



How the diversity of constructed wetlands improves the plankton communities discharged into a protected Mediterranean wetland

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Abstract The effectiveness of constructed wetlands (CWs) created to improve water quality has been demonstrated. However, their role in enhancing biodiversity, such as in plankton communities, is still understudied. To assess this, we analysed, over two years, the plankton of three structurally different CWs which are intermediaries between low-quality waters and a protected Mediterranean wetland (*Albufera de València* Natural Park). We estimated the alpha-diversity of each CW and the beta-diversity among their different sectors. In two CWs, the diversity decreased

as water flowed from the Inlet (a species mix from anthropically disturbed environments) to the Outlet, due to natural assembly processes. In the other CW, as it received water dominated by a few species, the emerging assemblages increased the diversity. Moreover, comparing the three CWs, the most divergent communities were those in the outlets (due to the emergence of exclusive species, biovolume differences, etc.). Therefore, they contributed to beta-diversity as they acted as generators of communities, which were characterized by the loss of cyanobacteria and chlorophytes, the dominance of large copepods or cladocerans and the presence of unshared species. We emphasize the importance of having structurally and functionally different CWs to enhance biodiversity and improve biological water quality in natural parks.

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Introduction

Wetlands are vulnerable ecosystems that, despite offering numerous environmental services, have been systematically degraded (due to drying up, being used as wastewater drains, etc.), as stressed by Verhoeven (2014). Therefore, artificial or constructed wetlands (hereafter CWs) have been created worldwide (Scholz & Lee, 2007; Moshiri, 2020) to halt the degradation

of natural wetlands. The CWs ecological engineering is an established option for water management with numerous effective applications that have been proven around the world providing several environmental and economic advantages (Vymazal, 2011; Stefanakis, 2019). Moreover, their green infrastructure provides important ecosystem services (e.g. promoting biodiversity, improving water quality, contributing to flooding protection, etc.). Two of these services are considered crucial: the maintenance and enhancement of biological diversity (Zhang et al., 2020) and the improvement in the quality of the received water through the removal of suspended material, microalgae (mainly those potentially toxic), nutrients and hazardous substances (Rodrigo et al., 2013a, 2022; Land et al., 2016; Jamion et al., 2022). This is of special relevance when the CWs are acting as intermediaries between low-quality waters and protected wetlands, the latter being the receptor system (Kadlec & Wallace, 2008).

Changes in species richness, as well as other community features, based on species composition and distribution (i.e. ecological and functional diversity, evenness, beta-diversity), have been tied to ecosystem functioning and are, therefore, likely to influence the services they provide (Balvanera et al., 2014). In this vein, the use of diversity indices on the plankton community (which mostly dominates in inland aquatic systems; Suthers et al., 2009) can contribute to the knowledge of the functioning of CWs, as well as bring about further management strategies, since good environmental management must ensure, or even enhance, the diversity of organisms and their functions (Ghosh & Biswas, 2015). In CWs, this can be achieved when the water in the outlets is of better biological quality than that in the inlets, thus, providing the receptor system with the biodiversity generated within the CWs. Biological water quality improves within a CW if the plankton composition changes towards a higher diversity of roles (Declerck et al., 1997; Rojo et al., 2010), which allows a more efficient transference of energy and matter, and a higher stability in the food web leading to an improvement in ecosystem services (Puche et al., 2021).

There are only few studies on the diversity of plankton communities in CWs (Luyiga & Kiwanuka, 2003; Chen et al., 2011; Li et al., 2014; Castro-Castellon et al., 2016) and even fewer regarding the changes between their inlets and outlets (Rodrigo & Segura,

2020). It has been shown that the changes in plankton diversity are not the same in all seasons (Kagalou et al., 2010; Travaini-Lima et al., 2016; Latinopoulos et al., 2020) nor in all the CWs (Calero et al., 2015). Moreover, if different parts or sectors have been built within the CWs to simulate different habitats, those changes are also not the same (Calero et al., 2015). It has been observed that, in some cases, plankton diversity increases (Hu et al., 2012) and in others, it hardly varies (Calero et al., 2015; Travaini-Lima et al., 2016). These facts highlight the need for further research to elaborate a review of the plankton in CWs, which resemble natural wetlands, and to enhance the ability of these systems to provide ecosystem services through the transformation of plankton communities. In our study, we examined three structurally different Mediterranean CWs (i.e. heavily modified waterbodies) created between 2009 and 2011 within the European Water Framework Directive (2000/60/CE) of the European Community water policy (European Commission Directive 2000/60/CE) to improve the water quality which, after flowing through these CWs, is released into one of the largest Mediterranean coastal lagoons, the hypertrophic *Albufera de València* (AV) lagoon which is a relevant component of the homonymous Natural Park (Hernández-Crespo et al., 2017).

The transition from a highly anthropically disturbed lotic environment (water inlet channels) to a more lentic wetland environment (within the CWs) with no anthropic alterations, and most likely with vegetation, will favour the change from a plankton community, which is a miscellany originated in the agricultural fields, sewage treatment plants and irrigation channels (Vera-Herrera et al., 2022), towards a community where selective predation, competition and rapid growth allow the development of certain species and dominant roles (Calero et al., 2015; Travaini-Lima et al., 2016; Rodrigo et al., 2018). We already know that the composition of the planktonic communities in the inlets and outlets in these CWs is different (Rodrigo & Segura, 2020), but this composition could also be different between the different sites inside each CW, as occurs in natural wetlands (Rojo et al., 2012). Thereby, we hypothesize that alpha-diversity in the plankton communities will decrease as the community is modified within the CW. We also hypothesize that the beta-diversity of the area, measured as the dissimilarity of communities, will increase due to the spatial heterogeneity found within

each CW and between neighbouring CWs, providing the Natural Park with greater planktonic biodiversity, which is one of the environmental services expected from the CWs.

Within the framework of a “science-based governance” LIFE12 ENV/ES/000685 Project, chemical and biological water quality in the three above-mentioned CWs was monitored for 2 years (2014–2015). Hernández-Crespo et al. (2017) proved that the three CWs are capable of reducing abiotic material but showed clear differences in their performance due to their different design and features. More recently, Rodrigo and Segura (2020) reported how the phytoplankton biomass was reduced in the outlets and the zooplankton biomass was increased within the CWs. Completing this panorama, this study aims, by means of diversity indices, to analyse how these CWs influence the diversity of their planktonic communities, and, therefore, the diversity of the wetland complex.

Materials and methods

Description of the CWs

The three studied CWs, *Tancat de la Pipa* (TP hereafter; 39°22'04"N; 0°20'46"W), *Tancat de Mília* (TM hereafter; 39°18'40"N; 0°21'21"W) and *Tancat de L'Illa* (TLI hereafter; 39°16'42"N; 0°17'20"W) are located within the *Albufera de València* Natural Park (Valencia, Spain; Fig. 1). This Mediterranean Coastal Park (Hernández-Crespo et al., 2017) is a Ramsar and Natura 2000 site (Council Directive, 92/43/EEC; Directive, 2009/147/EC; MITECO, 2021) and hosts one of the largest Mediterranean coastal lagoons, the hypertrophic *Albufera de València* (AV) lagoon, which has long suffered from high urban, agricultural and industrial pressure. The three CWs were created in 2009 (TP) and 2011 (TM and TLI) in the framework of the European Community water policy (European Commission, 2000) to improve the water quality of the AV lagoon.

