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Seasonal variations of waterbird ecological networks under different saltpans management

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ABSTRACT

Habitat change has increased the loss of wetlands and impacted highly on coastal biodiversity. Consequently, wetland-dependent species such as waterbirds have experienced a decline in their populations. This study proposes an application of bipartite networks using both the sampled sites and species as nodes to assess seasonal variations in waterbirds composition and habitat specialization in response to the abandonment of saltpans. The sampling was carried out in active and abandoned saltpans of the Ria Formosa (Portugal) over four sampling periods to evaluate the temporal change in waterbird communities. Abundance was twice and species richness 14% higher in active saltpans than in abandoned ones. About 60% of the waterbirds indicated a high specificity towards active saltpans. Saltpans showed a high β-diversity and seasonal dynamic of waterbird community composition. Network dissimilarity across the year was dominated by turnover of the edges rather than species turnover. Dynamics in network structure and composition seemed to be related to bird dispersal, migration phenology, and habitat specialist strategies. Overall, this study highlights the importance of preserving the activity of saltpans as it conditions abundance, richness and dynamics of waterbird populations. Continued efforts are needed to reduce threats to coastal wetlands and restore abandoned saltpans worldwide, since these are key habitats for the conservation of resident and migratory waterbirds.

1. Introduction

Wetland ecosystems are known to support a rich biodiversity and deliver a large number of services that contribute to human well-being (Millennium Ecosystem Assessment, 2005; Mitsch and Gosselink, 2015). Despite wetlands' ecological and economic significance, conservation actions started late in the twentieth century, when more than half of the world's wetlands was lost (Davidson, 2014; Gardner et al., 2015; Mitsch and Gosselink, 2015). Human factors such as land conversion and eutrophication caused that deterioration and loss were faster in wetlands than in other ecosystems. This rapid degradation of wetlands has affected globally to the species dependent on these habitats. Waterbirds, a major group of wetland-dependent species, have experienced a decline in their coastal populations: from the populations of world waterbirds for which trends are known, 38% are in decline and only 20% increasing (Millennium Ecosystem Assessment, 2005; Wetlands International, 2012). Moreover, waterbirds provide a huge range of ecosystem services (Green and Elmberg, 2014), so they can be used as relevant indicators when addressing the trade-off between land use change and conservation of coastal wetlands.

Coastal saltpans (also called *salinas*, salines, saltworks or salterns) have been identified as complementary foraging and roosting habitats contributing to the conservation of global waterbird population (e.g. Barnagaud et al., 2019; Collazo et al., 1995; Lei et al., 2018; Masero, 2003; Rufino et al., 1984; Sripanomyom et al., 2011; Warnock et al., 2002). Within a global context of abandonment of saltpans and land use change, this study is an example of how a combination of statistical and network analysis can be used to assess seasonal species composition under different land uses. Ecological networks have typically been applied to study interactions among species (e.g. host and parasites, plant-pollinator), and have increasingly been used through multiple environmental gradients and levels of biological organization (Guimarães, 2020; Tylianakis and Morris, 2017), even to study interactions at the cellular level (e.g. protein-protein) (Wagner, 2003). Networks become "bipartite" when interacting species are divided in two disjoint sets (e.g. by trophic level, host-parasites) (Bascompte and

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Jordano, 2007; Dormann et al., 2008). The spatiotemporal comparison of multiple networks allows viewing ecological networks as dynamic entities for which we can quantify species and interaction turnover, a network modelling approach that is increasingly applied in community studies (CaraDonna et al., 2017; Poisot et al., 2012a; Tylianakis and Morris, 2017). Understanding how the structure and dynamics of species interactions are affected by anthropogenic disturbance such as habitat loss is paramount, and it has been studied in host-parasitoid (Tylianakis et al., 2007), plant-pollinator (e.g. Spiesman and Inouye, 2013; Traveset et al., 2018) and hybrid networks (Morrison et al., 2020). However, so far, little attention has been paid to explore biological networks using spatial topographies as nodes of networks such as, for example, temporary ponds (Fortuna et al., 2006), roosting trees for shelter (Fortuna et al., 2009), or locations of tagged species (Jacoby et al., 2012).

This study uses sites with different management as nodes of bipartite networks to assess the effect of land use change on seasonal waterbird composition. I assess the temporal beta diversity of saltpans waterbird communities and analyse their temporal dynamics related to phenology, dispersal and habitat specialization. The study estimates the impact of the abandonment of saltpans on the seasonal composition, abundance and turnover of bird communities found in saltpans with different management throughout the year. I firstly investigate the seasonal variations in composition and abundance of bird communities and their ecological networks. Then, I explore the dissimilarities and temporal dynamics of bird assemblages by assessing: i) the variability in the composition of communities between the two managements of saltpans, ii) the degree of habitat specialization of waterbirds, and iii) the beta diversity in interaction networks quantifying the relative importance of species turnover and rewiring of interactions among shared species. The presented method introduces a new approach to the analysis of species communities in relation to land use.

2. Material and methods

2.1. Study area

The saltpans are located in the Ria Formosa Natural Park (7° 49′ W, 37° 1′ N), which extends along a coastal lagoon system in southern Portugal (Fig. 1). The park covers an area of 179 km^2 consisting mostly of a system of barrier islands, channels and inlets. Due to its ecological importance, the Ria Formosa has been included in the Natura 2000 Network, it is a Ramsar Convention site (http://www.ramsar.org/), and a BirdLife Important Bird and Biodiversity Area (IBA) (BirdLife International, 2020a).

Saltpans are man-made wetlands protected by the Ramsar Convention. The Iberian Peninsula, an important breeding and wintering area for birds, has developed traditional salt exploitation during centuries. Some studies have provided information on variation of waterbirds in specific saltpans of the Ria Formosa, reporting that saltpans play an important role as breeding and feeding habitats (e.g. Batty, 1992; Fonseca et al., 2005; Rufino et al., 1984). However, no quantitative analysis has examined the seasonal difference between active and abandoned saltpans across the entire Natural Park to assess the effect of the abandonment of saltpans on waterbirds in the Ria Formosa.

