977–1994) (see Appendix 2 for the whole list of traits). These traits are either qualitative or quantitative and measure different aspects of resources used by birds. In order to decrease the potential influence of highly correlated traits, the multivariate technique of Hill & Smith (1976) was applied to create scaled orthogonal composite traits. This multivariate analysis allows the creation of independent composite traits with mixed quantitative variables and factors (Devictor et al. 2010). The first six axes of this multivariate analysis were kept as they contribute to 60% of the inertia, and they were considered independent composite traits to compute each functional diversity index.

Thirdly, the relative abundance of rare versus common species within bird communities was calculated. The three different forms of rarity

developed by Rabinowitz (1981) were used: rarity due to restricted range, due to low individual abundance and due to a high degree of habitat specialization (see Godet et al. 2015a for an application to French breeding birds). These three indices were calculated using the data from the French Breeding Bird Survey (Jiguet et al. 2012). For each species, a Species Abundance Index (SAI) was first calculated as the opposite value of the mean log-transformed abundance per point from 2001–2012 where the species was contacted in France. In other words, a high SAI means that the species has, on average, low local abundance and is thus rare from an abundance point of view. Then, a Species Range Index (SRI) was calculated as the opposite value of the number of sites where the species was contacted from 2001–2012 in France. In other words, a high SRI means that the species has a restricted range and is thus rare from a geographical range point of view. Habitat specialization was estimated using the Species Specialization Index (SSI) developed by Julliard et al. (2006) and widely used to characterize habitat specialization in birds (e.g. Devictor et al. 2008a, Filippi-Codaccioni et al. 2010a, Barnagaud et al. 2011, Le Viol et al. 2012). A high SSI means that the species has a high degree of habitat specialization and is thus rare from a habitat specialization point of view.

Lastly, the CAI (Community Abundance Index), CRI (Community Range Index), and CSI (Community Specialization Index) representing the community weighted mean indices calculated with SAI, SRI and SSI, respectively, were calculated for each point. A given community weighted mean was calculated as $CXI = \Sigma\ (a_iX_i)/A$ where "a_i" designates the abundance of species "i" in this assemblage, "X_i" the specific index of species "i", and "A" the total abundance. To sum up, high values of CRI, CAI and CSI correspond to a community dominated by species rare from a geographical range point of view, rare from their local abundance point of view, and rare from their habitat specialization point of view, respectively.

Statistical analyses

Each landscape and biological metric was standardized, site by site, as follows: $C_i = (x_i-x)/\sigma$, with x_i being the value of a landscape (or biological) metric for a square buffer or a point count respectively, x being the average of the values of this landscape (or biological) metric in all the buffer (or point count) of the site, and σ being the standard deviation of the values of this landscape

(or biological) metric in all the buffers (or point count) of the site.

Because the biological metrics used may display spatial autocorrelation within each site, the data used may not be independent. Therefore, the within-site spatial autocorrelation of each biological metric was explored. For each site and each biological metric, a generalized least square (gls) model was applied with the biological metric as the dependent variable and the landscape characteristics as the independent variables in which the spatial structure of observations was considered. The variograms of these models were then used to characterize the spatial structures of the residuals. A spatial autocorrelation was assumed when the variance between the pairs of points increased with the increase in distance between these pairs. The signature of intra-site spatial autocorrelation was not found for any variable at any site (detailed results can be given on request by the authors). Therefore, we assume a spatial independence of the observations presented in the results.

The relative importance of each landscape metric (and therefore of landscape composition vs. landscape configuration) on bird assemblages was then hierarchized. The nine biological metrics (abundance, species richness, species diversity, functional richness, functional evenness, functional divergence, community specialization index, community abundance index, community range index) were used as dependent variables and the six landscape metrics (TA, LR, LD, PU, PS, CO) as independent variables. "Site" was also systematically included as a grouping factor to account for inter-site effects. Hierarchical partitioning of R^2 was used in order to determine the proportion of variance of each biological metric explained independently by each landscape metric (Chevan & Sutherland 1991, Mac Nally 2000). This method enables the identification of variables whose independent correlation with the dependent variable is large, in contrast to variables that have little independent effect but a high correlation with the dependent variable resulting from joint correlation with other independent variables. Landscape metrics were then identified that independently explained a larger proportion of variance than could be explained by chance, by comparing the observed value of the independent contribution to the explained variance (I) to a population of Is from 1000 randomizations of the data matrix. Significance was accepted at the upper 95% confidence limit (Z-score of 1.65; Mac Nally 2000, Walsh et al. 2004). Note that, although the

partitioning of variance does not require non-correlated factors, pairs-correlation between each of the six landscape indices never exceeded $R^2 > 0.51$. To assess if each landscape metric is positively or negatively linked with each biological metric, we used the slope of simple linear regressions between each pair of landscape and biological metric.

RESULTS

Bird species
Over the 172 point-counts, each representing two periods of 5 min of census (i.e. more than 28 hours of effective field sampling), 69 terrestrial bird species were detected (Appendix 3).