The CWs were former rice fields transformed via ecological engineering into heavily modified Mediterranean waterbodies, with the aim of improving the quality of the water entering the lagoon and providing habitats for wildlife. In TP, the water in the Inlet is a mixture of recirculated water from the AV lagoon and water collected from different agricultural

and urban discharges (Fig. 1). In the same way, TLI also receives water from the AV lagoon mixed with water from a small lagoon (*Estany de la Plana*), formed in the past from one of the connections of the AV lagoon to the Mediterranean Sea (Fig. 1). Water mixing at the inlets depends on the water level of the AV lagoon, which varies mainly due to agricultural demands for rice cultivation by flow management through the opening and closing of floodgates (Soria, 2006). However, in TM the input water comes exclusively from the southern part of the AV lagoon by recirculation via a pump (Fig. 1). The waters from the three CWs are finally released into the AV lagoon or into the *Estany de la Plana*, which is connected to the AV lagoon. The hydraulic retention time during the study period was between 2.3 and 9.3 days in TP, 1.9–7.1 days in TM and 14.6–23.3 days in TLI (Hernández-Crespo et al., 2017).

The three CWs are divided into different sectors. TLI and TM have an initial sector of horizontal subsurface flow; however, the sector in TLI is much smaller than the one in TM, which was planted with *Phragmites australis* (Cav.) Trin. ex Steud., 1840 (Fig. 1). TP lacks this sector. The second ones are free-water surface flow sectors (divided into sub-sectors) planted with emergent vegetation: in TP, a mixed community (*P. australis*, *Typha angustifolia* L., *Sparganium erectum* L. and *Iris pseudacorus* L.) was planted, and TM and TLI were mainly planted with *T. angustifolia* (Hernández-Crespo et al., 2017; Rodrigo & Segura, 2020). The CWs also have a shallow pond located at the end of the systems, mostly without vegetation (in TM this had some inner areas with emergent vegetation).

Sampling and plankton analyses

Water samples were collected seasonally from January 2014 to December 2015: each year, one sampling took place in winter (January), three in spring (March, April and May), one in summer (July) and another one in autumn (October) in the context of a LIFE project (LIFE12 ENV/ES/000685). In each CW, four sampling sites were chosen (Fig. 1): the Inlet, two inner sites (Site-2, Site-3) and the Outlet. Both phytoplankton and zooplankton samples were taken with a handmade sampler from the shore at a depth of approximately 25 cm. We included in our “plankton” analyses all the species found in the samples collected

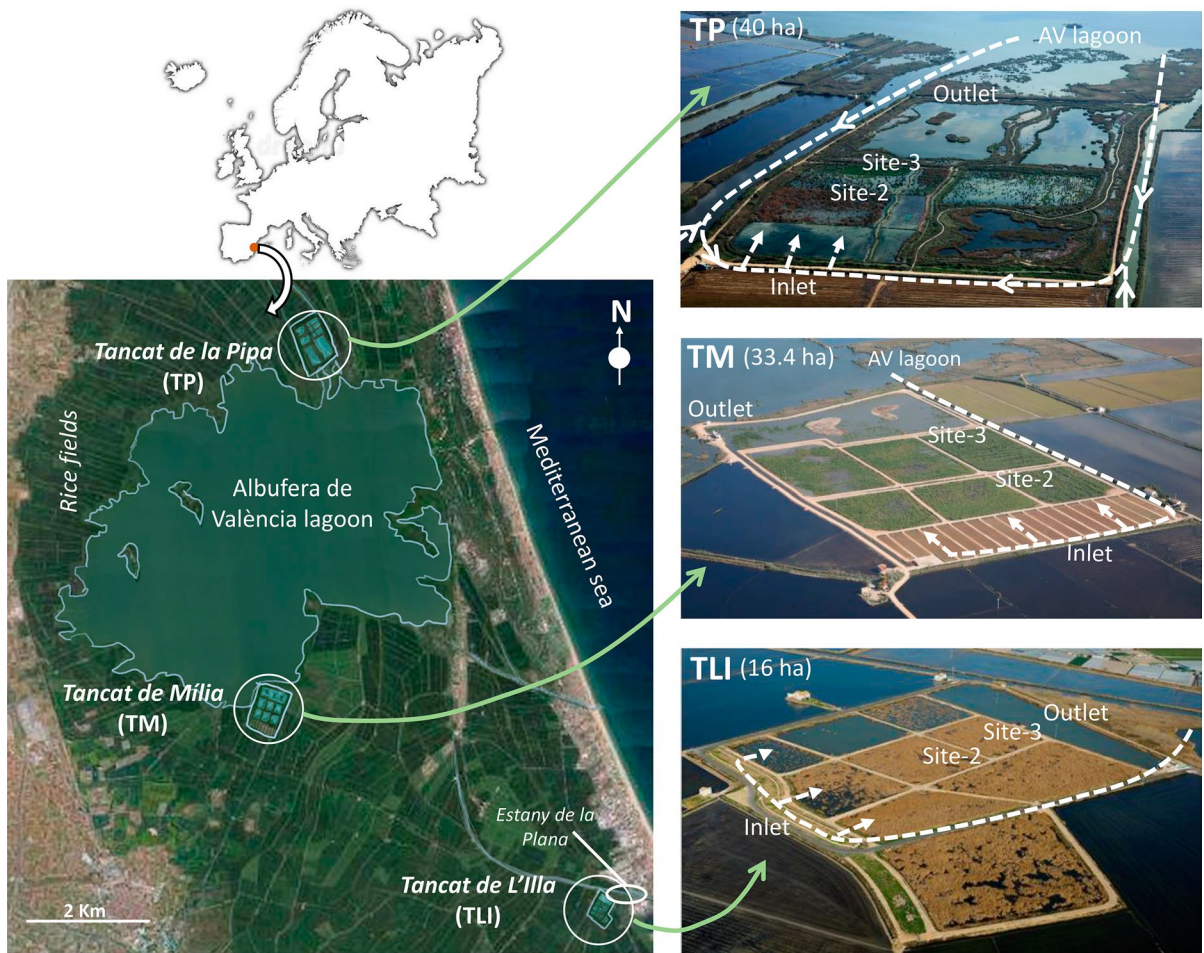


Fig. 1 Location of the Albufera de València Natural Park, Albufera de València lagoon (AV lagoon), the three constructed wetlands (Tancat de la Pipa –TP-, Tancat de Milia –TM- and Tancat de L'illa –TLI-) and the Estany de la Plana.

The four sampling stations for each CW (Inlet, Site-2, Site-3 and Outlet) and the main water flow direction are also indicated

from the water column, including the benthic organisms (which were also present in these kinds of samples since the wetland is a shallow system with vegetation) because they are a relevant part of the aquatic network (Puche et al., 2021).

