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RESEARCH

Differing responses of functional and taxonomic waterbird diversity to vegetation height and water level variation in a coastal wetland

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Abstract

The conservation of wetland biodiversity is a major global issue. In anthropogenic landscapes, it requires the identification of environmental conditions and management practices that sustainably maintain the diversity of the communities. We carried out a six-year survey over 18 sites (78 ha) in the Marais Breton, lowland grazing marshes on the western coast of Europe in France. We tested the influence of the spatio-temporal dynamic of vegetation heights, water depth and the proportion of flooded areas on the taxonomic and functional diversity of wading birds and ducks at the site scale. Taxonomic diversity was enhanced by higher spatial heterogeneity of water level and reduced by higher spatial heterogeneity of vegetation height. In sharp contrast, functional diversity was not influenced by spatial heterogeneity of water level and increased with spatial heterogeneity of vegetation height. Additionally, the effect of the spatio-temporal heterogeneity of water level and vegetation height was guild-dependent. Based on our results we encourage a management at the landscape scale integrating multiple land ownerships to promote a taxonomic and functional diversity rather than at the site scale only.

Keywords Wetland management · Ducks · Waders · Habitat · Functional diversity

In coastal wetlands, the ever-changing hydrological conditions (i.e., alternating periods of flooding and drying induced by tides, precipitation, topographic variations, and practices) create spatial and temporal heterogeneity of water levels which in turn influence the cover, structure and composition of vegetation (Keddy 2001; Pennings and Bertness 2001; Herteux et al. 2020). Such environmental variability creates a fine-grained mosaic of habitat types which allows these particularly productive ecosystems to host a diverse and specific biodiversity. Thus, by providing different foraging, roosting, and nesting sites, coastal wetlands harbor numerous breeding and migrating waterbirds with contrasting ecological requirements and conservation status (Delany et al. 2009). These avian communities support several economic and recreational activities — e.g., tourism birdwatching and hunting (Green and Elmberg 2014).

However, coastal wetlands are among the most threatened ecosystems with a decline of their total surface estimated at over 50% over the last century (Davidson 2014; Li et al. 2018), mainly due to the intensification of human activities - e.g., extensive drainage, urban development, industrial activities, water regulation and intensive agriculture (Ferrarini et al. 2023; Gedan et al. 2009; Lee et al.

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2006; Leung et al. 2024; Zedler and Kercher 2005). They are also particularly vulnerable to climate change hazards such as sea-rise level, storm surge, and higher dessication risk (Cahoon et al. 2006; Spencer et al. 2016; Grieger et al. 2020; van der Pol et al. 2024). Therefore, most bird species relying on these habitats are declining (Studds et al. 2017; Clausen and Clausen 2014; Erwin 2002; Taft et al. 2002). Most conservation efforts focus on natural and large freshwater systems such as rivers and lakes. Nevertheless, the high ecological value of lowland grazing marshes in Europe is recognised for their ability to support a diversity of freshwater and wetland species. These coastal areas provide alternative or complementary high-quality habitats to many waterbirds. They are of major conservation concern both from an ecological and socio-economic perspective (Sutton-Grier and Sandifer 2019).

One strategy to maximize waterbird diversity in wetlands is to increase the spatio-temporal heterogeneity of the habitats. At the species level, habitat heterogeneity largely contributes to habitat selection for many species (González-Gajardo et al. 2009; Lorenzón et al. 2016; Elliott et al. 2020). For species foraging on a variety of resources, heterogeneous areas are more attractive than homogeneous areas (Dunning et al. 1992). At the community level, the classical niche theory is often invoked to predict a positive relationship between habitat heterogeneity and species richness (Kadmon and Allouche 2007). For a given surface area, heterogeneous environments are expected to provide more potential niches and host more species than homogeneous ones. In wetlands, habitat heterogeneity is driven by the change both in hydrological conditions and vegetation cover (Ma et al. 2010). For instance, spatial heterogeneity of water level creates different foraging habitats for waterbirds (Kushlan 1986), and allows the coexistence of species with different diets and ecomorphological niches (Baschuk et al. 2012; Brandolin and Blendinger 2016; Desgranges et al. 2006). Similarly, spatially heterogeneous vegetation cover offers suitable nesting and foraging conditions for more species than homogeneous environments providing a minimal area is available (Nudds 1983).

Nevertheless, the generality of the positive relationship between habitat heterogeneity and species diversity is still debated (Stein et al. 2014) as it may depend on the taxonomic group, the habitat type (Tews et al. 2004), or even the spatial scale of the study (Allouche et al. 2012; Laanisto et al. 2013). Furthermore, most studies focused on the response of taxonomic diversity while less attention has been paid to functional diversity. Functional diversity estimates the variation in functional traits such as diet, foraging behavior and migratory status among species within a community. It provides a deeper ecological understanding of communities and ecosystems by highlighting the contribution of species to ecosystem functions. This approach is relevant from an ecological and conservation perspective because functional traits influence individual and population performance and ecosystem functioning (Gagic et al. 2015; Tilman et al. 1997).