Relative effects of landscape characteristics on the three facets of biodiversity
Landscape characteristics (all landscape indices pooled) mainly explain the taxonomic characteristics (multiple linear regressions: species richness — $R^2 = 0.39$; species diversity — $R^2 = 0.37$; abundance — $R^2 = 0.19$), the presence of two types of rare species within the assemblages (specialist species (CSI) — $R^2 = 0.19$; and localized species (CRI) — $R^2 = 0.18$), and functional richness ($R^2 = 0.24$) (Fig. 2). Landscape features explain to a much lesser extent functional evenness ($R^2 = 0.09$), functional divergence ($R^2 = 0.08$) and the community abundance index ($R^2 = 0.06$). Note that there are no significant site effects whatever the biological index considered (Fig. 2).

Relative effects of landscape composition versus landscape configuration
Decomposing the relative influence of landscape composition versus configuration on each facet of bird assemblages reveals an overall higher importance of landscape composition than landscape configuration when the three indices of each of these landscape components are pooled (Fig. 2). Overall, among landscape composition indices, landscape diversity and the total amount of terrestrial area explain most of the variance in almost every characteristic of bird assemblages (Fig. 2). Among landscape configuration indices, cohesion explains most of the variance in species richness and diversity, followed by patch simplicity, whereas the three configurational indices explain a similar proportion of the variance of bird abundance. Lastly, patch simplicity is the factor that best explains functional richness, CSI and CRI among landscape configuration indices (Fig. 2).

Positive versus negative relationships between landscape characteristics and the three facets of biodiversity
The less extreme landscape features for terrestrial species (corresponding to the highest values of each landscape index) that significantly influence bird assemblage characteristics are positively linked with taxonomic and functional indices (Fig. 2). Functional evenness is the only functional characteristic negatively linked with landscape diversity but, as seen above, the landscape indices only explain a low proportion of the variance of functional evenness ($R^2 = 0.09$). On the other hand, these less extreme landscape features tend to decrease the presence of rare species among bird assemblages: specialist species (CSI), localized species (CRI) and species with low local abundance (CAI).

Overall, these results suggest that less extreme landscapes promote taxonomic abundance, species richness, species diversity, functional richness and functional divergence, but tend to decrease the presence of rare species, including specialist species, localized species and species with low abundance.

DISCUSSION

**Effects of landscape composition versus configuration on bird assemblages**
Landscape composition was found to play a more important role than landscape configuration in bird assemblages and this influence is greater on taxonomic characteristics. This corresponds to most studies demonstrating that composition plays a greater role than configuration, which is known as the "landscape composition hypothesis" (Fahrig 2003) as opposed to the "landscape configuration hypothesis" (Villard et al. 1999, Betts et al. 2006). For example, by considering the two different aspects of fragmentation, most studies have demonstrated that the breaking up of a habitat (assessed in this study by the two indices "PU" and "CO"), independent of habitat loss (assessed here by the index "TA"), has rather weak effects on biodiversity (Fahrig 2003).

Among the three landscape indices related to landscape composition, the amount of terrestrial habitat (TA) is one of the factors that best explains all biodiversity indices. This relationship between species richness and TA fits with one of the oldest laws of biogeography, the Arrhenius law (Arrhenius 1921): $S = C.A^z$ where S is the number

TAXONOMIC INDICES
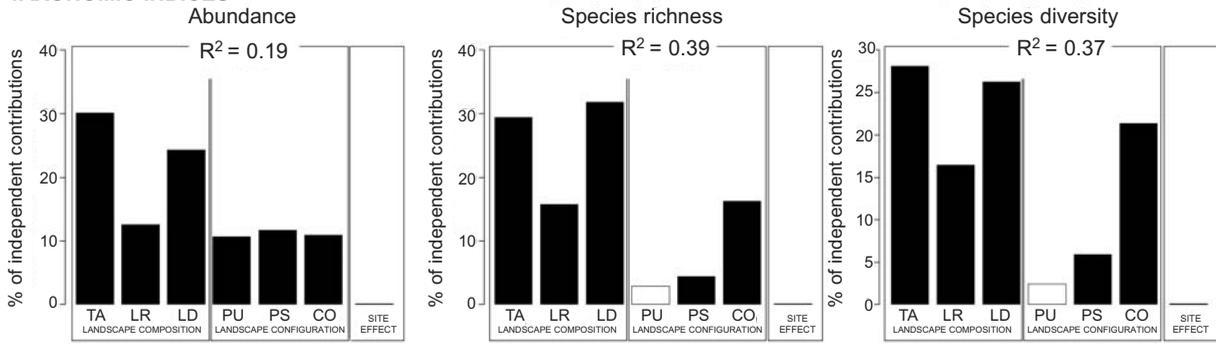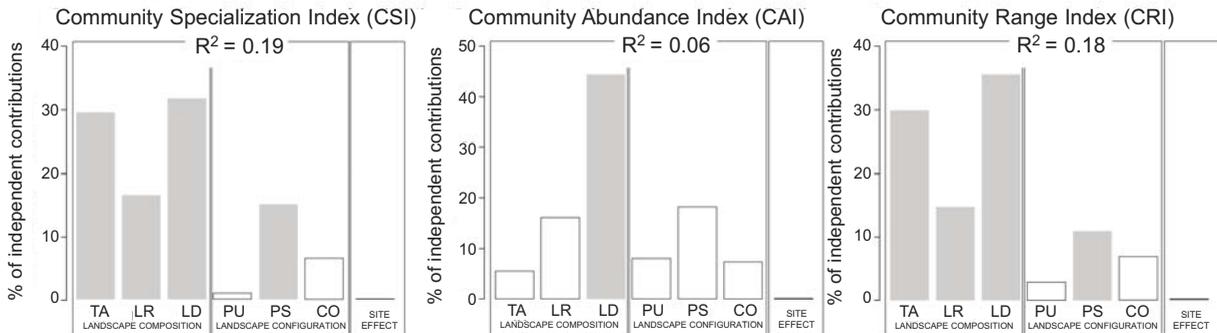