All saltpans are situated at sea level and have similar semi-arid Mediterranean climatic conditions: precipitations are weak and irregular, with a prolonged dry season during the summer months and an average value of 450 mm/yr; temperatures are mild, ranging from 7 °C to 30 °C throughout the year; and the insolation is high, with approximately 3150 h/yr (http://www2.icnf.pt).

2.2. Survey design

Inter-seasonal raw abundance of waterbirds was estimated on active and abandoned saltpans of the Ria Formosa from April 2015 to January 2016 using line transect sampling. I surveyed on foot a total of 52 randomly located line transects, covering practically all localities with saltpans in the Ria Formosa (Fig. 1 and Table 1). The counts were made by the same observer from the banks of the saltpans using 10 × 40 binoculars, extending only one side of the line transect, and lasting 15 min per transect. All saltpans have a rectangular shape so line transects were straight and had a mean length of 195.3 m in active and 194.4 m in abandoned transects (Table 1). The distance between transects was variable, being 40 m the minimum distance to the nearest transect and 9.3 km the maximum separation between transects of different localities (between Fuseta and Santa Luzia). Saltpans are in open habitats with high visibility so detection distances were large: ranging from 70 m for the smallest birds (e.g. *Charadrius alexandrinus*) to 400 m for the biggest

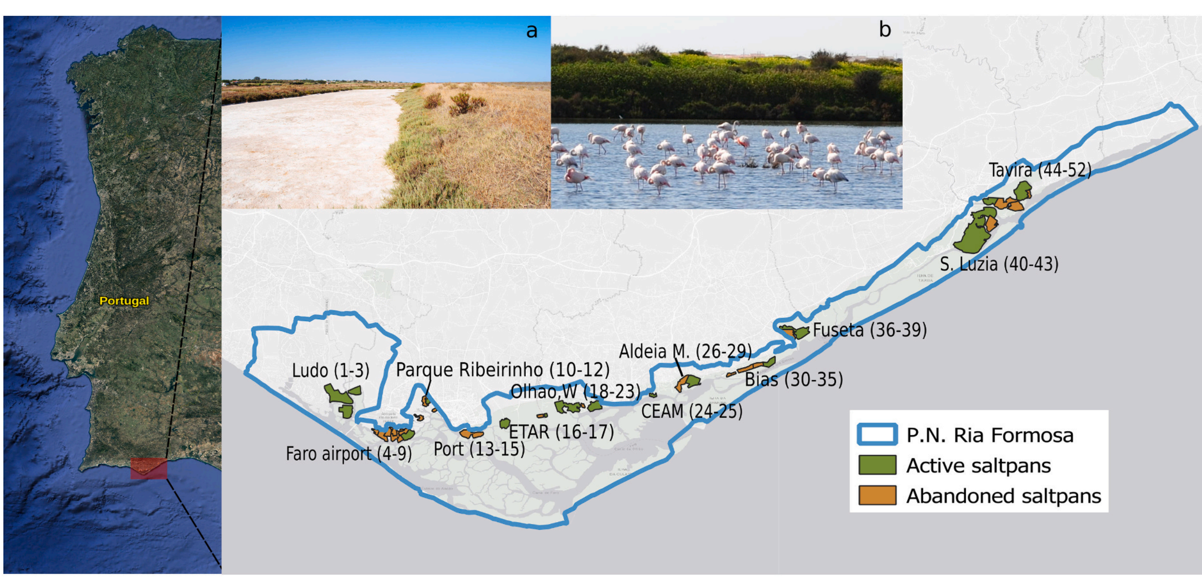

Fig. 1. Location of saltpans complexes in Ria Formosa Natural Park where the composition of waterbird communities was sampled. a) Abandoned saltpan desiccated during summer; b) Active saltpan in winter. Active and abandoned saltpans at the moment of the survey (2015–2016) are shown. Numbers correspond to the line transects surveyed (see Table 1).

Table 1
Line transects surveyed in this study covering practically all localities with saltpans in the Ria Formosa (Algarve, Portugal). Line transects are labelled from West to East (see Fig. 1). The type of management in the saltpans and the length of the transects are shown.

Transect ID	Locality	Type	Length (m)
1	Ludo	Active	214
2	Ludo	Active	207
3	Ludo	Active	199
4	Faro airport	Abandoned	215
5	Faro airport	Abandoned	199
6	Faro airport	Abandoned	208
7	Faro airport	Abandoned	220
8	Faro airport	Abandoned	199
9	Faro airport	Abandoned	185
10	Parque Ribeirinho, Faro	Abandoned	140
11	Parque Ribeirinho, Faro	Active	220
12	Parque Ribeirinho, Faro	Active	208
13	Faro, commercial port	Abandoned	197
14	Faro, commercial port	Abandoned	202
15	Faro, commercial port	Abandoned	192
16	Faro, ETAR	Active	222
17	Faro, ETAR	Active	213
18	Olhao, west	Abandoned	151
19	Olhao, west	Active	164
20	Olhao, west	Active	191
21	Olhao, west	Abandoned	167
22	Olhao, west	Active	179
23	Olhao, west	Active	193
24	Olhao, CEAM PN Ria Formosa	Abandoned	221
25	Olhao, CEAM PN Ria Formosa	Abandoned	226
26	Aldeia Marim	Active	180
27	Aldeia Marim	Active	222
28	Aldeia Marim	Active	201
29	Aldeia Marim	Abandoned	216
30	Bias do Sul	Abandoned	186
31	Bias do Sul	Abandoned	178
32	Bias do Sul	Abandoned	184
33	Bias do Sul	Abandoned	211
34	Bias do Sul	Active	186
35	Bias do Sul	Active	199
36	Fuseta	Abandoned	236
37	Fuseta	Active	204
38	Fuseta	Abandoned	179
39	Fuseta	Active	178
40	Santa Luzia	Active	185
41	Santa Luzia	Active	187
42	Santa Luzia	Active	205
43	Santa Luzia	Active	207
44	Tavira	Active	204
45	Tavira	Abandoned	169
46	Tavira	Abandoned	142
47	Tavira	Abandoned	221
48	Tavira	Active	119
49	Tavira	Abandoned	215
50	Tavira	Abandoned	197
51	Tavira	Abandoned	185
52	Tavira	Abandoned	201

species (*Phoenicopterus roseus*). Besides, waterbirds tended to stay still while foraging during sampling, so practically all birds within the saltpans covered by the transects were detected. Ubiquitous species such as *Ciconia ciconia* or seagulls were not included in the study.