To design efficient wetland management practices for waterbirds, two criteria must be met. First, it is essential to identify the ecological requirements of the different components constituting the local waterbird communities (Almeida et al. 2018, 2020; Brandolin and Blendinger 2016; Maleki et al. 2020). In this regard, spatial and temporal heterogeneity of habitat features (including water levels and vegetation cover) are recognized as major ecological factors driving waterbird communities in wetlands (González-Gajardo et al. 2009; Lorenzón et al. 2016; Quiroga et al. 2021; Tavares et al. 2015). Second, it is crucial to propose clear and applicable guidelines that would enhance the engagement of local stakeholders and, eventually, the application of measures favorable to biodiversity (Williams and Madsen 2013). We attempted to fulfill both objectives in the present work.

Our study was carried out in wetlands of the Marais Breton on the French Atlantic coast that is used by large numbers of waterbirds as wintering, breeding and staging sites (Schmaltz et al. 2019). These marshes are of international importance for wintering bird species according to the Ramsar Convention. They are part of the EU Natura 2000 network, hosting, each year, over 60,000 waterbirds distributed in 96 species (https://rsis.ramsar.org/fr/ris/2283). They represent the most important national breeding area for the northern shoveler (*Spatula clypeata*), the black-tailed godwit (*Limosa limosa*), the redshank (*Tringa totanus*) and the lapwing (*Vanellus vanellus*) (Marchadour 2014).

We investigated how a protocol used by local managers can (i) inform on the influence of water level and terrestrial vegetation dynamic on the taxonomic and functional diversity of waders and ducks, and (ii) provide insight into the management of this particular wetland to maintain waterbird diversity. Coastal wetlands are important for wintering waterbirds (Saeijs and Baptist 1980). However, we focused on spring staging and breeding time since these periods of the year are particularly crucial for waterbird population dynamics (Lindström 2003; Arzel et al. 2006; Newton 2008). We tested the effect of spatial and temporal heterogeneity of water level and vegetation height on taxonomic and functional diversity of waterbirds with a focus on the two major groups in the study area, namely waders (i.e., Charadriiformes) and ducks (i.e., Anatidae). Furthermore, we analysed whether taxonomic and functional diversity respond in the same way to habitat heterogeneity. According to the general theoretical expectations, we expected positive relationships between habitat heterogeneity and waterbird diversity and abundance (Griffin et al. 2009). However, foraging behavior and nesting requirements differ substantially between the two groups so it is unclear whether habitat heterogeneity would benefit each group equally (Smart et al. 2006). Based on our results, we identify management practices that would promote either one group of waterbirds or one type of diversity (taxonomic or functional) depending on conservation priorities.

Methods

Study sites

The study was conducted in the "Marais Breton" (46°51'7 "N, 2°3'11 "W), a coastal wetland area of approximately 32,000 hectares located on the French Atlantic coast (Fig. 1). The Marais Breton is a dammed marsh, structured by a dense and complex network of ditches. In summer, it is irrigated through a hydraulic system connecting the marshes to the Loire river. In winter, 20% of its surface is flooded independently of the irrigation network connected to the Loire river. Thus, all waterbodies in this study are freshwaters uninfluenced by salinity. Although relatively far from urban centres and unlike most marshes, it is inhabited, with a few main or secondary residences and farms. Thermoatlantic subhalophilic meadows (EUNIS code A2.523, CORINE biotopes code 15.52) are the main land use and are mainly exploited for extensive farming systems, oriented towards cattle production and rearing, or mixed production (milk and meat) (Le Floch, Candau, 2001). These meadows constitute open ecosystems, marked by the rare presence of shrubs or trees along the ditches. Hence, the spatio-temporal dynamic of the water levels and the terrestrial vegetation cover is largely dependent on the management decisions of each private landowner (farmers, hunters). The climate is temperate-oceanic with mild, wet winters and relatively cool summers.

We got access permissions to 18 land ownerships in the Marais Breton. According to the local manager's knowledge, these study sites are representative of private hunting estates in terms of surface (mean area = 4.42 ± 1.01 ha), vegetation development and hydrological units. These hunting estates are usually delimited by ditches, composed of wet meadows and one to four permanently flooded ponds (among our 18 study sites, one contained no ponds). Seven ponds contained from one to three islets (mean number for all sites = 1.43 ± SD 2.92) of a dozen square meters. The average distance to the nearest study site is 1,393 m ± SD 1,415 m (Fig. 1). Each site constitutes an independently managed unit. Hunting occurs on and around most study sites but outside the study period (September-January). Thus, potential disturbances outside the hunting season are limited to water level management and farming practices.

A team of two observers visited each site bimonthly from March 1 to July 31. Twelve sites were monitored for six years (2015–2020) and six sites were added to the study and monitored for three years (2018–2020). All the sites were surveyed 9–10 times per year except two sites that were visited 3–6 times in some years (see details in Table S1) due to financial and manpower constraints.