FUNCTIONAL INDICES
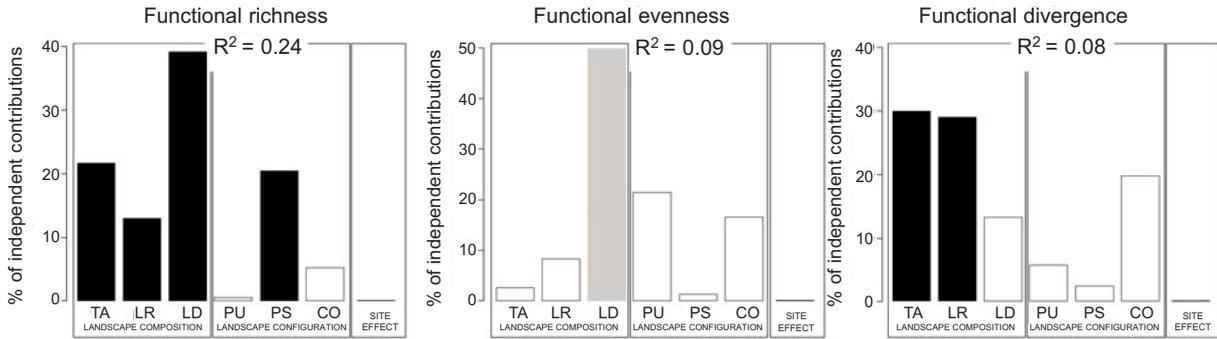
RARITY INDICES

Fig. 2. Relationships between landscape metrics and bird assemblages. Bar charts indicate the percentage of explained variance in bird assemblage characteristics for each landscape index. The three first landscape indices (left part of each graph) correspond to landscape composition, the three others (right part) correspond to landscape configuration. Black and gray bars represent significant independent correlates with positive and negative relationships, respectively, tested by simple linear regressions. White bars correspond to non-significant correlates. Each R^2 corresponds to the coefficient of determination of a multiple linear regression using the biological index as a dependent variable and all the landscape indices as factors. For the abbreviated names of the landscape indices, see Table 2.

of species, A the total area, and C and Z are constants. In our data set, if raw values of TA and species richness are taken, the following relationship is found: $S = 4.93.A^{0.2018}$ (power regression, $R^2 = 0.1331$, $p < 0.01$). In several other studies, the extent of suitable habitat has also been identified as the major driver of species richness (see Bennett et al. 2006 for a review). The two other indices of landscape composition, landscape richness (LR) and landscape diversity (LD), also demonstrate a strong influence on species richness and diversity, which fits with a niche filtering

process (Hobson & Bayne 2000): each landscape unit creates a potential ecological niche for a species. At the scale of the salinas, the increase in landscape richness and diversity is mainly due to an ecotone effect where the boundaries of the salinas are more dominated by residential (parks and gardens) and agricultural areas, which contribute to a higher landscape heterogeneity.

Among landscape indices related to configuration, landscape cohesion plays a significant, positive and more important role than some other landscape composition indices in species richness

and species diversity. The cohesion of the terrestrial patches within the salinas can therefore be viewed as corridors, which may compensate for fragmentation (Saunders & Hobbs 1991). This demonstrates that there is a positive effect of corridors on species other than walking ones such as mammals, as shown in a few other studies on birds (Johnson & Adkinson 1985, Dmowski & Kozakiewicz 1990, Clergeau & Burel 1997). Assessing whether landscape cohesion plays a more important role in bird assemblages when the amount of terrestrial habitats (TA) drops below a particular threshold could be a future development of this study. This premise, known as the "fragmentation threshold hypothesis", has been demonstrated by both theoretical (e.g. Bascompte & Solé 1996) and empirical (e.g. Betts et al. 2007) studies (see Ritchie et al. 2009).

Extreme landscapes decrease taxonomic and functional characteristics but promote the presence of rare species

Nevertheless, although the areas with the largest extent of terrestrial habitat, and the richest, most diverse and most cohesive landscapes, promote bird abundance, species richness and diversity, they decrease the occurrence of rare species. The most extreme landscapes are therefore dominated by rare species, including mainly specialist and localized species. The richest and most diverse terrestrial landscapes that dominate the periphery of the salinas may benefit generalist species that can exploit a large range of different habitats (Kassen 2002, Marvier et al. 2004). The relatively lower abundance of generalists in extreme landscapes may be explained by the fact that landscapes of the core of the salinas are just too hostile for them. In fact, highly generalist species such as Great Tit *Parus major*, Blackbird *Turdus merula*, Chaffinch *Fringilla coelebs* and Wood Pigeon *Columba palumbus* were scarce within the core of the salinas. On the other hand, the specialist species, which were found mainly within extreme landscapes, were mostly associated with aquatic areas. The 15 species characterized by the highest specialization scores included wetland specialists (Bluethroat *Luscinia svecica namnetum*, Great-Reed Warbler *Acrocephalus arundinaceus*, Eurasian Reed Warbler *Acrocephalus scirpaceus*, Sedge Warbler *Acrocephalus schoenobaenus*, Reed Bunting *Emberiza schoeniclus*, Sand Martin *Riparia riparia*, Zitting Cisticola *Cisticola juncidis*, Marsh Harrier *Circus aeruginosus*) that could find suitable habitats in the salinas.