The same 52 transects were visited four times (once per season) embracing spring (19th April - 17th May), summer (11th - 25th July), autumn (15th October - 12th November) and winter (14th - 30th January). The number of transects needed to cover the entire Ramsar site meant that it was not possible to survey only at low or high-tide. The potential effect of tidal variation on waterbirds abundance was reduced by randomizing the order of visits to the 52 transects through the four seasons. The saltpans were classified into two types according to their land-use: “active saltpans” (24 transects) and “abandoned saltpans” (28 transects) (Fig. 1).

2.3. Statistical analysis

I tested if there was a significant variation in the composition between the bird communities found in the two types of saltpans during each season by using an analysis of similarities (ANOSIM; Clarke, 1993). The ANOSIM statistic (R) computes the difference of mean ranked dissimilarities between groups (B) and within groups (W), being N the number of observations:

$$R = (B - W)/(N(N-1)/4)$$

R value ranges from -1 to 1, and a value equal to 0 indicates completely random grouping. ANOSIM was computed using the Bray-Curtis dissimilarity index (which ranges between 0 if the two sites share the same number of each species, and 1 if the two sites share none of the species) and 999 permutation tests. Before performing ANOSIM, empty sites (saltpans without birds) were removed from the abundance data matrix. ANOSIM was performed using the R package “vegan” (Oksanen et al., 2019).

2.4. Bipartite network analysis

I constructed a weighted bipartite network per season based on the raw abundance of species found in saltpans. Both the sites and bird species were considered as the vertices (nodes) of the network linked between them by the edges. The width of the edges were weighted by the abundance of each species in each connected transect. Waterbird species absent in each season were removed. Ecological networks were visualized using the 52 sites and the “igraph” package (Csardi and Nepusz, 2006). The function “visweb” from package “bipartite” (Dormann et al., 2008) was additionally used to visualize the bipartite networks.

Network dissimilarity between seasons was quantified using the function “betalinkr_multi” (Poisot et al., 2012a). This function decomposes multiple-network dissimilarity into species and interactions turnover components. It calculates the dissimilarity in species composition (β_S). Besides, the computed dissimilarity of the whole-network structure (β_{WN}) is decomposed into two additive components: one compositional component related to species turnover (β_{ST}) and one component related to interactions turnover between shared species (β_{OS}) (Poisot et al., 2012a). The function “betalinkr_multi” was computed with the abundance data (binary = F), using the recommended setting (“commondenom”) for partitioning of β_{ST} and β_{OS} components and the Jaccard Index to calculate similarity between networks (the Jaccard Index computes the size of the intersection divided by the size of the union of the samples). In the present study, an interaction would indicate the occurrence of a bird species in a surveyed saltpan with the weighting of the edges relative to the abundance of each species in each connected transect. When measuring the dissimilarity of networks as proposed by Poisot et al. (2012a), only one set of nodes of the bipartite network (the species) will experience turnover over time as the other set of nodes (the sites) remain static. The ecological interactions (edges linking birds and saltpans) are in this case unidirectional, thus, the component related to interactions turnover between shared species to both realisations (β_{OS}) will be named hereafter “edges turnover”. Multiple-network dissimilarity between consecutive and non-consecutive seasons was assessed. For comparison purposes, beta diversity was calculated both using the data on the 52 transects and also rearranging the sites according to the type of management of the saltpans (active vs. abandoned).

The specialization of birds in relation to the type of saltwork (active vs. abandoned) was characterized using the Paired Difference Index (PDI). PDI was selected due to its better performance with quantitative data in comparison with other indices (see Poisot et al., 2012b). PDI for a species is computed as:

$$PDI = \sum_{i=2}^{R} (P_1 - P_i) \Big/ (R - 1),$$

where P_1 is the highest interaction strength on a resource, P_i are the remaining link strengths, and R is the number of resources (here, the two types of saltpans) (Dormann et al., 2008; Poisot et al., 2012b). PDI values were normalised so that they could range from 0 (generalist) to 1 (specialist). To calculate PDI, singletons (species with only one observation) were removed because they always render a specialization equal to 1 (Dormann, 2011). Network descriptors were computed with package "bipartite" (Dormann et al., 2008) and a dotmap to visualize the PDI values was produced using the "BoutrosLab.plotting.general" package (Boutros, 2020). All analyses were performed in R v3.2.2 (R Core Team, 2020).

3. Results

Raw abundance data found in all saltpans during the four seasons is presented in Appendix A. A total of 25 native waterbirds were observed in the saltpans: 11 resident species, 13 non breeding and 1 breeding species (Table 2). From these species, 10 were observed in all seasons. Overall species richness was similar among seasons: 18 species in autumn, 20 in summer and spring, and 21 species in winter. The highest abundance was found in autumn (1935 individuals) and the lowest during winter (1444 individuals). The overall sum of abundance and species richness in active saltpans were, respectively, 46% and 14% higher than in abandoned ones (Fig. B.1., Appendix B), even despite the fact that more inactive than active saltpans were sampled. Abandoned saltpans only showed slightly higher abundance in winter and higher richness in spring than active ones. When compared the mean abundance and richness to consider the effect of the different number of transects surveyed in each type of saltpans, species richness per transect in active saltpans is higher across the year, and abundance also, except during the winter, when abundance is similar between types of saltpans (Fig. 2). The number of empty sites (transects in which no birds were found) was higher during spring ($n = 19$) and summer ($n = 18$) than in autumn ($n = 11$) and winter ($n = 9$). Empty sites were mostly abandoned saltpans, ranging from 78% in summer to 95% in spring (see Fig. 3).