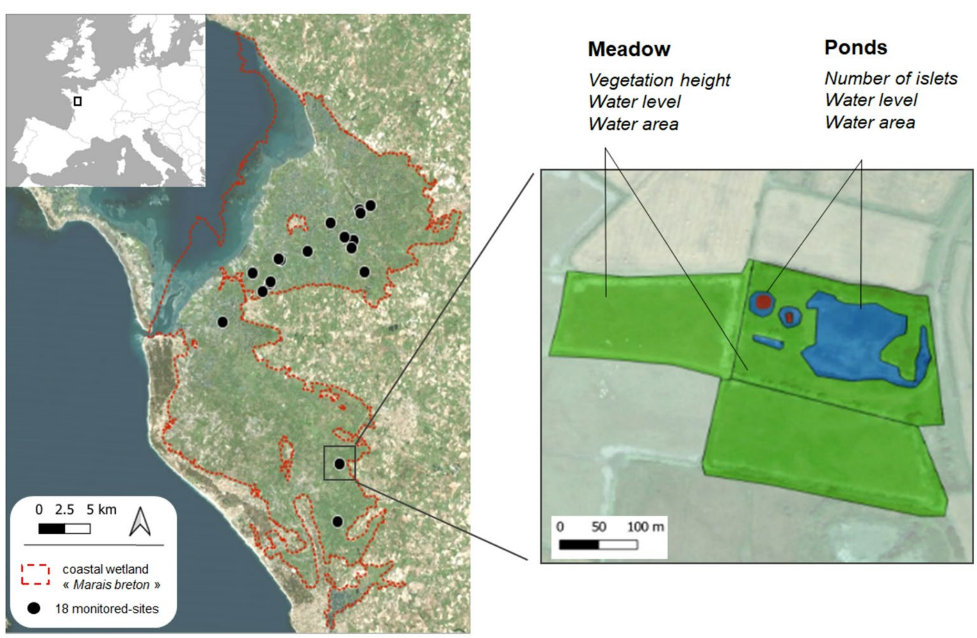

Fig. 1 Location of the Marais Breton in Europe and France (left panel),and illustration of the habitat predictors measured on each on 18 monitored sites (right panel)

Bird survey, species traits and diversity indices

Waterbird censuses were carried out in the morning. In bad weather conditions monitoring was shifted by one day. Observers walked around each site, usually along the bordering ditches, and then around the pond. Censuses lasted up to 30 min and were carried out by two observers using a spotting scope (Zeiss 85 T*, 45°, 20-75x) and binoculars (Zeiss 8*56 HD). All adult waterbirds observed on land and on the pond within the site were identified to the species level and counted while those in flight were excluded. We studied two guilds of waterbirds: wading birds (Charadriiformes) and ducks (Anatidae), including dabbling ducks, diving ducks and shelducks (see Table S2 for a complete species list of each group). We used species richness and abundance to describe taxonomic diversity. For functional diversity, we calculated for each species "diet plasticity" (DIET) and "foraging strata plasticity" (FOR) by tallying respectively the number of different diet items (1 to 7: invertebrates, fish, vertebrates, carcasses, fruits, seeds or other types of plant material), and the number of habitat strata used (1 to 4: water below surface, water surface, ground or above ground). Note that this last habitat stratum includes the original categories "understory", "mid-high" and "canopy" as defined in the EltonTraits database (Wilman et al. 2014) (see Table S3 for trait values of each species). For both diet and foraging traits, we computed two functional dispersion diversity indices ($FDIS_{DIET}$; $FDIS_{FOR}$) that are the mean distance of individual species to the centroid of all species by trait (DIET or FOR) in the community (Laliberté and Legendre 2010) using the R-package *FD* (Laliberté et al. 2015).

Habitat variables

The habitats were characterized by variables related to vegetation, water levels, and islets in ponds. Vegetation height and water depth were measured daily census day. Following previous studies we defined five vegetation height classes that encompass the variation in wader preferences for this habitat feature (Clausen et al. 2013; Durant et al. 2008): 1–7 cm; 8–15 cm; 16–30 cm; 31–50 cm and >50 cm. We then visually estimated the percentage cover of each class rounded to the nearest 5% in the wet but not flooded meadows. We used a measuring stick to estimate water depth. We sought to limit as much as possible the disturbance caused by the survey during the breeding period. Therefore, the number of measurements was not fixed but depended on the known topography of each site (Tanneberger et al. 2011). We considered five classes of water level (Bolduc and Afton 2008; Colwell and Taft 2000; Taft et al. 2002): "wet" (no standing water, not included in analysis); 1–5 cm; 6–10 cm; 11–15 cm; > 15 cm. We estimated the proportion of the entire site area covered by each class of water depth (including the ponds).

We then calculated a heterogeneity index for vegetation (VH) and water depth level (WDH) using the following equation, that is essentially the standard deviation of cover values in a site (Fig. 2):

$$(1)\ VH\ or\ WDH = 1 - \sqrt{\frac{\sum_{i=1}^{n}(x_i - \overline{x})^2}{n}}$$

With x_i = proportion cover x of class i ; $\overline{x}$ = average proportion cover for a census date and n = number of classes ($n_{vegetation}$ = 5, n_{water} = 4). The standard deviation was subtracted from 1 so that a VH or WDH value close to 1 represents a high level of heterogeneity and a value close to 0 represents a low level of heterogeneity.

We recorded also water area (WA) as the proportion of an entire site under water as estimated by eye. For each site, we calculated the yearly means and standard deviations of VH, WDH and WA (i.e., 3, 6, 9 or 10 censuses depending on the site) (Table S1). The mean values represent the overall "spatial heterogeneity" during the year survey while the standard deviations represent the temporal variation over the monitoring season (i.e., the level of change over time).