The hostile landscapes are also probably subject to a much lower interspecific competition in terms of food resources for example. Furthermore, in addition to specialist species, extreme landscapes promote the presence of species that are rare for their national geographical range. However, there is a significant relationship between species specialization and species range index (linear model, $R^2 = 0.69$, $p < 0.05$) which makes it difficult to dissociate the influence of these two facets of rarity. In our dataset, most of the specialist species also have restricted geographical ranges, as species with large ranges are often less specialized in their habitat than those with restricted ranges (Gaston & Spicer 2001). In our study, the wetland specialists cited above also have a restricted range at a national scale. However, a few generalist species have a rather restricted range and were found preferentially among extreme landscapes, such as the two raptors Montagu's Harrier *Circus pygargus* and Eurasian Sparrow Hawk *Accipiter nisus* as well as Meadow Pipit *Anthus pratensis* and Grey Partridge *Perdrix perdrix*, which may benefit from open landscapes at the core of the salinas.

Landscape characteristics scarcely explain the functional composition of bird assemblages. The only functional characteristic responding to landscape characteristics is functional richness, but this is strongly and positively correlated with species richness (see Villéger et al. 2008).

Our results fit with several studies demonstrating opposite values of bird species richness or diversity with community specialization. Along a vegetation gradient Reif et al. (2013) demonstrated an increase in species richness and a decrease in the specialization of the community from open habitats to young forests. Filippi-Codaccioni et al. (2010b) also showed that species richness and the specialization of the community are negatively correlated in agricultural areas. Other authors showed that species richness and the specialization index of bird communities may have different temporal trends: Kerbiriou et al. (2009) demonstrated a long-term increase in bird species richness and a collapse of bird community specialization in a French island over 100 years. Such results highlight that biological metrics such as bird abundance, species richness or diversity are often insufficient indicators of environmental factors as they fail to incorporate ecological differences between species (Devictor & Robert 2009).

The importance of considering different landscape attributes together with different biological facets

This study demonstrates the importance of taking into account different components of both landscape and biological features. Taxonomic indices, which are widely used in the literature, do not consider the identity of species. No important effects of landscape characteristics on the functional characteristics of bird assemblages were found. However, their effects on the presence of rare species are significant and large. Considering only the taxonomic aspect of biodiversity, one could conclude that salina landscapes are hostile for terrestrial birds because they tend to decrease abundance, richness and bird diversity, whereas these landscapes can also be viewed as promoters of original assemblages, including specialist species and localized species also harboring unique functional traits (Mouillot et al. 2013). Similarly, the different components of the landscapes may act differently on biodiversity. Although a majority of studies focus on the amount of available habitat, other components of landscape composition, such as landscape richness and diversity, also play an important role in structuring bird assemblages, as do other landscape configuration features, although with less influence.

Note however that this study only deal with terrestrial birds and that coastal salinas are important habitats for aquatic birds. Coastal salinas are both attractive as feeding and roosting sites for waterbirds, as demonstrated in south-east Asia (Sripanomyom et al. 2011, Green et al. 2015), western Europe (Masero et al. 2000) and North America (Warnock et al. 2002). If different ecological parameters controlling the attractiveness of the ponds for waterbirds (e.g. water level in the ponds; Green et al. 2015) have been tested, the effect of landscape structures of the ponds (and not only of the clay banks) on aquatic birds could be also investigated in the future.

Conservation implications

The coastal salinas of Western France are very old, and their landscape structures remain unchanged for centuries and will doubtless long remain so. Management or conservation measures cannot promote any changes in terms of landscape characteristics, but we can however identify areas where the highest conservation challenges are concentrated. One of the challenges could be the conservation of the areas hosting bird assemblages peculiar to and typical of salinas. As we approach the heart of the salinas, there is an increase in landscape fragmentation lato sensu, and a decrease in landscape richness and diversity. This landscape gradient from the periphery to the heart of the salinas is accompanied by a decrease in taxonomic diversity, but it promotes original bird assemblages composed of specialist species, that are also present at low abundances in France and that have restricted geographical ranges at a national scale. If we want to preserve particular bird assemblages, landscapes located at the heart of the salinas should be conserved as a priority. At the species level, the Bluethroat *Luscinia svecica namnetum* is a good example of a subspecies endemic to the French Atlantic coast during the breeding period, which is preferentially found at the core of the salinas, where the landscapes seem to be the most hostile for most of the terrestrial species (Dominik et al. 2012). Godet et al. (2015b) recently showed how the breeding males of this subspecies are able to offset such landscape constraints by expanding their home ranges.