ANOSIM found the bird communities were similar within and between the types of saltpans (summer: $R = 0.046$, $p = 0.143$; spring: $R = 0.022$, $p = 0.326$; winter: $R = 0.037$, $p = 0.128$). Slightly higher compositional dissimilarities between the two types of saltpans than within types were found only during autumn ($R = 0.14$, $p = 0.003$).

The bipartite ecological networks showed differences among the seasons (Fig. 3). In overall, the highest number of links across the year occurred between birds and active saltpans. The bird species most abundant during the year were *Limosa limosa, Calidris alpina* and *Phoenicopterus roseus* (Fig. 3 and Figs. B.2.-B.5. of Appendix B).

Beta diversity among seasons was higher when all sites were pooled than when sites were split by types of saltpans (Table 3). Once the multiple-network dissimilarity was calculated by rearranging all the sites into the two types of saltpans, the highest dissimilarity in species composition (β_S) was found between autumn and winter (and spring). Taking all sites pooled together, the highest dissimilarity in species composition was also between autumn and spring. In both cases, the dissimilarity of interactions between the whole networks (β_{WN}) was due to a greater extent to the edges turnover between shared species (β_{OS}) than to the species turnover (β_{ST}).

Two singleton species (*Netta rufina* and *Gallinula chloropus*) were removed from PDI analysis. Around 74% of the waterbirds analysed showed PDI $\geq$ 0.8 at least one season of the year (Fig. 4 and Table B.1. in Appendix B). PDI analysis showed a higher specificity of waterbirds towards active than towards abandoned saltpans. About three-quarters of the waterbirds analysed indicated a habitat specialist strategy, and, among them, more than 75% (13 waterbirds) showed a high specificity

Table 2
Native birds observed during the survey in the Ria Formosa Natural Park. IUCN Red List categories and seasonality for each species according to birds' global distributions are shown (BirdLife International, 2020b). Seasonality describes the period in the species life cycle in which it occurs in the Ria Formosa. The Spanish Red List (Madroño et al., 2004) and the Portuguese Red List (*; Cabral et al., 2005) categories are also shown if different to that from IUCN. Categories: LC: Least Concern, NT: Near Threatened, VU: Vulnerable, EN: Endangered, CR: Critically Endangered. (†): personal observation: the Common Shelduck (*T. tadorna*) was observed breeding in active saltpans near Faro city in spring, being this population the only one present in Portugal during the spring (http://www.avesdeportugal.info/contacto.html); (‡): species sighted in all seasons.

Scientific name	Common name	Abbreviation	IUCN/Spanish/Portuguese* Red Lists	Occurrence in Ria Formosa (seasonality)
Himantopus himantopus‡ (Linnaeus, 1758)	Black-winged Stilt	H.him	LC	resident
Calidris alpina‡ (Linnaeus, 1758)	Dunlin	C.alp	LC	non breeding
Charadrius hiaticula‡ (Linnaeus, 1758)	Common Ringed Plover	C.hia	LC	non breeding
Charadrius alexandrinus‡ (Linnaeus, 1758)	Kentish plover	C.ale	LC/VU	resident
Sternula albifrons (Pallas, 1764)	Little Tern	S.alb	LC/NT/VU*	breeding
Limosa limosa‡ (Linnaeus, 1758)	Black-tailed Godwit	L.lim	NT/VU	non breeding
Phoenicopterus roseus‡ (Pallas, 1811)	Greater Flamingo	P.ros	LC/VU*	resident
Arenaria interpres‡ (Linnaeus, 1758)	Ruddy Turnstone	A.int	LC	non breeding
Tadorna tadorna (Linnaeus, 1758)	Common Shelduck	T.tad	LC/NT	resident†
Recurvirostra avosetta‡ (Linnaeus, 1758)	Pied Avocet	R.avo	LC/NT*	resident
Egretta garzetta‡ (Linnaeus, 1766)	Little Egret	E.gar	LC	resident
Anas strepera (Linnaeus, 1758)	Gadwall	A.str	LC/VU*	resident
Tringa totanus‡ (Linnaeus, 1758)	Common Redshank	T.tot	LC/VU/CR*	resident
Anas platyrhynchos (Linnaeus, 1758)	Mallard	A.pla	LC	resident
Numenius phaeopus (Linnaeus, 1758)	Whimbrel	N.pha	LC/VU*	non breeding
Netta rufina (Pallas, 1773)	Red-crested Pochard	N.ruf	LC/VU	non breeding
Gallinula chloropus (Linnaeus, 1758)	Common Moorhen	G.chl	LC	resident
Pluvialis squatarola (Linnaeus, 1758)	Grey Plover	P.squ	LC	non breeding
	Grey Heron	A.cin	LC	non breeding

(continued on next page)

Table 2 (*continued*)

Scientific name	Common name	Abbreviation	IUCN/Spanish/ Portuguese* Red Lists	Occurrence in Ria Formosa (seasonality)
Ardea cinerea (Linnaeus, 1758)				
Calidris ferruginea (Pontoppidan, 1763)	Curlew Sandpiper	C.fer	NT/VU*	non breeding
Platalea leucorodia (Linnaeus, 1758)	Eurasian Spoonbill	P.leu	LC/VU/VU*	resident
Anas clypeata (Linnaeus, 1758)	Northern Shoveler	A.cly	LC/EN*	non breeding
Phalacrocorax carbo (Linnaeus, 1758)	Great Cormorant	P.car	LC	non breeding
Anas crecca (Linnaeus, 1758)	Common Teal	A.cre	LC/VU	non breeding
Anas acuta (Linnaeus, 1758)	Northern Pintail	A.acu	LC/VU	non breeding
Vanellus vanellus (Linnaeus, 1758)	Northern Lapwing	V.van	NT/LC/LC*	non breeding
Tringa nebularia (Gunnerus, 1767)	Common Greenshank	T.neb	LC	non breeding

towards active saltpans. Only 4 species showed high affinity (PDI $\geq$ 0.8) towards abandoned saltpans, while 14 species were active specialists during at least one season of the year (Fig. 4). Neither species showed a consistent pattern of high affinity (PDI $\geq$ 0.8) over the entire year for either type of saltpans, partly because most species were not seen all year. Among the species sighted in all seasons, *Arenaria interpres* showed the highest overall affinity towards active saltpans.