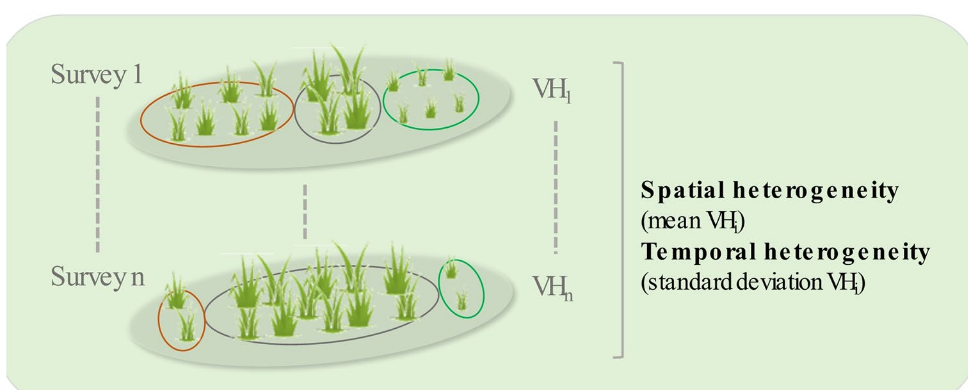

Fig. 2 Computation of the heterogeneity indices as illustrated for vegetation cover. On each survey, the proportion of the site covered by each class of vegetation height (shown by the circles of different colours) is recorded. The index is computed following (1) in the text. Spatial heterogeneity is the mean and temporal heterogeneity is the standard deviation of all index values recorded on a site for a given year

Finally, we counted the number of islets (nb.islets) in each pond each year, knowing that several islets had been created, for waterbird breeding during the study period in five sites (sites 3, 4, 9, 12 and 17). All GIS analyses were processed in QGIS software (version 3.10.12, 2020). Basic statistics of each variable are presented in Table S4.

Statistical analyses

We summed the values calculated for all censuses per species, site and year, which resulted in a dataset of 90 surveys (Table S5). We calculated change in species richness (ΔS) and turnover (gain and loss of species) between consecutive years (Avolio et al. 2019) for each site (R-package *Codyn* (Hallett et al. 2020) to assess the stability of species composition during the study. We then assessed the response of waterbird taxonomical and functional diversity to habitat predictors by using generalized linear mixed models using the R-package *glmmTMB* (Magnusson et al. 2020). We used species richness and abundance as response variables for taxonomic diversity, and functional dispersion indices ($FDIS_{FOR}$, $FDIS_{DIET}$) for functional diversity. All full models contained the habitat predictors (VH_{mean}, WDH_{mean}, WA_{mean}, VH_{sd}, WDH_{sd}, WA_{sd}, nb.islets) and the two categorical variables site area and year. The former was included as a random factor in the analysis, and the latter was kept as a fixed factor because of the small number of categories (6 years). The number of censuses per year was included as an offset to adjust for the different sampling effort between surveys (Table S1).

Prior to statistical analyses, we checked for evidence of heteroscedasticity, outliers in response variables, predictor collinearity, overdispersion, and residual normality (Zuur et al. 2010). No heteroscedasticity and outlier problems were detected (R-package *Performance*, Lüdecke et al. 2021). We estimated collinearity using the Variance Inflation Factor (VIF) and considered values greater than 3 as problematic (Zuur et al. 2010). Mean water area (WA_{mean}) was the only predictor that exhibited strong collinearity values (VIF = 5–10), and was therefore excluded from all models. Quantitative predictors were scaled before computing the models to more precisely estimate the relative influence of each predictor. Only the model for abundance was fitted with a negative binomial distribution because it showed overdispersion. For species richness, we compared the performance of models fitted with a Poisson and Gaussian distribution of errors and selected the model with the lowest Akaike Information Criterion (AIC). Functional diversity was modeled using a Gaussian distribution too.

For each response variable, we ranked the competing models using the Akaike Information Criterion (AIC). We conducted model averaging on the subset of competing models (ΔAIC < 2) because many models had similar AIC and weights (Grueber et al. 2011). These analyses were performed with the R-package *MuMIn* (Barton 2018).

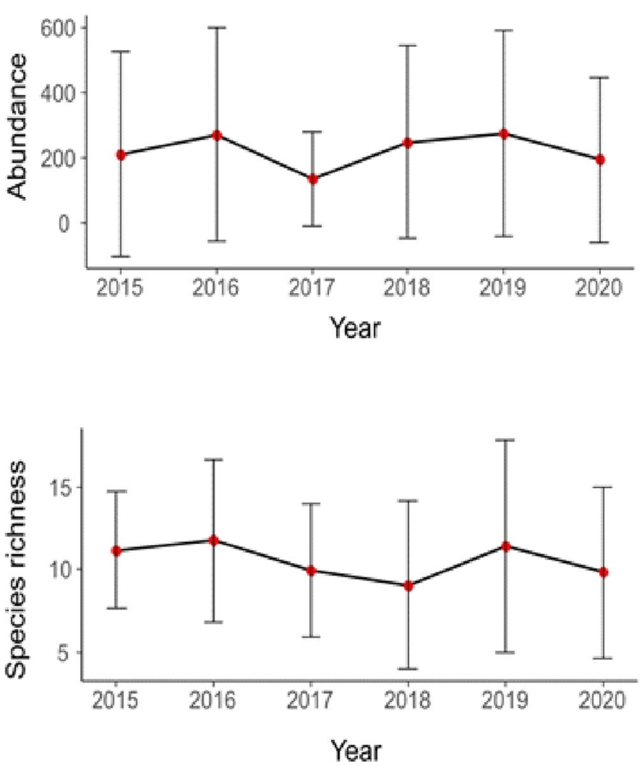

Fig. 3 Mean ± standard deviation of abundance and species richness of waterbirds for each year of the monitoring period. Note that 12 sites were monitored in 2015-2015 and 18 sites were monitored afterwards