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STRESZCZENIE

[Krajobrazy o bardzo uproszczonej strukturze charakteryzują się niską różnorodnością taksonomiczną i funkcjonalną ptaków, ale przyciągają gatunki rzadkie]

Działalność człowieka może prowadzić do upraszczania krajobrazu i nadawania mu struktury geometrycznej, tj. zbudowanej z prostoliniowych i powtarzalnych jednostek (np. pola uprawne). Podczas gdy rozmieszczenie ptaków w różnych krajobrazach jest często badane, znacznie mniej uwagi poświęca się znaczeniu samej konfiguracji krajobrazu i jego struktury. Jako strukturę należy rozumieć relatywną reprezentację różnych środowisk w danym krajobrazie, zaś konfiguracja to ich przestrzenne ułożenie oraz geometria poszczególnych płatów.

W pracy badano wpływ tych dwóch komponentów krajobrazu — tj. struktury i konfiguracji na trzy różne aspekty zgrupowań ptaków: ich charakterystykę taksonomiczną i funkcjonalną, oraz obecność rzadkich gatunków. Badania prowadzono na terenie czterech salin — obszarów, na których pozyskuje się sól poprzez odparowanie wody z solanki pochodzącej z morza (Fig. 1). Wybór takiego typu krajobrazu wynikał z faktu, że na tych zmienionych przez człowieka terenach każda jednostka krajobrazu jest łatwa do zdefiniowania i opisania, a także dlatego, że struktura tego typu krajobrazu nie ulegała zmianom przez stulecia, w związku z czym badane zależności pomiędzy cechami krajobrazu i bioróżnorodnością nie mogą być tłumaczone przez zmiany które zaszły w ostatnim
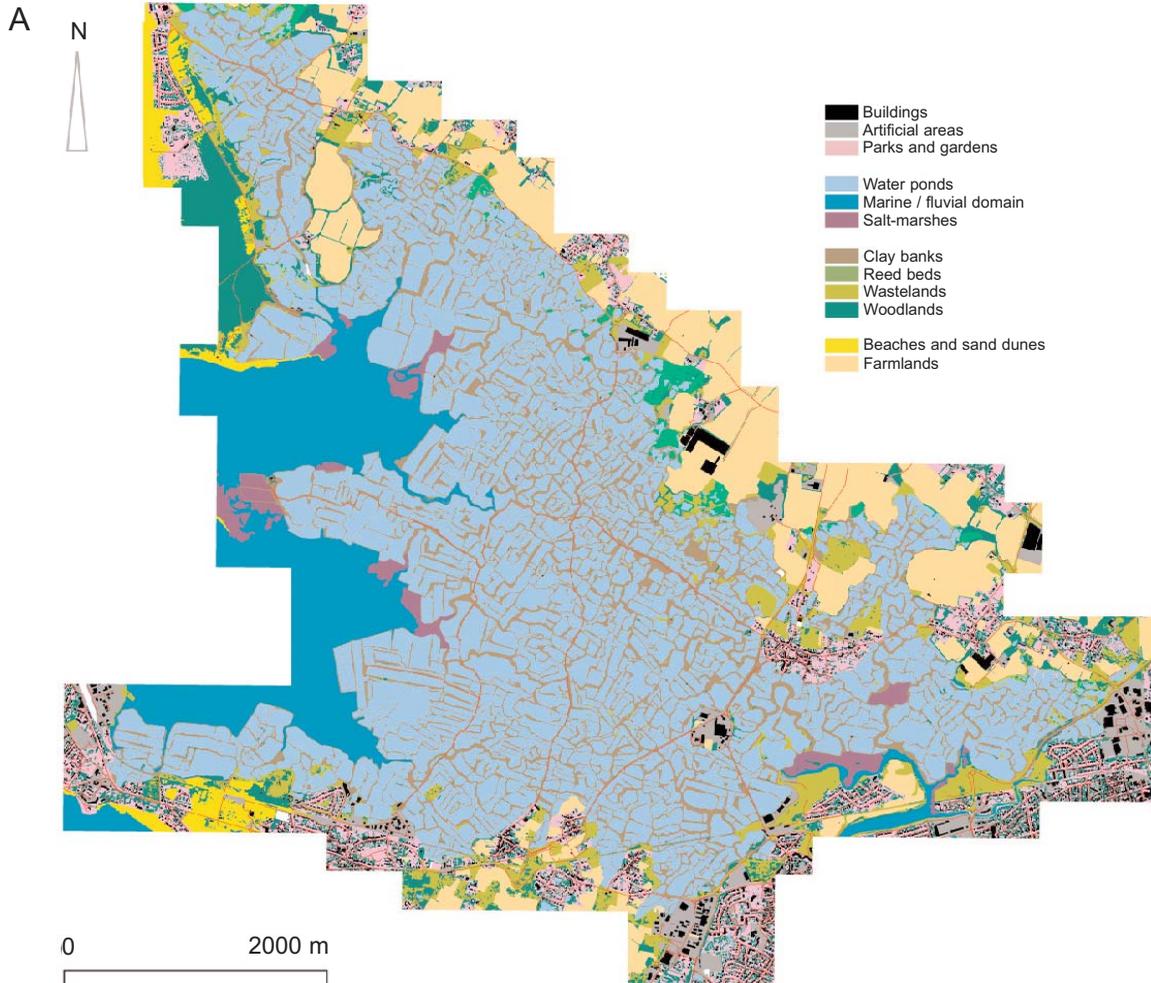
czasie. Dla każdego z terenów opisywano 12 różnych środowisk (Tab. 1, Apendyks 1).