4. Discussion

4.1. Bipartite networks in beta diversity analysis

Ecological networks have increasingly been used to explore community responses to environmental gradients (Tylianakis and Morris, 2017). In this study, seasonal variations of biological communities in relation to land use change have been explored using a less frequent approach of bipartite networks analysis, because both the sampled sites and bird species are used as the vertices (nodes). The conversion of sampled sites into individual nodes to construct the bipartite network, instead of pooling the sites by type of environment (in this case, saltpans with different management), allows us to visualize the occurrence pattern of species in different sites within the network structure. Perturbations, cascading effects, and a wide range of ecosystem alterations can be easily visualized using ecological networks (Pocock et al., 2016). In this study, the links of the networks indicate a one-sided relationship reflecting the preference of habitat by birds. Thus, the networks presented allow a visualization of the effect of land-use change on species diversity as it illustrates spatiotemporal changes in richness and abundance.

Moreover, the approach presented here allows to integrate in the analysis empty sites over time and environment (i.e. plots/transects with zero total counts). Zero count data can be difficult to handle when analysing temporal beta diversity because they require transformations prior to multivariate analyses which involves deciding if double zeros (e.g. two species jointly absent at different transects) are ignored (Legendre and Borcard, 2018; Zuur et al., 2010). Here, bird species showed a high frequency of zero abundance but these zeros are ecologically meaningful because they inform on the unfavourable conditions of some saltpans, and the approach used here allows to correctly interpret the data.

4.2. Waterbirds abundance and species richness under different saltpans management

This study has shown that the activity of saltpans is relevant for maintaining abundance and species richness of key wetland dependent species of waterbirds. Overall abundance was twice and species richness 14% higher in active saltpans than in abandoned ones. The fact that most (78% - 95%) of the transects without birds were located in abandoned saltpans suggests that the cessation of activity in the saltpans of the Ria Formosa results in a loss of habitat for waterbirds. A possible explanation for this might be that the groundwater table begins descending in spring and abandoned saltpans are usually desiccated during summer in the Ria Formosa (Chefaoui and Chozas, 2019; Costa et al., 1996). Water level is known to affect foraging activity of waterbirds in saltpans since it regulates the availability and composition of benthic invertebrates (Velasquez, 1992). In this study, more than a third

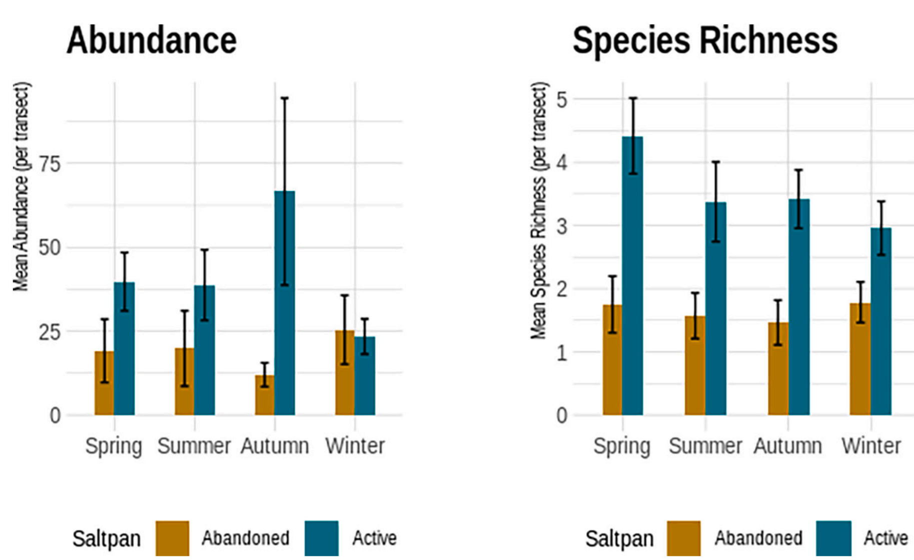

Fig. 2. Seasonal mean abundance and mean species richness of waterbirds sampled in the abandoned (n = 28) and active (n = 24) saltpans complexes of the Ria Formosa Natural Park. Error bars indicate standard errors.