Phytoplankton samples (250 ml) were fixed with lugol and counted in Utermöhl chambers with an inverted microscope (Olympus CK2) at 400 magnifications to obtain the density. At least 400 individuals of the most abundant population were counted, implying a 10% error (Lund et al., 1958). Each species was taxonomically identified to the lowest possible taxonomic level by a qualified researcher. Algal biovolume (μm^3) was calculated with cell densities and cell

volume, measuring sizes from at least 20 individuals, and following Rott (1981) and Hillebrand et al. (1999). Water samples for metazooplankton (approximately 3 l) were filtered through 45 μm Nyltal mesh and preserved with a formalin solution (4%, final concentration). Density (ind l^{-1}) was calculated by counting with an inverted microscope (Olympus CK2) at 100 magnifications (Suthers et al., 2009; Rodrigo & Segura, 2020). Taxonomic determination and biomass ($\mu\text{gDW l}^{-1}$) were obtained following the methods described in Rojo et al. (2012); the manuals used for the identification were those of Dussart (1967, 1969), Koste (1978), Segers (1995), Einsle (1996), Orlova-Bienkowskaja (2001) and Nogrady and Segers

(2002). For biomass determination, at least 20 individuals of each species were measured. Rotifer and ostracod biovolumes were calculated assimilating body shapes to geometrical bodies. Biovolume was converted to biomass, assuming a body density of 1 g cm^{-3} . Crustacean biomass was obtained with length-dry weight regressions and a 1/10 proportion for dry/wet weight. The cumulative mass production was expressed in carbon units using the conversion $1 \text{ gDW}=0.4 \text{ g C}$ for Rotifera, Cladocera and Copepoda (Reiss & Schmid-Araya, 2008).

Diversity indicators and statistical analyses

The alpha-diversity indicators, or community diversity indicators used were: (i) specific richness (S), (ii) the Shannon index (H), (iii) effective number of species (EN) and (iv) evenness (EV). The H index was selected as the diversity index because it is sensitive to less frequent species (Shannon & Wiener, 1949), and it was calculated in natural logarithms based on biovolume (phytoplankton) and biomass (zooplankton). EN was calculated as the exponential of the Shannon index (e^H) following MacArthur (1965), Hill (1973) and Jost (2006); this indicator allows an accurate comparison between values of different samples and the calculation of their average, which would not be possible using H (Jost, 2006). The EV ($e^{H/S}$), being richness constant, covaries with H, expressing if the abundance distribution is in a more or less equitable manner (Hill, 1973). The Pearson correlation between diversity indicators was also calculated to highlight the percentage of variance of H due to S or EV. These correlations were calculated by compiling the values of all the sampling sites and all the dates in each CW.

To gain insights into the dynamics of heterogeneity fostered by the CWs, we calculated the beta-diversity comparing, pairwise, the sampling sites both within and between the CWs to evaluate: (i) whether it was at the Inlet, in the inner sectors (Site-2 and Site-3) or at the Outlet of the CWs where there was a greater difference in community composition; (ii) the transformational effectiveness of each CW and (iii) the likely divergence in the trajectory of community transformation from the Inlet to the Outlet. To assess this, we calculated the number of shared and exclusive species, the Bray–Curtis dissimilarity index (abundance data; Bray & Curtis, 1957) and Sørensen dissimilarity index (presence/absence data; Sørensen,

1948). Furthermore, the overall beta-diversity was calculated based on the composition of the four sampling sites of each CW on each sampling date. This beta-diversity was obtained with the Harrison index (Harrison et al., 1992; Koleff et al., 2003) according to the following equation:

$$\text{Harrison index} = \frac{\left(\frac{S}{\alpha}\right) - 1}{[N - 1]}$$

where S is the total number of species, α is the average number of species and N is the number of samples. The Harrison index takes the number of compared assemblages into account, resulting in a useful measure of spatial heterogeneity (Jost, 2007).

Comparisons of means between alpha-diversity and beta-diversity indicators were carried out with one-way ANOVA tests after checking the normality (Shapiro–Wilk test) and homoscedasticity (Levene test) with the subsequent post hoc analyses (Tukey’s pairwise comparisons). When both conditions were not verified, non-parametric tests were used (Kruskal–Wallis or Mann–Whitney test). These statistical analyses were performed using the statistical package IBM SPSS 19.0 and PAST version 4.08 (Hammer et al., 2001), considering statistically significant differences at a probability $P < 0.05$. Venn diagrams with the number of exclusive and shared species were obtained with the *VennDiagram* package (Chen, 2013) and then plotted with the *venn.diagram* function. Heat-maps were done using a Bray–Curtis dissimilarity matrix with the *vegan* package (Oksanen et al., 2018) and plotted with the *heatmap* function. Both the Venn diagrams and the heat-maps were performed with the free software R, version 4.1.3 (R Development Core Team, 2018).

Biological water quality assessment

The metrics from the European Water Framework Directive (2000/60/CE) to estimate water quality based on plankton, were specially designed for lakes and reservoirs. The studied CWs are shallow systems, hence these metrics cannot be applied. In this context, and following Willén (2000), we have used the phytoplankton biovolume to evaluate how the trophic state and ecological status changed as the water flowed through the CWs. Phytoplankton biovolume can be used as an indicator to assess water quality since their

rapid response to environmental condition changes, their primary role in the food web and their impact on other organisms (Willén, 2001); therefore, they properly reflect the effectiveness of the CWs. Apart from this, we calculated the rotifer/cladoceran richness ratio for each site to discover the changes throughout the CWs. Rotifer and cladoceran richness are influenced by clear water/turbid state in shallow wetlands (Cottenie & Meester, 2003), nutrients (Jeppesen et al., 2000) and primary productivity (Dodson et al., 2000). Therefore, we used this ratio as an indirect way to assess biological water quality.

Results

Alpha-diversity indicators in each CW and comparison

Taking into account the three CWs, during the two years of monitoring, the total identified phytoplankton and zooplankton taxa were 219 and 93, respectively (Online Resource Table S1). For phytoplankton, chlorophytes were the group with the highest number of species (39–54 taxa; Table S1), followed by cyanobacteria (20–28 taxa; Table S1). For zooplankton, the rotifer group was the one that contributed most to the richness in the three CWs (36–53 taxa; Table S1). The number of cladoceran species ranged between 10

and 17, which is substantially higher than the number of copepod species (2 taxa) and ostracods (1 taxa).

Regarding TP and TLI phytoplankton assemblages, the S, EV and EN and their means, were lower in the outlets than in the inlets (Table 1, S2; Fig. 2). Sometimes the main change occurred in the first sector of the CWs, after the water flowed through Site-2 and Site-3, whereas on other dates the main changes occurred within the pond towards the end of the CWs. However, TM acted the opposite way, showing an increase in the alpha-diversity values from the Inlet to the Outlet (Fig. 2). Despite this observable trend in the means, significant differences ($P < 0.05$) between sites were sporadic (Table S3). Regarding zooplankton assemblages, the diversity, when differences were significant, followed a pattern similar to that of phytoplankton (Fig. 2; Table S3).