Results

We observed 20,306 individuals from 48 species, five of which representing nearly 70% of the cumulative abundance (Common shelduck *Tadorna tadorna*, Northern shoveler *Anas clypeata*, Black-tailed godwit *Limosa limosa*, Mallard *Anas platyrhynchos* and Black-winged stilt *Himantopus himantopus*). Among the observed species, 18 were wading birds (38%, $n = 8832$) and 8 were ducks (17%, $n = 8803$) which constituted the two major guilds. Relative abundance of each species as well as basic statistics summarizing diversity indices measured in the 90 surveys are presented in Tables S2 and S5. The longitudinal analysis revealed some variation in species composition during the monitoring period but no clear trend in species number and turnover rate, thus suggesting a relative temporal stability of species composition during over the timeframe (see Fig. 3 and ESM_1 for further details).

The monthly variation of vegetation cover was similar across years for the higher vegetation class (Fig. 4), which depicts vegetation growth with a peak in late May and early

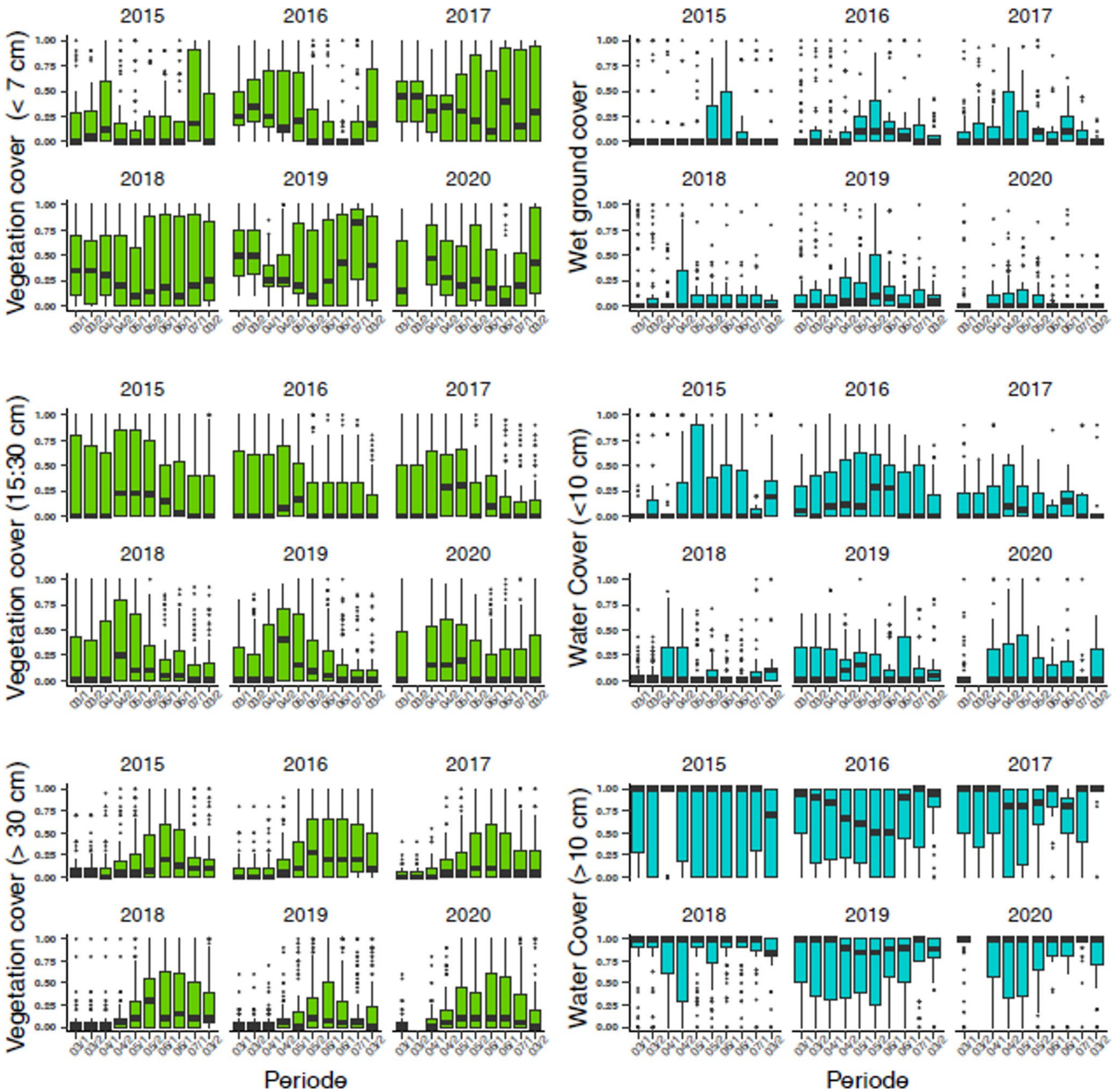

Fig. 4 Monthly variation of vegetation and water cover and among the sites during the six years of the survey. The panels show results for three height strata of vegetation (< 7 cm, 15-30 cm, > 30 cm) and three water levels (wet ground with no standing water, < 10 cm, > 10 cm)

June and then a reduction due to the asynchronous onset of mowing and grazing between sites. The shortest height class was the most variables among years. The monthly variation in cover for water levels was more variable between years due to different weather conditions, particularly for the class > 10 cm in particular).