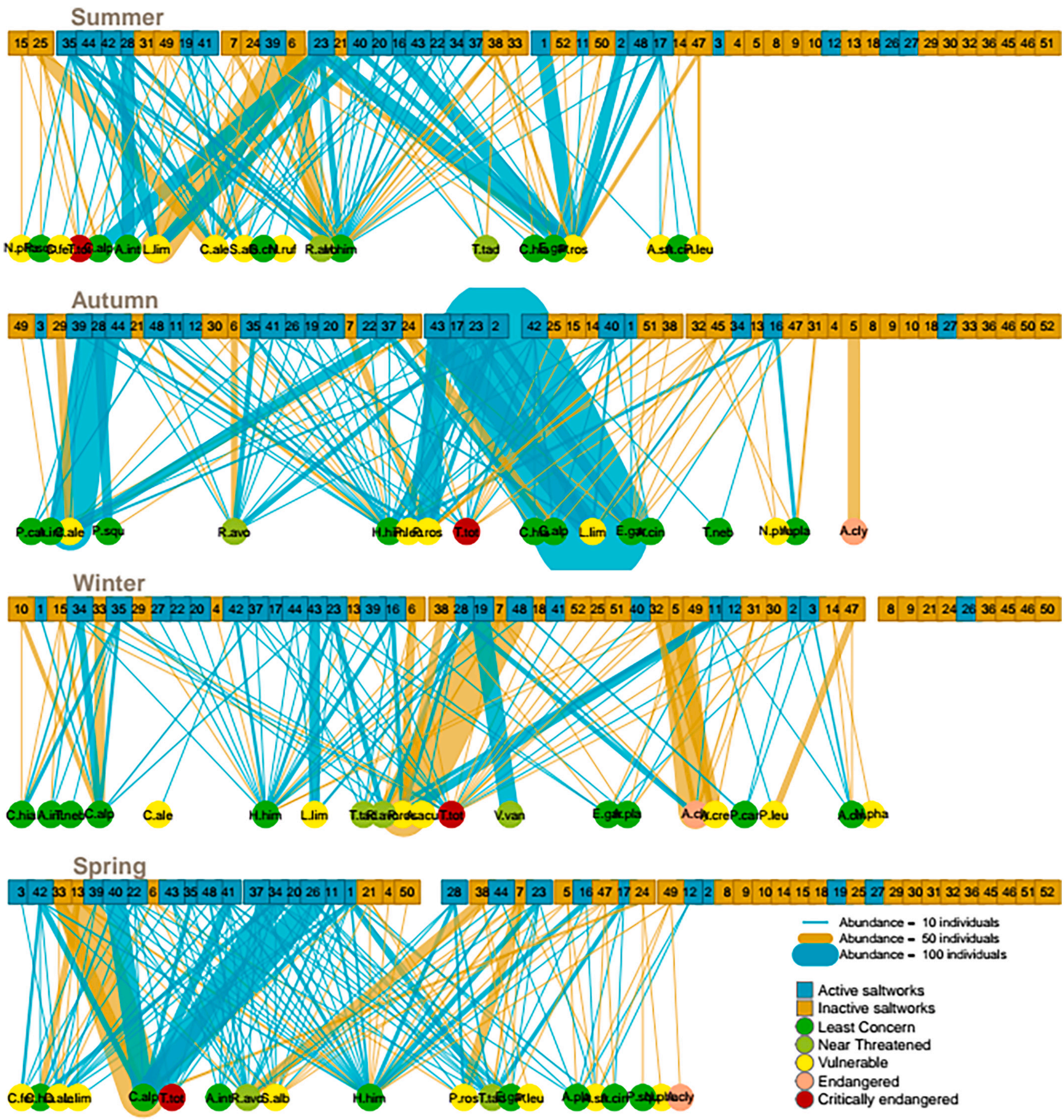

Fig. 3. Bipartite networks modelling relations between the bird species and surveyed saltpans in the Ria Formosa. The width of the edges are weighted by the abundance of each species in each connected numbered transect (see Table 1 for a description of the transects). Since the order of the nodes are optimized to minimize edge crossings, empty sites at the moment of sampling appear in the right without edges. Bird species are coloured according to their IUCN Red List categories (see Table 2). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

of transects had no birds during spring and summer, thus desiccation of abandoned saltpans during the drier seasons is diminishing both breeding habitat and waterbirds abundance and richness. In winter, there were less empty saltpans and higher species richness, suggesting that rain can facilitate the seasonal change of desiccated abandoned saltpans into available feeding habitats for wintering bird populations. Indeed, a higher mean abundance in abandoned saltpans was only found during winter, while over the whole year mean abundance and richness was twice higher in active saltpans. Abundance in active saltpans could probably have been even higher, at least in the migrations and winter, if samplings had been done only at high tide, when other foraging grounds such as the intertidal is flooded. In accordance with the present results, previous studies have demonstrated that active saltpans were preferred over inactive by waterbirds in the Portuguese saltpans of the Mondego (Múrias et al., 2002) and the Guadiana estuary (Dias, 2009). In the Ria Formosa, the abandonment also affects the type and degree of

Table 3
Partitions of beta diversity on all the possible pairs between the networks of the four seasons. Beta diversity was measured in two ways: by types of saltpans (active vs. Abandoned) and considering all sites pooled. β_S: dissimilarity in species composition. β_{OS}: the dissimilarity component explained by the interactions among shared species. β_{WN}: the dissimilarity between the two networks. β_{ST}: the dissimilarity component explained by difference in species community composition.

	By types of saltpans				All sites pooled			
Consecutive seasons	β_S	β_{WN}	β_{OS}	β_{ST}	β_S	β_{WN}	β_{OS}	β_{ST}
Spring 2015 - Summer 2015	0.45	0.74	0.73	0.01	0.72	0.92	0.71	0.21
Summer 2015 - Autumn 2015	0.42	0.69	0.62	0.07	0.65	0.92	0.82	0.09
Autumn 2015 - Winter 2016	0.62	0.74	0.63	0.1	0.74	0.91	0.76	0.15
Mean	0.5	0.72	0.66	0.06	0.7	0.92	0.76	0.15
Non-consecutive seasons								
Spring 2015 - Winter 2016	0.56	0.76	0.65	0.11	0.75	0.87	0.65	0.22
Spring 2015 - Autumn 2015	0.6	0.81	0.74	0.07	0.81	0.93	0.64	0.28
Summer 2015 -Winter 2016	0.47	0.77	0.55	0.22	0.7	0.92	0.69	0.22
Mean	0.54	0.78	0.65	0.13	0.75	0.91	0.66	0.24

vegetation cover on the dykes separating the saltpans, and some of the abandoned saltpans are covered by dense mats of the invasive *Carpobrotus edulis* (Chefaoui and Chozas, 2019). Once this change in vegetation cover happens, roosting habitat available for ground-nesting waterbirds such as *Charadrius alexandrinus* and *Himantopus himantopus* might be irreversibly reduced.