Zgrupowania ptaków zostały scharakteryzowane na podstawie liczeń punktowych (łącznie 172 punkty). W analizach uwzględniono wyłącznie gatunki dzienne związane ze środowiskami lądowymi. Dla każdego z punktów, w których liczone były ptaki, obliczono następujące wskaźniki — dla struktury krajobrazu: całkowitą powierzchnię obszarów lądowych (TA), bogactwo środowisk (liczba różnych środowisk, LR), różnorodność środowisk (na podstawie wskaźnika Shannona, LD); dla konfiguracji krajobrazu — liczbę płatów środowisk lądowych (PU), kształt płatów (PS) oraz zwartość płatów (CO) (Tab. 2). Zgrupowania ptaków opisano za pomocą: liczebności, bogactwa gatunkowego i różnorodności gatunkowej oraz udziału gatunków rzadkich i pospolitych. Dodatkowo określono różnorodność funkcjonalną na podstawie trzech wskaźników: b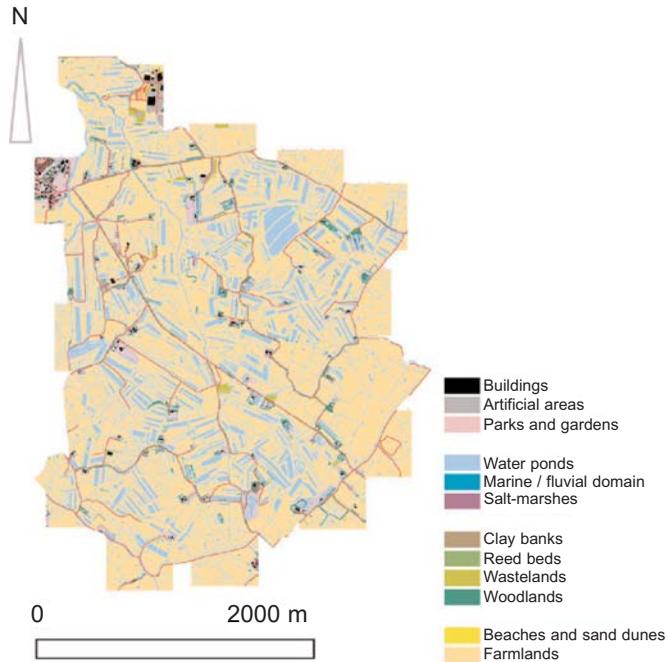ogactwa (FRic), równomierności (FEve) i dywergencji (FDiv). Do analizy różnorodności funkcjonalnej wzięto pod uwagę 21 cech historii życia stwierdzonych gatunków ptaków (Apendyks 2).

We wszystkich liczeniach punktowych stwierdzono łącznie 69 gatunków ptaków (Apendyks 3). Struktura krajobrazu miała znacznie silniejszy wpływ na zgrupowania ptaków niż jego konfiguracja (Fig. 2). Nie stwierdzono natomiast wpływu powierzchni badań (Fig. 2). Krajobrazy najbardziej nieprzyjazne — z małą powierzchnią terenów lądowych, niskim bogactwem i różnorodnością środowisk oraz niską zwartością płatów, oraz środowiska bardzo pofragmentowane ze złożonym układem płatów, charakteryzowały się najniższym bogactwem gatunkowym, różnorodnością taksonomiczną i funkcjonalną. W środowiskach tych występowały jednak gatunki rzadkie — przystosowane do życia w środowiskach podmokłych (jak potrzos) czy takie, mające ograniczone zasięgi (jak podróżniczek).

Appendix 1. Detailed maps of studied areas. A — Guérande, B — Marais Breton, C — Ré Island, D — Oléron Island.