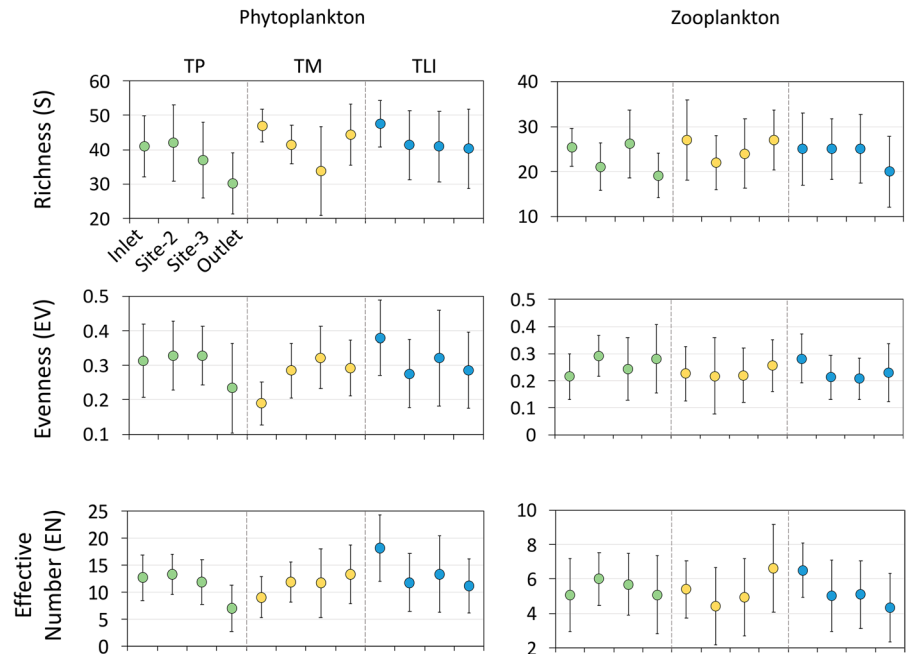
There were significant correlations for the phytoplankton in the three CWs, between H and S (0.61–0.67) and H and EV (0.70–0.84). For zooplankton, the correlation between H and S was significant only in TLI (0.44) and also between H and EV in the three CWs (0.54–0.75); for both phytoplankton and zooplankton EV was more correlated to H than to S in all CWs (Table S4). Although there were similarities between the dynamics of the mean of the phytoplankton and zooplankton diversity indicators (Fig. 2), when phytoplankton data were correlated against zooplankton data for each CW, the correlation

Table 1 Minimum and maximum values for each alpha-diversity indicator (S: richness, H: Shannon diversity index, EV: evenness, EN: effective number of species) for phytoplankton and zooplankton assemblages

Assemblages were from the different sampling sites (Inlet, Site-2, Site-3 and Outlet) of the three constructed wetlands (TP: *Tancat de la Pipa*, TM: *Tancat de Mília* and TLI: *Tancat de L'illa*) during the monitoring period (2014–2015)

	Phytoplankton				Zooplankton			
	S	H	EV	EN	S	H	EV	EN
TP								
Inlet	24–56	1.9–2.9	0.2–0.6	6.7–18.9	20–34	0.7–2.1	0.1–0.4	2.0–8.2
Site-2	27–58	2.0–3.0	0.2–0.5	7.4–20.7	12–29	1.4–2.3	0.2–0.4	4.1–10.0
Site-3	17–52	1.6–2.9	0.2–0.5	5.0–17.9	9–34	0.6–2.2	0.1–0.5	1.7–8.6
Outlet	17–46	0.6–2.8	0.1–0.5	1.9–16.4	10–25	0.6–2.2	0.1–0.5	1.8–9.0
TM								
Inlet	39–55	1.5–2.9	0.1–0.3	4.7–17.6	20–46	0.8–2.1	0.1–0.4	2.2–8.2
Site-2	34–52	1.8–2.8	0.1–0.4	6.0–16.5	12–32	0.2–2.2	0.1–0.5	1.2–9.0
Site-3	14–58	0.9–3.0	0.2–0.4	2.6–20.7	10–37	1.1–2.2	0.1–0.4	3.0–9.0
Outlet	32–60	1.8–3.1	0.1–0.4	6.1–21.4	19–38	0.5–2.3	0.1–0.4	1.6–10.0
TLI								
Inlet	39–61	2.3–3.4	0.2–0.6	10.2–30.8	14–40	1.5–2.3	0.2–0.4	4.5–10.0
Site-2	26–56	1.2–3.0	0.1–0.4	3.2–19.5	12–34	0.8–2.3	0.1–0.3	2.3–10.0
Site-3	26–62	1.4–3.4	0.2–0.6	4.1–28.5	13–38	0.9–2.2	0.1–0.4	2.6–9.0
Outlet	15–57	1.5–2.9	0.2–0.4	4.6–18.7	7–35	0.4–2.1	0.1–0.4	1.5–8.2

Fig. 2 Mean values and standard deviations of the alpha-diversity indicators for phytoplankton and zooplankton assemblages at the different sampling sites within each constructed wetland (TP: *Tancat de la Pipa*, TM: *Tancat de Mília* and TLI: *Tancat de L'illa*). Note that: (i) the Y-axis scales of phytoplankton figures are not always the same as those of zooplankton and (ii) H is not represented, because H must not be mathematically averaged. The X-axis legend is only indicated in the upper-left graph, it is the same in the rest



was not significant for any of the alpha-diversity indicators in TP and TM, or low correlation was found in TLI (Table S4).

Beta-diversity within and between the CWs

Comparing sectors of the same CW, between 13 and 25% (depending on the CW) of the phytoplankton species were only found in one sector (Fig. 3). These algae species were mainly chlorophytes (around 50%) followed by diatoms and cyanobacteria. However, the highest percentage of zooplankton taxa found only in one sector (mainly rotifers), did not exceed 12% (Fig. 3). Comparing the three outlets, 33% and 22% of the phytoplankton and zooplankton taxa, respectively, were only found in one of the outlets. Focusing on the inner sites of the CWs (Site-2 and Site-3), 25% of phytoplankton taxa and 14% of zooplankton taxa were exclusively found there (Table S5). More specifically, 9%, 12% and 16% of the total phytoplankton richness and 5%, 4% and 11% of total zooplankton richness were found exclusively within TP, TM and TLI, respectively; only one of these taxa, the benthic rotifer *Mytilina mucronata* (Müller, 1773), was shared by the three CWs (Table S5).

A high heterogeneity (dissimilarity) was observed between the Inlet community and those generated within the CW (Fig. 4, S6; Table S7); these

dissimilarities followed different patterns of community changes inside the CWs (Fig. 4): in TP the greatest change occurred in the Outlet; in TM it was at the beginning when the water passes from the Inlet to the first CW sector (i.e. the horizontal subsurface flow sector); in TLI, for phytoplankton, the main change occurred after the Inlet, and for zooplankton, it was in the first inner site (Site-2; Fig. 4). Comparing the CWs, the most different phytoplankton assemblage was the one entering TM (Inlet). However, for zooplankton, TP showed greater differences compared to the two other CWs and also the inner sites of TM (Site-2 and Site-3; Fig. 4). The correlation between the Bray–Curtis and Sørensen dissimilarities indices showed that the phytoplankton and zooplankton changes between the sectors of TP were mainly due to a species substitution (Fig. S6). However, in comparisons between the sites of TM and TLI, the differences mainly occurred due to a change in the biovolume of the species and, in the case of zooplankton also by a species substitution, but in a lower proportion (Fig. S6).