4.3. Habitat specialization of waterbirds

Around 60% of the waterbirds analysed indicated a high specificity towards active saltpans at least in one season. The season with the highest number of active specialists was autumn, with 8 waterbird species (Fig. 4). The reason can be that desiccation is still affecting abandoned saltpans during this season, so the wintering birds that start arriving might gather in active saltpans suitable for feeding. Considering the year as a whole, *Arenaria interpres* was sighted in all seasons and showed a high affinity towards active saltpans over the entire year, even though this species is known to prefer tidal flats and to use saltpans only as supplementary feeding grounds (Dias, 2009; Lei et al., 2018).

Among the species found to be specialists of active saltpans in this analysis, 4 species are considered resident (*Charadrius alexandrinus, Egretta garzetta, Phoenicopterus roseus* and *Tadorna tadorna*), and 2 are breeding (*Sternula albifrons* and *Tringa totanus*) in the Ria Formosa (BirdLife International, 2020b; Table 2). The importance of active saltpans as breeding habitats, in addition to its use for foraging, has been confirmed for several species such as *P. roseus* and *C. alexandrinus,* (Béchet et al., 2009; Tinarelli and Baccetti, 1989). *P. roseus* is wholly dependent on the presence of small crustaceans such as *Artemia salina,* only present in saltpans under certain levels of salinity (Cabral et al., 2005), so active saltpans are specially important during the incubation and chick rearing periods (Béchet et al., 2009).

Probably, higher levels of affinity could have been found both within seasons and over the entire year if sample replications could have been made at each season. Despite this, these results agree with previous studies that have demonstrated the relevance of active saltpans for the maintenance of waterbirds populations of *Limosa limosa*, *Charadrius alexandrinus*, *Himantopus himantopus* and *Recurvirostra avosetta* in the Iberian Peninsula (Catry et al., 2011; Dias, 2009; Masero, 2003; Múrias et al., 2002; Rufino et al., 1984), showing that active saltpans are used more by these species than abandoned ones.

With respect to the abandoned saltpans, only three species showed an exclusive specificity: the Northern Shoveler (*Anas clypeata*), the Common Teal (*Anas crecca*) and the Whimbrel (*Numenius phaeopus*) (Fig. 4). The two anatids (*A. clypeata* and *A. crecca*) were only observed in flooded abandoned saltpans during winter, but never in active saltpans. *N. phaeopus* was sighted infrequently as solitary individuals in flooded abandoned saltpans as well. Besides showing a strong affinity towards active saltpans in autumn, the Eurasian Spoonbill (*Platalea leucorodia*) also showed a high specificity towards abandoned saltpans during summer and winter. Similarly, the abandoned saltpans in which *P. leucorodia* was observed were exclusively saltpans flooded throughout the year, located in "Ilha de Tavira". A possible explanation for this affinity towards flooded abandoned saltpans could be that their salinity is lower than in the active ones (Chefaoui and Chozas, 2019), and the macrofauna of saltpans of lower salinity resembles that of intertidal mudflats and natural coastal lagoons, allowing birds to find suitable food such as polychaetes (Evagelopoulos et al., 2008; Velasquez, 1992).

4.4. Seasonal turnover

The role that saltpans management plays with respect to the temporal distribution of birds has an ecological interest in the present study. Thus, saltpans are used as nodes, and the term "edges turnover" is used instead of "interactions turnover" (β_{OS}) to account for the one-sidedness of the ecological relationship between the sets of nodes (birds and saltpans).

Overall inter-seasonal β-diversity of waterbird communities was high. There was a high seasonal dynamic, only 40% of waterbird species were observed in all seasons. Despite this temporal variation, dissimilarity between the whole networks (β_{WN}) was due to a greater extent to edges turnover between shared species (β_{OS}) than to species turnover. Thus, the dispersal of birds among the relatively close saltpans of the Ria Formosa seems to be playing an important role in network organization. These results are in agreement with ANOSIM analysis which showed that compositional dissimilarities between the types of saltpans and within types were practically equal in all seasons. Dispersal is known to affect network reorganization by ensuring a low interspecific variation, so networks retain similar structure and composition (Thompson and Gonzalez, 2017).

Overall seasonal network dissimilarity was consistently higher when considering all transects pooled in an undifferentiated way than when measured by type of saltpans management. Given that interactions of shared species (β_{OS}) is insensitive to changes in network size (Poisot et al., 2012a), this finding suggests that networks structure is driven partially by the management of saltpans, as many birds showed specificity towards active saltpans for breeding and feeding.

Migration phenology was better reflected when non-consecutive seasons were compared as edges turnover and β-diversity of species composition were greatest. In the case of consecutive seasons, the highest dissimilarity in species composition (β_S) was found in the transition from autumn to winter, coinciding with the time of arrival of wintering birds. Phenology is considered a relevant key predictor of interaction network properties (CaraDonna et al., 2017).

4.5. Conservation implications

This research has demonstrated that the abandonment of saltpans reduces abundance and richness of waterbird populations and affects their seasonal dynamics. Besides, around 60% of the waterbird species showed breeding and feeding specificity towards active saltpans. Ria Formosa is important for numerous waterbirds as a breeding and wintering ground, holding more than 20,000 species on a regular basis (BirdLife International, 2020a). Some species found abundantly in Ria Formosa's saltpans during this survey are, however, red listed species regarded as under threat in the rest of the Iberian Peninsula (Fig. 3 and Table 2). Thus, threatened Iberian waterbird populations could