B

N

Buildings
Artificial areas
Parks and gardens

Water ponds
Marine / fluvial domain
Salt-marshes

Clay banks
Reed beds
Wastelands
Woodlands

Beaches and sand dunes
Farmlands

0   2000 m

C

N

Buildings
Artificial areas
Parks and gardens

Water ponds
Marine / fluvial domain
Salt-marshes

Clay banks
Reed beds
Wastelands
Woodlands

Beaches and sand dunes
Farmlands

0   2000 m
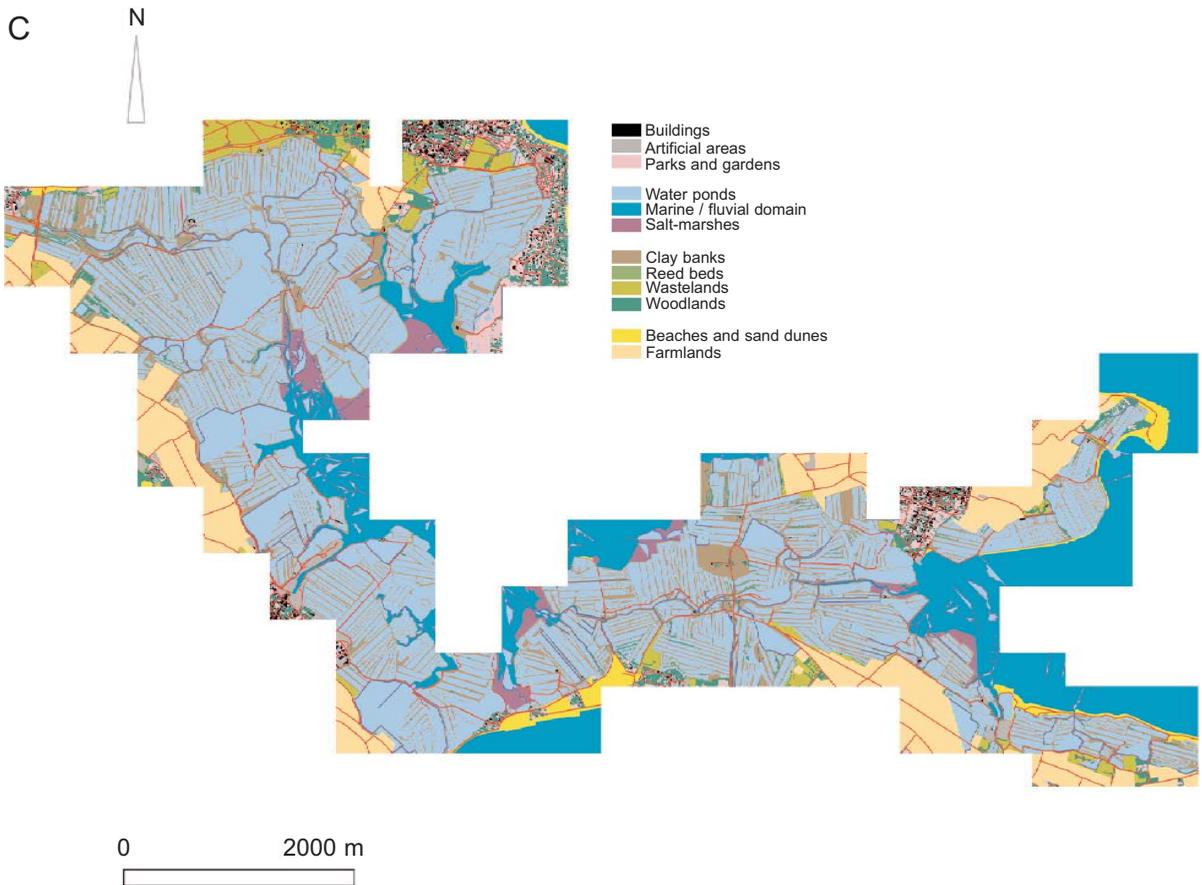
D

Appendix 2. List of functional traits used to calculate functional richness, evenness and diversity.

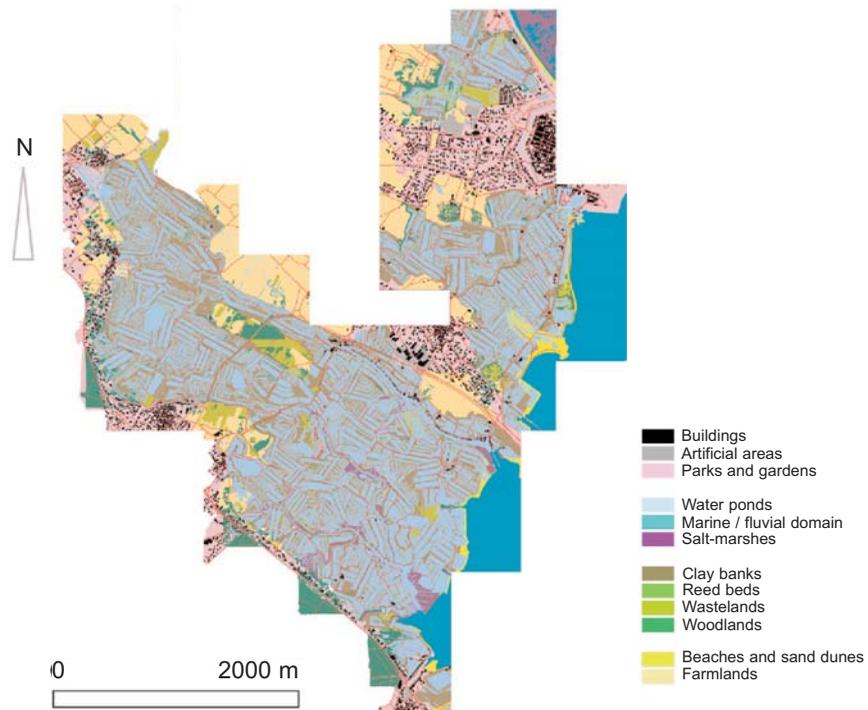| Traits	Values
Migratory status	Sedentary/Migratory
Average weight (in g)	0 to n
Mean number of eggs per year	0 to n
Relation between weight and wing length	0 to n
Longevity (in years)	0 to n
Position of the nest	On the ground, on vegetation, on a cliff, in a cavity or a combination of the four
Feeds on vertebrates	Yes/No
Feeds on invertebrates	Yes/No
Feeds on plants	Yes/No
Feeding strategy: pursues its prey	Yes/No
Feeding strategy: gleans its prey	Yes/No
Feeding strategy: pounces on its prey	Yes/No
Feeding strategy: grazes	Yes/No
Feeding strategy: digs	Yes/No
Feeding strategy: scavenges	Yes/No
Feeding strategy: probes	Yes/No
Feeding in water	Yes/No
Feeding in mud	Yes/No
Feeding on ground	Yes/No
Feeding among vegetation	Yes/No
Feeding in air	Yes/No

Appendix 3. List of the terrestrial bird species detected in the four study sites. "+" indicate the presence of a species in a site.