For all response variables except wader richness, the best model included the habitat variables and performed better than the null model (ΔAIC > 2) (Table 1). Spatial vegetation height heterogeneity (VH_{mean}) was the most important variable across the six averaged models (mean importance 0.75) followed by the two descriptors of water level heterogeneity (mean importance: WDH_{mean} = 0.50, WDH_{sd} = 0.43), water area (mean importance WA_{sd} = 0.38), temporal heterogeneity of vegetation height (mean importance VH_{sd} = 0.22) and the number of islets (mean importance nb.islets = 0.03).

Table 1 Comparison of generalized linear mixed models predicting waterbird taxonomic (abundance and species richness) and functional diversity (FDIS) based on AIC for null models (no variables) and full models with (2 covariates and 6 habitat variables). Random effects are present in all models including null models. Functional dispersion of diet-related traits ($FDIS_{DIET}$) and foraging strata-related traits ($FDIS_{FOR}$)

	Null model		Model with habitat variables	
	ΔAIC	*weight*	*ΔAIC*	*weight*
Species richness				
All birds	>2		0.0	0.53
Wading birds	0.04	0.36	0.0	0.45
Ducks	>2		0.0	0.39
Abundance				
All birds	>2		0.0	0.63
Wading birds	>2		0.0	1.00
Ducks	>2		0.0	0.66
Functional diversity				
$FDIS_{DIET}$	>2		0.0	0.23
$FDIS_{FOR}$	>2		0.0	0.19

Taxonomic and functional diversity

Spatial heterogeneity of vegetation height (VH_{mean}) negatively influenced the richness and abundance of the two guilds and positively both functional diversity indices (Table 2 A). Water level heterogeneity (WDH_{mean}) positively influenced the richness and abundance of the two guilds but it did not explain the variation in functional dispersion (DIET and FOR). Temporal variation in water depth heterogeneity (WDH_{sd}) negatively influenced functional indices (DIET and FOR) but had little or no importance for species richness and abundance. Temporal variation of vegetation height heterogeneity (VH_{sd}) and water area variation (WAsd) had usually weaker influences in the models but their averaged coefficients were always positive. The number of islets (n.islets) was only retained in one model, but with a low importance (Table 2 A).

Ducks and wading birds

None of the predictors explained the variation in wading bird richness, whereas duck richness was mostly explained by spatial heterogeneity in vegetation height (VH_{mean}) and water level (WDH_{mean}) with negative and positive coefficients, respectively. The averaged models for abundance also yielded contrasting outputs between the two guilds. Spatial heterogeneity of vegetation height (VH_{mean}) had the strongest importance with a negative effect on wading bird abundance, but it did not explain the variation in duck abundance. In contrast, water level heterogeneity (WDH_{mean}) and temporal variation of water level heterogeneity (WDH_{sd}) had a positive and negative influence on duck abundance, respectively. Nevertheless, these predictors were not kept in the averaged models for wading birds. As for the variation in water area (WA_{sd}), it had a strong effect on the abundance of the two guilds. However, the effect was positive for wading birds and negative for ducks. The temporal variation of vegetation height (VH_{sd}) and the number of islets (nb.islets) contributed to a lower extent to the wading bird abundance (Table 2B).

Discussion

Opposite responses to the spatiotemporal heterogeneity of the habitat

We showed that spatial and temporal heterogeneity of vegetation height and water level, measured at the scale of sites covering a few hectares, significantly affected waterbird diversity. As expected, the effect of spatial and temporal heterogeneity of the habitat depended on the ecological guild. More surprisingly, taxonomic and functional diversity exhibited opposite responses to some of these habitat predictors. Long-term trends in abundance and richness may affect the estimation of the effect of current ecological condition. Because practices were fairly constant and the bird community show little fluctuation during the time frame of the study (see Fig. 3 and Supplementary material). we are confident about the effects of the local ecological factors that we detected.

An important result is that vegetation height and water level heterogeneity affected the diversity of waterbirds in opposite directions. Bird richness and abundance increased with spatial heterogeneity of water level and decreased with increasing spatial heterogeneity of vegetation height. Variable water depths likely provided more foraging opportunities for species with different eco-morphological constraints, such as the maximal length of bill, leg or neck (Arzel and Elmberg 2004; Guillemain et al. 2002; Kooloos and Zweers 1991; Nudds et al. 2000) and promoted richer communities (Ma et al. 2010; Sebastián-González and Green 2014). Water depth variability also influences plant communities and water salinity which in turn affects the diversity of aquatic invertebrates (Batzer et al. 2004; Tolonen et al. 2003), an important food resource for waterbirds (Baschuk et al. 2012; Bolduc and Afton 2004). The negative effect of spatial heterogeneity of vegetation height on bird diversity may seem surprising. Although less individuals may be detected in higher vegetation, we do not expect this potential effect to drive the observed response because we surveyed all birds, not only the nesting ones, and wading birds and ducks did not show the same response to vegetation height heterogeneity. We may have missed individuals, as