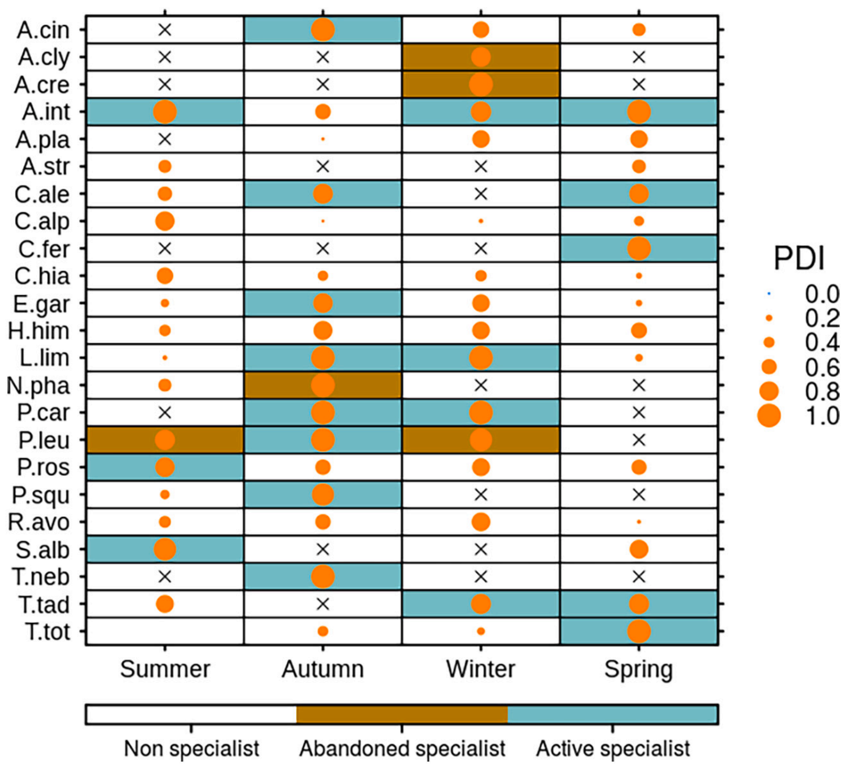

Fig. 4. Paired Difference Index (PDI) analysis to distinguish specialist from generalist waterbirds on the two types of saltpans. Dot size indicates the magnitude of PDI, a PDI value of zero indicates a generalist species, while values of 1 indicate that the species is specialist. Background colours (blue and brown) indicate a high specialization (PDI ≥ 0.8) towards active and abandoned saltpans, respectively. Crosses represent species not found in that season. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

experience, to some extent, a "rescue effect" from these populations, as suggested for *Charadrius alexandrinus* (Figuerola et al., 2004).

This work contributes to our understanding of the importance of maintaining saltpans for the benefit of waterbird populations. In sum, the possible factors explaining the different network structure found in abandoned saltpans in the Ria Formosa are: i) the desiccation of the saltpans during the dry season (Chefaoui and Chozas, 2019; Costa et al., 1996); ii) the degradation of the dykes separating the saltpans, which are often invaded by *Carpobrotus edulis* (Chefaoui and Chozas, 2019); and iii) drop in salinity that can affect the macrofauna that serves as food for birds (Cabral et al., 2005; Chefaoui and Chozas, 2019; Evagelopoulos et al., 2008; Velasquez, 1992). These conditions can be further aggravated for birds if abandonment entails a drastic change in land use (e.g. urbanization, industrialization) as happened in Greece (Crisman et al., 2009).

Since Ria Formosa's saltpans were built on saltmarshes instead of intertidal areas (Batty, 1992), it is evident that saltpans favoured the availability of feeding areas for waterbirds. But saltpans are human-made wetlands that periodically are transformed or abandoned. Southern Europe saltpans have been disappearing since the twentieth century (Crisman, 1999) and more than 90% of Portuguese saltpans ceased their activity in the last six decades (Neves, 2005; Rodrigues et al., 2011). Given that natural coastal wetlands are being degraded, saltpans created centuries ago are vital for the conservation of resident and migratory waterbirds. Such is the case of many wetland-dependent species analysed here: *Calidris ferruginea, Charadrius alexandrinus, Limosa limosa, Numenius phaeopus, Phoenicopterus roseus, Recurvirostra avosetta, Sternula albifrons* and *Tringa totanus*. For these waterbirds, the abandonment of saltpans and their transformation into marine aquaculture is considered a major threat (Cabral et al., 2005; Madroño et al., 2004). Besides, Southern Europe saltpans are used as stopover sites by many migratory waterbirds analysed in this study, such as the Flamingo (*Phoenicopterus roseus*) and the Pied Avocet (*Recurvirostra avosetta*), the latter having its main Portuguese breeding population in the Ria Formosa (Cabral et al., 2005).

The findings of this study will be of interest to assess the role of Ria Formosa as a key site of the East Atlantic flyway. The analysis of ecological networks undertaken here has proven useful in understanding the relationship between bird communities and land-use management, and provides a methodology that is applicable to any species. Visualising networks, a valuable tool for investigating ecosystem alterations, can also be useful to engage with decision-makers (Pocock et al., 2016). Future research considering a larger temporal scale to compare results across years and more stopovers along flyways should be undertaken to investigate further the migratory phenology of birds through ecological networks.

The restoration of abandoned saltpans would be desirable in the Natural Park of Ria Formosa, where cultivation of salt is a sustainable economic activity that is beginning to diversify into new products (e.g. "flor de sal"). It has been suggested that restored saltpans could also be used for the cultivation of *Artemia* sp., an euryhaline crustacean that, besides feeding birds, can favour salt production and be used in aquaculture (Vieira and Bio, 2011). Rehabilitated saltpans provide ecotourism opportunities based on salt museums and centres for nature interpretation (Crisman et al., 2009; Rodrigues et al., 2011), so birdwatching could also be a profitable ecotourism activity. Moreover, a number of ecosystem services provided by saltpans have been identified throughout the world. Apart from maintaining biodiversity, cultural values and provisioning salt, salpans have been related to the supply of oxygen and medicinal resources, and the regulation of pests and water quality (de Melo Soares et al., 2018). Thus, continued efforts are needed to reduce threats that affect coastal wetlands and restore abandoned saltpans worldwide.

Declaration of Competing Interest

None.

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Research data

R script to reproduce the analysis is available at https://github.com/Chefaoui/Chefaoui_2021

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoinf.2021.101364.

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