Common name	Scientific name	Marais Breton	Ré island	Oléron island	Guérande
Skylark	*Alauda arvensis*	+	+	+	+
Common Swift	*Apus apus*	+	+	+	+
Common Linnet	*Linaria cannabina*	+	+	+	+
European Greenfinch	*Carduelis chloris*	+	+	+	+
Cetti's Warbler	*Cettia cetti*	+	+	+	+
Zitting Cisticola	*Cisticola juncidis*	+	+	+	+
Common Wood-Pigeon	*Columba palumbus*	+	+	+	+
Carrion Crow	*Corvus corone*	+	+	+	+
Common Kestrel	*Falco tinnunculus*	+	+	+	+
Eurasian Chaffinch	*Fringilla coelebs*	+	+	+	+
Barn Swallow	*Hirundo rustica*	+	+	+	+
Bluethroat	*Luscinia svecica*	+	+	+	+
Black Kite	*Milvus migrans*	+	+	+	+
White Wagtail	*Motacilla alba*	+	+	+	+
Blue Tit	*Cyanistes caeruleus*	+	+	+	+
Great Tit	*Parus major*	+	+	+	+
House Sparrow	*Passer domesticus*	+	+	+	+
Common Pheasant	*Phasianus colchicus*	+	+	+	+
Black-billed Magpie	*Pica pica*	+	+	+	+
Dunnock	*Prunella modularis*	+	+	+	+
Eurasian Collared-Dove	*Streptopelia decaocto*	+	+	+	+
European Turtle-Dove	*Streptopelia turtur*	+	+	+	+
Common Starling	*Sturnus vulgaris*	+	+	+	+
Common Whitethroat	*Sylvia communis*	+	+	+	+
Eurasian Wren	*Troglodytes troglodytes*	+	+	+	+
Eurasian Blackbird	*Turdus merula*	+	+	+	+
Common Buzzard	*Buteo buteo*		+	+	+
Marsh Harrier	*Circus aeruginosus*	+	+		+
Eurasian Jackdaw	*Corvus monedula*	+		+	+
Common Cuckoo	*Cuculus canorus*	+		+	+
House Martin	*Delichon urbicum*		+	+	+
Cirl Bunting	*Emberiza cirlus*		+	+	+
European Robin	*Erithacus rubecola*		+	+	+
Western Yellow Wagtail	*Motacilla flava*	+	+	+	
Northern Wheater	*Oenanthe oenanthe*	+	+		+
Common Chiffchaff	*Phylloscopus collybita*		+	+	+
Black Redstart	*Phoenicurus ochruros*	+	+	+	
European Serin	*Serinus serinus*		+	+	+
Blackcap	*Sylvia atricapilla*		+	+	+
Eurasian Sparrowhawk	*Accipiter nisus*	+	+		
Sedge Warbler	*Acrocephalus schoenobaenus*		+		+
Eurasian Reed-Warbler	*Acrocephalus scirpaceus*			+	+
Long-tailed Tit	*Aegithalos caudatus*			+	+
Red-legged Patridge	*Alectoris rufa*	+	+		
Medow Pipit	*Anthus pratensis*		+		+
Rock Pigeon	*Columba livia*		+		+
Common Reed Bunting	*Emberiza schoeniclus*	+	+		
Eurasian Jay	*Garrulus glandarius*		+		+
Melodious Warbler	*Hypolais polyglotta*		+	+	
Common Nightingale	*Luscinia megarhynchos*		+	+	
Golden Oriole	*Oriolus oriolus*		+	+	
Green Woodpecker	*Picus viridis*	+			+
European Stonechat	*Saxicola rubicola*			+	+
Song Thrush	*Turdus philomelos*			+	+
Eurasian Hoopoe	*Upupa epops*			+	+
Great Reed Warbler	*Acrocephalus arundinaceus*			+	
Tree Pipit	*Anthus trivialis*			+	
Montagu's Harrier	*Circus pygargus*	+			
Stock Dove	*Columba oenas*	+			
Rook	*Corvus frugilegus*	+			
Lesser Spotted Woodpecker	*Dendrocopos minor*				+
Eurasian Hobby	*Falco subbuteo*		+		
Common Grasshooper	*Locustella naevia*				+
Corn Bunting	*Emberiza calandra*	+			
Grey Patridge	*Perdix perdix*	+			
Bonelli's Warbler	*Phylloscopus bonelli*			+	
Sand Martin	*Riparia riparia*				+
Garden Warbler	*Sylvia borin*				+