Table 2 Multi-model (GLMMs) averaged estimates of standardized coefficients (± standard error) and p-values for the site-scale habitat predictors of (A) taxonomic diversity and functional diversity of the waterbird communities and (B) taxonomic diversity of waders and ducks. Significant variables (p-value ≤ 0.05) are in bold. The relative importance of each predictor was computed by summing its Akaike weights in all the models from the model subset (ΔAIC < 2) where it was included. Two covariates (site area and year) were included in all models but their estimated coefficients are not displayed in the table. Standardized regression coefficients with error standard (std.coef ± se); mean water level heterogeneity (WDH_{mean}); mean vegetation heterogeneity (VH_{mean}); standard deviation of water level heterogeneity (WDH_{sd}); standard deviation of vegetation heterogeneity (VH_{sd}); standard deviation of water area (WA_{sd}); number of Islets (nb.islets)

Predictor	**Coefficient ± se**	**p-value**		**Importance**	
A. Taxonomic vs. Functional diversity					
SPECIES RICHNESS (2 models - gaussian)					
VH_{mean}	−2.49 ± 0.63	< 0.01		1	
WDH_{mean}	0.73 ± 0.33	0.03		1	
VH_{sd}	-	-		-	
WDH_{sd}	-	-		-	
WA_{sd}	-	-		-	
nb.islets	-	-		-	
ABUNDANCE (7 models - negative binomial					
VH_{mean}	−0.44 ± 0.16	< 0.01		1	
WDH_{mean}	0.23 ± 0.06	< 0.01		1	
VH_{sd}	0.08 ± 0.07	0.23		0.28	
WDH_{sd}	−0.04 ± 0.07	0.55		0.1	
WA_{sd}	0.05 ± 0.07	0.52		0.1	
nb.islets	0.04 ± 0.07	0.56		0.1	
FDIS.DIET (5 models - gaussian)					
VH_{mean}	0.32 ± 0.07	< 0.01		1	
WDH_{mean}	-	-		-	
VH_{sd}	0.12 ± 0.06	0.05		0.7	
WDH_{sd}	−0.25 ± 0.07	< 0.01		1	
WA_{sd}	0.14 ± 0.08	0.08		0.6	
nb.islets	-	-		-	
FDIS.FOR (4 models - gaussian)					
VH_{mean}	0.37 ± 0.08	< 0.01		1	
WDH_{mean}	-	-		-	
VH_{sd}	0.01 ± 0.07	0.15		0.44	
WDH_{sd}	−0.20 ± 0.07	< 0.01		1	
WA_{sd}	0.09 ± 0.08	0.24		0.35	
nb.islets	-	-		-	
B. Wading birds vs. Ducks					
Predictor	Coefficient ± se	*p*-value	*p*-value	Importance	Importance
SPECIES RICHNESS					
Wading birds (no candidate model)					
Ducks (5 models - Poisson)					
VH_{mean}	−0.64 ± 0.18	< 0.01		1	
WDH_{mean}	0.36 ± 0.16	0.02		1	
VH_{sd}	-	-		-	
WDH_{sd}	−0.21 ± 0.15	0.18		0.35	
WA_{sd}	-	-		-	
nb.islets	-	-		-	
ABUNDANCE					
Wading birds (3 models – negative binomial)					
VH_{mean}	−0.70 ± 0.14	< 0.01		1	
WDH_{mean}	-	-		-	
VH_{sd}	0.15 ± 0.11	0.17		0.37	
WDH_{sd}	-	-		-	
WA_{sd}	0.36 ± 0.11	< 0.01		1	
nb.islets	0.06 ± 0.10	0.57		0.17	
Ducks (2 models – negative binomial)					

Table 2 (continued)

Predictor	Coefficient ± se	p-value	Importance
VH_{mean}	-	-	-
WDH_{mean}	0.31 ± 0.06	<0.01	1
VH_{sd}	-	-	-
WDH_{sd}	-0.16 ± 0.07	0.02	1
WA_{sd}	-0.20 ± 0.07	<0.01	1
nb.islets	-	-	-

we would have done with any current method. An alternative technique would have been to flush the birds repeatedly during the survey, which is questionable from a conservation perspective and might lead to nest abandonment. However, within a fixed area, increasing habitat heterogeneity eventually reduces the size of key habitats for foraging or nesting, which may limit site attractiveness. Hence, although more heterogeneous environments contain more habitats that could potentially support more species (Kadmon and Allouche 2007), an "area-heterogeneity trade-off" may prevent this potential from being realized (Allouche et al. 2012). Such an explanation is plausible for our sites given their size (Table S1). Maximum heterogeneity values were observed in sites where vegetation was tall (>30 cm). High and dense vegetation could benefit vegetation gleaners but most waterbird groups prefer non-vegetated or short and sparsely vegetated habitats for foraging (Bancroft et al. 2002; Douglas and Pearce-Higgins 2014; Tavares et al. 2015). In addition, small wading birds may avoid sites with high vegetation (high heterogeneity in our study) that reduces predator detection (Brindock and Colwell 2011; Pomeroy 2006).

Guild-specific responses As anticipated, the two guilds responded differently to spatio-temporal heterogeneity of the habitat. The abundance of wading birds was negatively related to spatial heterogeneity of vegetation height and duck abundance positively to spatial heterogeneity of water level. Ducks preferred areas with stable water levels while wading bird favored sites with alternating periods of submersion/emersion (Aharon-Rotman et al. 2017), which can be explained by differences in their foraging behavior and feeding resources. Most wading birds consume invertebrates in the ground, particularly on mudflats. The response of ducks mainly reflects the ecology of the two dominant species in our dataset, the shelduck and the shoveler (15 and 14% of the total abundance). They feed partly (shelduck) or exclusively (shoveler) in the water column and tend to forage in sites with relatively deep waters (Guillemain et al. 2000) less exposed to drying. Such sites are favorable to aquatic invertebrates, especially crustaceans (Thorp and Rogers 2019) which provide important resources for these species.