Taking into account the assemblages from the same sectors of the three CWs (Harrison index) for each date at the same time and also as an average of the whole study period, the beta-diversity for the three outlets was higher most of the time compared to the beta-diversity for the three inlets (Fig. 5).

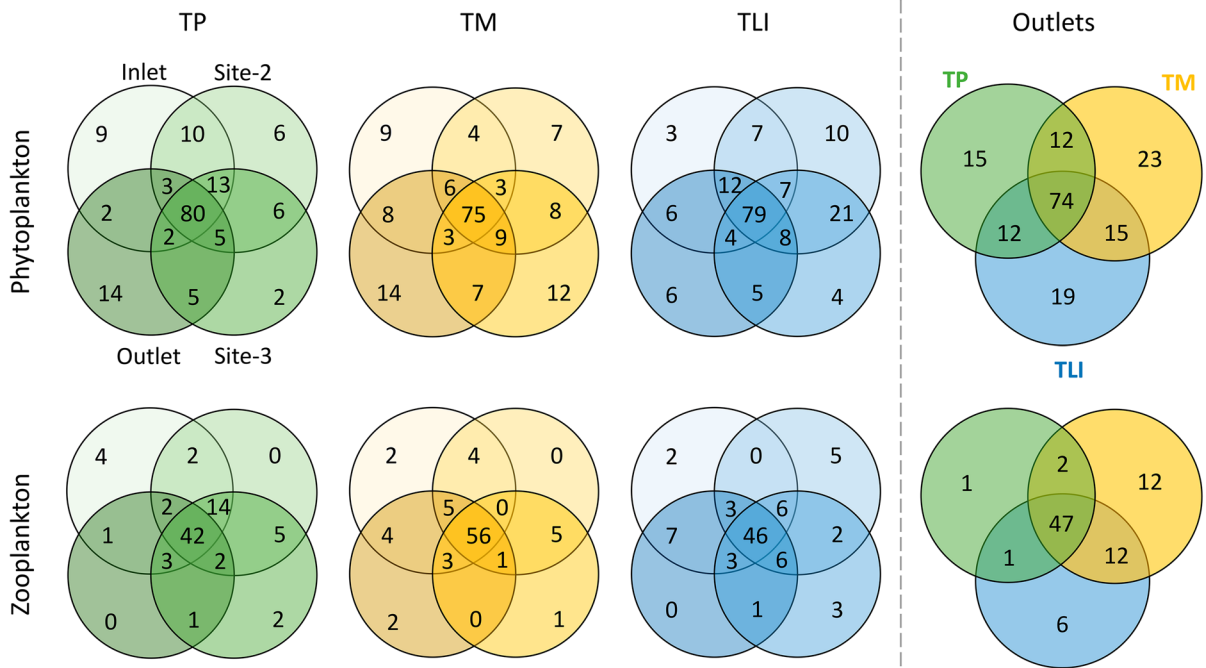


Fig. 3 Venn diagram illustrating the number of exclusive and shared species between sites of each constructed wetland (TP: *Tançat de la Pipa*, TM: *Tançat de Mília* and TLI: *Tançat de L'illa*) and between the three outlets (right part of the figure)

for phytoplankton and zooplankton assemblages. The sites for each constructed wetland are only shown in the first diagram, as they are the same for the others

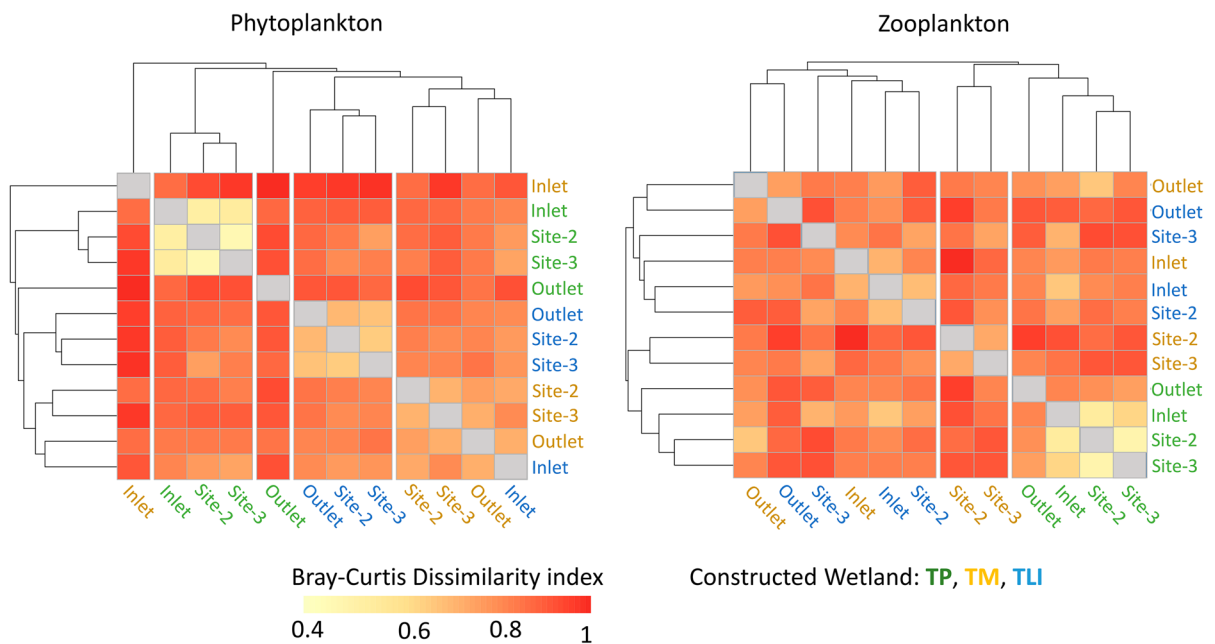
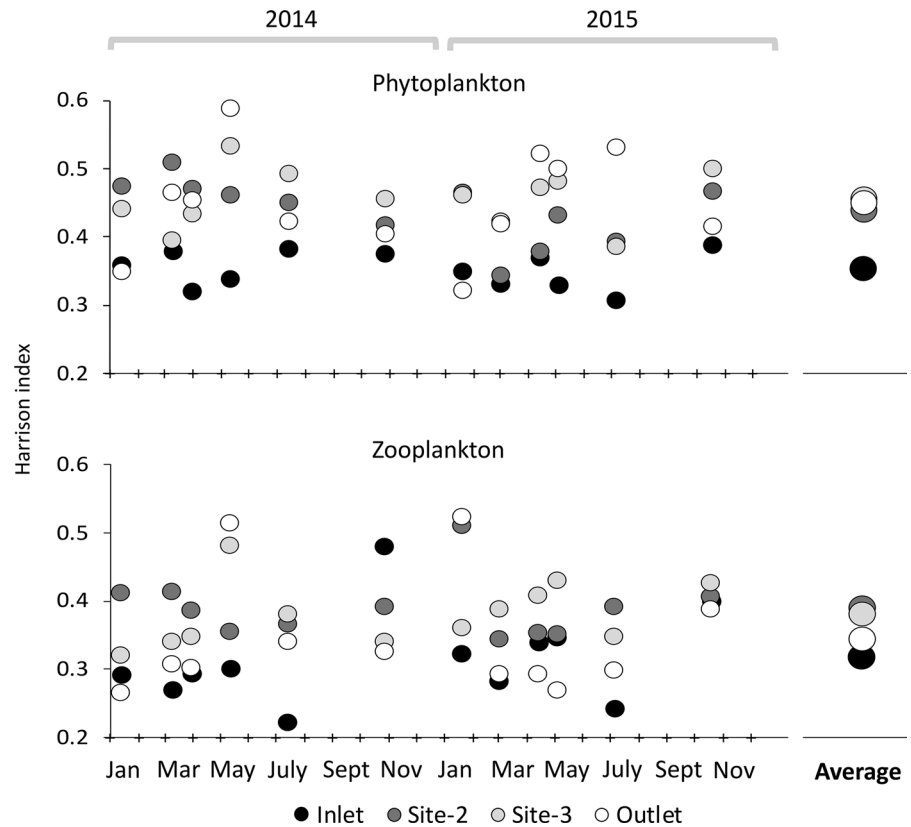