Responses of functional diversity Functional diversity of waterbirds also responded to habitat heterogeneity. Interestingly, while spatial heterogeneity of vegetation negatively affected taxonomic diversity, this variable had a positive effect on functional diversity indices of the waterbird community. Thus, increasing vegetation height heterogeneity did not allow more species or individuals to exploit the sites but allowed the coexistence of species that consume different food resources and exploit different vegetation strata for foraging. Although a general relationship between environmental heterogeneity and diversity is expected (Stein et al. 2014), a unimodal relationship (inverted U) between habitat heterogeneity and taxonomic diversity can also be predicted (Allouche et al. 2012). Our data support this latter prediction. The level of spatial heterogeneity of vegetation height in our study sites was likely located in the declining part of the relationship. Furthermore, both components of diversity also responded differently to variation in hydrological conditions. High temporal heterogeneity of water level resulted in a functionally less diverse guild but not taxonomically less diverse community, revealing a higher functional redundancy of species (more species sharing similar trait values) in more heterogeneous habitats (Altamirano et al. 2020). One explanation is that large changes in water depth over short periods, including drying, may prevent the settlement of populations of aquatic invertebrates, which are consumed by part of the bird community. The trade-off between heterogeneity and functional diversity is less well documented than for taxonomic diversity. It clearly deserves more investigation as our results and others (Lee and Martin 2017) support the view that both dimensions of diversity do not necessarily respond in the same way to environmental heterogeneity. Predation can be an important driver of bird abundance with individuals avoiding risky areas (Middleton et al. 2018) and some predators specializing on particular prey types (Pettorelli et al. 2011). While we did not monitor predator or evidence of predation during the survey, as we focused rather on vegetation structure in this study, it could be an interesting factor to consider in the future.

Implications for wetland management

Spatiotemporal heterogeneity of the habitats affects taxonomic and functional diversity differently. Because waterbird species have contrasting habitat requirements, specific management measures could induce different effects on distinct ecological guilds. Our results suggest that management solutions benefiting both guilds on the scale of our studied private hunting estates may not exist. Consequently, optimal wetland management for the whole bird community requires an assessment of conservation priorities and tradeoffs among different taxonomic or functional groups (Brandolin and Blendinger 2016; Stralberg et al. 2009; Luo et al. 2019). If the main goal is to maintain/increase functional diversity of waterbirds, a relevant strategy would be, for example, to implement extensive livestock grazing within grassland to create spatial heterogeneity vegetation height (Adler et al. 2001; Sabatier et al. 2010). Such a strategy may particularly benefit some species like the black-tailed godwit *Limosa limosa* (Schekkerman et al. 2008). However, it may be inefficient if the conservation goal is to maximize species richness or abundance of all species (Godet et al. 2016). At this spatial scale, a trade-off could exist between the heterogeneity level and the minimum area of each habitat required by individuals to nest or forage. Therefore, it may be more appropriate to manage habitats at a larger spatial scale (Fairbairn and Dinsmore 2001; Godet et al. 2016). Our results suggest that the management of water levels at the scale of our studied estates is a relevant strategy to promote richness and abundance of the two waterbird guilds. A network of wetlands including large ponds providing deeper water areas for ducks and shallower waters with short hydroperiods to create temporary mudflats for wading birds (Paracuellos 2006; Sebastián-González and Green 2014), could meet the habitat requirements of a wide range of species. Hence, an estate owner collaboration for a management at the landscape scale has the potential to promote taxonomic and functional diversity (Fairbairn and Dinsmore 2001; Godet et al. 2016).

Conclusion

The relationship between spatial and temporal heterogeneity of habitat on landownership scale depended on the response variable (vegetation or water level), the ecological guild (wading birds or ducks) and the diversity component (taxonomic or functional). The lack of congruent response of taxonomic and functional diversity indices is a crucial issue. Targeted management practices at the site scale could improve overall richness and abundance while selecting a reduced subset of functional traits and contribute to the loss of some waterbirds species. Therefore, the joint conservation of taxonomic and functional diversity may require planning both at the site and landscape scales. Integrating this set of constraints calls for coordination and cooperation at the landscape scale. The optimization of scenarios could be sought through landscape simulations explicitly accounting for habitat characteristics and species behavior which can be proposed to the local stakeholders.

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Author contributions JS contributed to data analysis and result interpretation and led the writing of the draft, GP analysed the data and contributed to the writing of the draft, CA and AD contributed to the interpretation of results and revised critically the draft. SF conceived the study contributed to the interpretation of results and revised critically the draft.

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Data availability Data are available at zenodo.org, DOI: 10.5281/zenodo.18161913

Declarations

Consent to publish All authors agreed with the manuscript content and all gave explicit consent to submit the version to be published.

Consent to participate The study was carried out on private lands which access has been granted by landowners. No animals were handled and observation time was limited as much as possible to reduce disturbances.

Competing interests The authors declare no competing interests.

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