Fig. 4 Heat map showing Bray–Curtis dissimilarities of phytoplankton (left) and zooplankton (right) assemblages between sites (Inlet, Site-2, Site-3 and Outlet) and constructed wetlands (TP: *Tançat de la Pipa*, TM: *Tançat de Mília* and TLI: *Tançat de L'illa*)

Fig. 5 Beta-diversity (Harrison index) comparing assemblages from the same sector of the three constructed wetlands for each date. The average for the Harrison index during the whole period is also indicated (right part of the graph)



Changes in the communities' composition

The H values changed due to the variations in specific richness (S) and/or evenness (EV). Several genera of potentially toxic cyanobacteria were detected in the three CW (e.g. *Aphanocapsa* Nägeli, 1849, *Pseudanabaena* Lauterborn, 1915 and *Planktolyngbya* Anagnostidis & Komárek, 1988), but their biovolume in the inlets ranged between 0.01 to 3.68 mm³ l⁻¹ and, exceptionally, 7.6 mm³ l⁻¹ in TM, whereas in the outlets the range was much lower (0.009 to 0.24 mm³ l⁻¹; Fig. 6; Table S1). The obtained trophic state indicated a maintenance or an improvement between the Inlet and the Outlet in 67%, 100% and 58% of the cases for TP, TM and TLI, respectively (Table S8). In TP and TM, there were three sampling dates in which the Outlet was oligotrophic water, and only one date in TLI. Considering the three CWs, the rotifer/cladoceran richness ratio decreased in 72% of the sampling moments from the inlets to the outlets (Fig. 6; Table S1).

Specifically, in the phytoplankton of TP there was a loss of some chlorophytes and an emergence

of dominant species (more than 50% of the biovolume) of the genera *Ochromonas* and *Chroomonas*. Regarding zooplankton, the Outlet of TP was characterized by the dominant taxa *Brachionus plicatilis* Müller, 1786 and a cyclopoid copepod (the latter together with *Daphnia magna* Straus, 1820 or the ostracod *Cypridopsis vidua* (O.F. Muller, 1776) (Fig. 6; Table S1). In TM, the Inlet was completely dominated by the cyanobacterial genus *Pseudanabaena*, but the abundance of this dominant taxa was already reduced from the Inlet to inner sites. However, the presence of different diatoms, cryptophytes and euglenophytes increased in the other sectors. In the same way, there was a decrease in the biomass of the cyclopoid copepod [*Acanthocyclops americanus* (Marsh, 1893)] followed by an increase in cladocerans (Fig. 6; Table S1). In TLI, some cyanobacterial species completely disappeared as the water flowed through the CW, such as *Synechocystis aquatilis* Sauvageau 1892., *Leptolyngbya* sp. or *Aphanocapsa* spp. There were two potential mixotrophs (an undetermined Chlorococcal and *Cryptomonas marssonii* Skuja 1948) which, in the Outlet, made up more than

Water flow		Inlet	Inner sites	Outlet
TP	Phytoplankton	<u>Cyanobacteria</u> : <i>Anabaenopsis</i> , <i>Aphanizomenon</i> , <i>Aphanocapsa</i> , <i>Raphidiopsis raciborskii</i> , <i>Planktothrix</i> , <i>Microcystis</i> , <i>Planktolyngbya</i> , <i>Pseudanabaena</i> , <i>Synechocystis aquatilis</i> <u>Chlorophyta</u> : <i>Chlamydomonas</i> , <i>Tetrademus</i> , <i>Scenedesmus</i> , <i>Desmodesmus</i>	<u>Diatoms</u> : <i>Chaetoceros muelleri</i> , <i>Gyrosigma macrum</i> , <i>Gomphonema</i> , <i>Naviculales</i> , <i>Skeletonema subsalsum</i> <u>Euglenophyta</u> : <i>Phacus</i>	<u>Diatoms</u> : <i>Naviculales</i> , <i>C. muelleri</i> , <i>S. subsalsum</i> <u>Chrysophyta</u> : <i>Ochromonas</i> <u>Cryptophyta</u> : <i>Chroomonas</i> <u>Mixotrophs</u> small flagellates
	Zoopl.	<u>Copepoda</u> : cyclopoid	<u>Rotifera</u> : <i>Colurella</i> sp., <i>Lecane hastata</i> <u>Cladocera</u>	<u>Rotifera</u> : <i>Brachionus plicatilis</i> <u>Cladocera</u> : <i>Daphnia magna</i> <u>Ostracoda</u> : <i>Cypridopsis vidua</i>
TM	P	<u>Cyanobacteria</u> : same as TP	<u>Diatoms</u> : <i>Naviculales</i> , <i>C. muelleri</i> , <i>G. macrum</i> , <i>S. subsalsum</i> <u>Euglenophyta</u> : <i>Phacus</i>	<u>Diatom</u> : <i>C. muelleri</i> , <i>Cyclotella</i> , <i>Fragilaria</i> , <i>Haslea spicula</i> , <i>Naviculales</i> , <i>S. subsalsum</i> <u>Cryptophyta</u> : <i>Cryptomonas</i> , <i>Plagioselmis</i> <u>Euglenophyta</u> : <i>Euglena</i> , <i>Lepocinclis</i>
	Z	<u>Copepoda</u> : cyclopoid	<u>Rotifera</u> : <i>Lecane pyriformis</i> <u>Cladocera</u>	<u>Ostracoda</u> : <i>C. vidua</i> <u>Cladocera</u> : <i>Ceriodaphnia</i> , <i>Daphnia</i>
TLI	P	<u>Cyanobacteria</u> : same as TP	<u>Diatoms</u> : <i>Bacillaria paxillifera</i> , <i>Mastogloia smithii</i> , <i>Rhopalodia gibba</i> , <i>Naviculales</i> , <i>C. muelleri</i> , <i>S. subsalsum</i> <u>Euglenophyta</u> : <i>Phacus</i>	<u>Diatoms</u> : <i>Naviculales</i> , <i>C. muelleri</i> , <i>S. subsalsum</i> <u>Cryptophyta</u> : <i>Cryptomonas marssonii</i> <u>Chlorophyta</u> : undetermined Chlorococcal
	Z	<u>Rotifera</u> <u>Copepoda</u> : cyclopoid	<u>Rotifera</u> : <i>Lecane aculeata</i> , <i>L. pyriformis</i> , <i>Lepadella acuminata</i> , <i>Lepadella rhomboides</i> , <i>Trichotria</i> sp. <u>Cladocera</u>	<u>Cladocera</u> : <i>D. magna</i> , <i>Acantholeberis curvirostris</i> <u>Ostracoda</u> : <i>Cypridopsis vidua</i> <u>Copepoda</u> : cyclopoid

Fig. 6 Summary table of the main taxa (P phytoplankton and Z zooplankton) in which there was a change in their biovolume/biomass as water flows through the different sites (Inlet,

Inner sites and Outlet) of the constructed wetlands (TP: *Tanquat de la Pipa*, TM: *Tanquat de Mília* and TLI: *Tanquat de L'Illa*)

50% of the total biovolume. Moreover, we found a less equitable distribution in the Outlet between zooplankton taxa; a cyclopoid copepod species, or a pair of cladoceran species [*Acantholeberis curvirostris* (O.F.Müller, 1776) and *D. magna*] made up more than 60% of the total biomass followed by a loss of rotifer species (Fig. 6; Table S1).

The taxa of diatoms exclusively found within the CWs (inner sites) were *Bacillaria paxillifera* (O.F. Müller) T.Marsson 1901, *Mastogloia smithii* Thwaites ex W.Smith 1856 and *Rhopalodia gibba* (Ehrenberg) O. Müller 1895 in TLI, *Gomphonema* spp. in TP and *Gyrosigma macrum* (W.Smith) J.W.Griffith & Henfrey 1856 in TM (Table S5). Other diatoms emerged within the CWs and continued to be present up to the Outlets (Fig. 6; Table S1). The increase in

euglenophyte species within these sites was notable. Moreover, several exclusive euglenophyte taxa could be found (Table S1). Regarding zooplankton, species mainly of the genera *Lecane* and *Lepadella* were only found in the inner sites.

Discussion

Our results make evident the role of CWs in the transformation of plankton communities. Alpha-diversity indicators give structural information on these plankton communities. The values attained in the studied CWs were similar to those found in Mediterranean natural wetlands with very different morphology and abiotic conditions, such as the AV lagoon and its

small surroundings waterbodies (Alfonso & Miracle, 1990; Anton-Pardo et al., 2013), the *La Safor* wetland (Rodrigo et al., 2003) or the *El Hondo* wetland (Rodrigo et al., 2001), as well as in the *Las Tablas de Daimiel* National Park in central Spain (Rojo et al., 2000). In TP and TLI the allochthonous plankton from a mixture of water arriving in these CWs (Vera-Herrera et al., 2022) had higher diversity than the plankton communities of natural Mediterranean wetlands. This lower diversity at the Outlets would be the result of interspecies interactions such as predation and competition, which might enhance the emergence of dominant species (Quintana et al., 2006). However, in TM, as it receives water only from the AV lagoon, which has a historical dominance of few cyanobacterial species (Romo & Miracle, 1993; Romo et al., 2013), the abundance of such dominant species was already reduced from the first sector. This allowed the presence of different algae genera and consequently, diversity (in terms of EV) in the water after passing through the CW was higher. Moreover, the reduction of cyanobacterial species could be observed, not only in TM but also in the other two CWs, some of them being toxic (Chorus & Bartram, 1999), resulting in an improvement in biological water quality.

These changes in the diversity of plankton as the water flowed through the structurally different CWs, produced a divergence between the three plankton communities that entered (which were more similar) and the three ones that were finally released into the AV lagoon (which were more different), being a source of beta-diversity to the Natural Park. In the CWs, some exclusive species were found in the different sites. As was expected by the relationship species/area, in TP and TM (the larger CWs in comparison to TLI) this proportion in phytoplankton was higher.

These differences, in TP, were due to a loss of cosmopolitan chlorophyte species and the emergence of species considered mixotrophs, feeding on bacteria and small cyanobacteria (Kugrens & Lee, 1990; Zhang et al., 2021). It is worth noting that TP was built 2 years earlier than the other CWs and this may mean that between its sectors the change in species composition is more pronounced because the different ecological processes that influence this are more consolidated. Regarding TLI, it is remarkable that the Outlet was also dominated by potential mixotrophs. The role of the horizontal subsurface flow sector of TM in the reduction of

phytoplankton biomass (Hernández-Crespo et al., 2017) has to be highlighted here. The water entering the intermediate sectors, after being filtered by the subsurface flow sector, was less enriched in phosphorus (Hernández-Crespo et al., 2017); this phosphorus reduction is related to the beneficial changes in the algal assemblage (i.e. better distribution of different algal groups; Villena & Romo, 2003). With respect to zooplankton, rotifers were the most represented group as expected, due to body size considerations (García-Chicote et al., 2018). The genera found, such as *Brachionus*, *Keratella* and *Polyarthra*, are indicators of eutrophic conditions (García-Chicote et al., 2018). However, after the water flowed through the CWs, there was a loss in rotifer species. The decrease in rotifer richness and the increase in cladoceran richness is another sign of an improvement in the trophic structure related to water quality. Cladocerans, being herbivores, are efficient at causing clear water phases due to their capacity to constrain microalgae. They also have a strong community structuring power, due to their selective grazing on some types of algae (Lampert, 1974; DeMott, 1981). On the other hand, rotifers are highly specialized suspension-feeders, feeding mainly on picoplankton and nanoplankton and not efficiently controlling algal biomass (Gosselain et al., 1998; Korosi et al., 2011). Apart from that, the higher representation of Cladocera over Copepoda in the Outlets in comparison to the inlets also indicated better water conditions, since the former are more sensitive to changes in specific habitat features such as transparency, conductivity and temperature (Jeppensen et al., 2011; Galir-Balkić & Ternje, 2018). The new composition of phytoplankton species inside the CWs appeared to result in a high biomass of cladocerans and the coexistence of several species (the main five species accounted for 2–50 μg dry weight l^{-1} in the outlets), in the same site and at the same time, despite the high competition that exists within this group. The low representation of copepods is usual in continental waterbodies (García-Chicote et al., 2019) and our Mediterranean, heavily modified, CWs can be considered as part of this group of waterbodies. Within this group, cyclopoid copepods are more frequent in eutrophic conditions than the larger calanoids, as the latter consume larger algal cells (Pinto-Coeelho et al., 2005). However, the cyclopoid copepod

species identified in the studied CWs [*A. americanus* (Marsh, 1893)] is an invasive species that displaces the native ones due to its fast growth and its omnivorous diet (Alekseev et al., 2021; Sarma et al., 2019). The naupliar stages of this species feed on phytoplankton and the adults exert effective predation even on other cyclopoid species. In TM and TLI, the replacement from a dominant cyclopoid to a greater distribution of biomass among cladocerans allowed the presence of different species of cladocerans at the Outlet of each CW. The development of ostracods, mainly of benthic features (Schmit et al., 2007), was clearly related to the existence of a high density of emergent vegetation found in the inner sites (Rodrigo et al., 2013a; Hernández-Crespo et al., 2017). This group have experienced an important loss of biodiversity in western Mediterranean wetlands (due to eutrophication and pollution; Poquet et al., 2008; Valls et al., 2016); thus, their development in the studied CWs represents a positive contribution of these systems to the biodiversity of the Natural Park.

In addition, the efficiency of the CWs in improving, most of the time, the trophic state of the outlets in comparison to the inlets should be highlighted. The structural characteristics of the CWs could be causing the differences in these efficiencies. TM has the largest sector of horizontal subsurface flow, and it was highly efficient because of the total dark conditions and the interception mechanism inside the substrate (Hernández-Crespo et al., 2017). These differences regarding the presence, or not, of a subsurface sector and its size might be causing the greatest differences between the inner sites in TM and those in the other two CWs. Moreover, the presence of reeds (*P. australis*) along this sector in TM, and their allelopathic effect on *Microcystis aeruginosa* (Kützing) Kützing 1846 (Chicalote-Castillo et al., 2017) might be related to the sharp decrease observed in this species after water flowed through the CW (up to 20 times lower biovolume in the Outlet than in the Inlet). Related to this, macrophytes in CWs also have a strong influence on the structure and dynamics of the plankton community, since their coverage is a major factor strongly modifying light conditions (Travaini-Lima et al., 2016). The TM and TLI inner sites, which were planted with *T. angustifolia*, and its impact on zooplankton community structure (Gebrehiwot et al., 2017), favoured the shared species between these two

CWs inner sites. Outlet sites were poorly vegetated, and the resuspension by wind, fish and aquatic avifauna could cause an increase of benthic species on the water column (Rodrigo et al., 2013b).

Special attention should be given to changes in the community in the inner sites of the CWs. The diatoms that emerged within them, and also the ones that continued to be present in the outlets, were mainly benthic, favoured by the presence of vegetation, and some of them related to brackish waters. This latter fact is in accordance with the conductivity rise experienced when the water passed through the different sectors of the CWs due to the high evapotranspiration, which increased 1.5-fold, on average, from the inlets to the outlets (Martín et al., 2013; Hernández-Crespo et al., 2017; Stefanidou et al., 2020). These mainly benthic taxa can migrate in the water column (Round & Eaton, 1966) and are related to mixotrophic feeding (Jones, 2000). In this way, their presence and biomass represent a considerable energy input to the plankton communities from the microbial food web (Calero et al., 2015), acting as a bypass of carbon flux toward the autotrophic food web (Medina-Sánchez et al., 2004; Puche et al., 2021). Unfortunately, we could not study ciliates and flagellates, which are also very important in the microbial loop and functioning in aquatic ecosystems (Gilbert et al., 1998). The presence of tico- and meroplankton species (mainly rotifers and diatoms) in the inner sectors of the CWs, is in accordance with the results of Puche et al. (2021) regarding the relevance of the benthic taxa and the mediation of the submerged vegetation in shallow aquatic ecosystems.

The CWs were able to internally generate their own communities, which did not share part of their composition with the others, resulting in a high spatial heterogeneity. This capacity produced, firstly, differences between sectors within each CWs and, secondly, differences between the CWs. Thus, the CWs promoted divergence in the trajectories of their assemblages (Drake et al., 1999; Rojo, 2021) and consequently, the communities of phytoplankton and zooplankton discharged to the AV lagoon is more diverse than if the water from the inlets had arrived directly into the lagoon without passing through the CWs. The heterogeneity in the composition of plankton within and between the CWs contributed to the beta-diversity, improving, in this way, the global biodiversity in the wetland region, as was observed in

other Mediterranean protected areas (e.g. in *Las Tablas de Daimiel*, Rojo et al., 2012). Hence, these CWs are fulfilling one of the expected ecosystem services: to provide biodiversity of aquatic organisms to the landscape (Zhang et al., 2021).

Final remarks and conclusions

Our results showed how alpha-diversity indicator values can decrease as water flows through the CWs (in TP and TLI); they may not change (but species change) or may even decrease (due to the loss of a miscellaneous mix reaching the wetland). Thus, to evaluate the effectiveness of CWs as water quality improvers in terms of planktonic composition, alpha-diversity indicators on their own do not seem to be the best choice. The information provided by these indices must be completed with a deeper ecological knowledge of the communities.

One of the most relevant questions to understand how CWs could improve water quality is to know whether they contribute to beta-diversity, generating new planktonic communities. Within each CW there is a set of basic ecological processes and relationships, but they are not exactly the same. This is influenced by the different structural features of the three CWs: their size, depth, hydraulic retention time, the composition and coverage of emergent vegetation (which have a great effect on plankton removal, Rodrigo et al., 2018; different allelopathic effects), trophic state, etc. All these different configurations, i.e. the diversity of constructed wetlands, have important positive effects on the planktonic diversity of the Natural Park. These CWs favoured species in phytoplankton and zooplankton assemblages which are related to better biological water quality; for instance, it is important to highlight the lack of development of potentially toxic cyanobacteria which were found in the inlet waters. Furthermore, inside the CWs, vegetation and the proximity of the sediment contributed, along with benthic biota, to the community found in the water column. This combination allows a very effective plankton-benthos network to be established in which benthic organisms play a central role in spreading the effects of disturbances to the community (Puche et al., 2021).

In conclusion, we have seen how CWs with different features have been beneficial to the

environment by improving the plankton communities. This is an ecosystem service that has to be appraised (Dumax & Rozan, 2021) in the process of expressing ecosystem goods and services. We recommend the construction of different structural and functional CWs within this Natural Park in the future, and in others with similar features, with the aim of improving aquatic diversity, and thus, ensuring ecosystem services.

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Author contributions NC, EP and CR statistically analysed, interpreted the data and wrote the manuscript, MAR designed the study and undertook the samplings, MS calculated abundance of populations, MAR and MS also contributed to the discussion of the manuscript.

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Data availability All data generated or analysed during this study are included in this published article and its supplementary information files.

Declarations

Conflict of interest The authors declare that they have neither conflict nor competing interests.

Ethical approval All authors have read, understood and have complied as applicable with the statement on “Ethical responsibilities of Authors” as found in the Instructions for Authors and are aware that with minor exceptions, no changes can be made to authorship once the paper is submitted.

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