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Mosaic of submerged habitats in the Venice lagoon shows signs of marinization

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A B S T R A C T

The relationships between habitat patterns and ecosystem functioning have been widely explored in terrestrial ecosystems, but less in marine and coastal ecosystems, calling for further research in this direction. This work focuses on the mosaic of submerged habitats in the Venice lagoon, Italy. It aims to describe the habitats' spatial patterns at multiple spatial scales, and to explore their linkages with the ecological status defined according to the EU Water Framework Directive (WFD, 2000/60/EC). The submerged habitats' mosaic has been analysed by calculating a set of seascape metrics at different spatial scales. These metrics have been linked with the biological quality elements (BQEs) that are monitored in the lagoon in compliance to the WFD. The results show that the habitats' spatial patterns differ between the areas of the lagoon with marine-like features and the areas which still retain more lagoon characteristics. The similarity between the pattern found in the whole lagoon and those found in marine-like areas suggests a general loss of lagoon characteristics at the lagoon scale. Regarding the ecological status, every BQE seems to be associated with a different habitat configuration at the water body scale. This does not facilitate the joint improvement of the BQEs, as required by the Directive. If we cannot achieve that, at some point we will probably have to choose what to prioritize. On a broader perspective, this calls for a reflection on what lagoon we want for the future, a vision that should be shared and account for the lagoon's complexity, current trends and challenges.

1. Introduction

The study of the relationships between habitats' spatial patterns and ecological functioning in terrestrial ecosystems has been the focus of landscape ecology for about half a century. The application of this analytical framework to coastal and marine ecosystems, known as seascape ecology, is however a relatively recent field, whose stage of development is comparable to that of landscape ecology back in the 1980s (Pittman et al., 2011). A seascape can be understood as a marine or coastal area containing a mosaic of patches, a spatial gradient, or other kinds of geometric patterning (Boström et al., 2011). One of the major criticalities concerning the application of landscape ecology to marine and coastal environment has been the clear identification of habitats boundaries and their mapping. Current advances in marine remote sensing technologies are progressively facilitating this task, especially in intertidal and shallow areas (Pittman et al., 2011; Wedding et al., 2011; Bell and Furman, 2017), with the result that most applications are focused on intertidal/benthic habitat types mainly located in coastal areas, such as salt marshes, seagrasses, coral reefs and macroalgae (Wedding et al., 2011; James et al., 2021; Santos et al., 2022), with only very recent studies going beyond this limit (Swanborn et al., 2022b, a). Although the appropriateness of the transposition of terrestrial methodologies to aquatic ecosystems is still debated (Manderson, 2016; Bell and Furman, 2017), the analysis of seascape structure mostly relies on the use of metrics designed for terrestrial ecosystems (Wedding et al., 2011), which are used to describe characteristics of the habitats mosaics. The way seascape structure is mapped and analysed depends on which of the following perspectives is adopted: (i) the patch-matrix model, based on island biogeography theory, which adopts a binary perspective that considers focal habitat patches embedded in a background matrix (e.g. seagrasses patches surrounded by unvegetated sand) (Wedding et al., 2011; Boström et al., 2011); (ii) the patch-mosaic model, which goes beyond this binary structure and represents the seascape as an heterogeneous assemblage of different patch types, in which the functioning of the whole mosaic is influenced by its composition (abundance and variety of patch types) and spatial configuration (geometric

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structure) (Wedding et al., 2011; Boström et al., 2011). Although this second perspective is intrinsic in the concept of landscape/seascape itself, the majority of the studies in coastal systems adopts a binary patch-matrix approach (focal versus non-focal habitats), and links seascape structures to faunal communities relative to a single patch type only (Boström et al., 2011). Therefore, the adoption of a broader and more systemic perspective is still an open frontier in marine and coastal applications.

The Venice lagoon (Italy) represents an interesting case study for a seascape ecology application. It is a complex social-ecological system in which the co-evolution between ecosystem and society has profoundly influenced both the lagoon morphology and the human lifestyle for centuries (Ravera, 2000; Solidoro et al., 2010). It currently faces several management challenges, among which the implementation of the EU Water Framework Directive 2000/60/EC (WFD) (European Commission, 2000). In this context, the shift from the monitoring to the implementation phase, that is, managing the ecosystem in order to achieve a good ecological status, is still an open issue.

Seascape ecology is a largely unexplored field in the Venice lagoon ecosystem. Only two studies of seascape ecology were carried out in the lagoon so far, one highlighting the influence of seagrass habitat structure on fish assemblages, at the local scale (Scapin et al., 2018), and another showing the influence of seascape structure on the target species of local fisheries (Scapin et al., 2022). This suggests that seascape structure could play an important role for the ecological functioning of the Venice lagoon, calling for further studies in this direction and rising the question if seascape ecology could contribute by bringing new perspectives within the context of the management strategies' implementation.

Taking up this challenge, this work addresses the whole mosaic of submerged habitats of the Venice lagoon from a seascape ecology perspective. The aim is to describe the spatial patterns of the Venice lagoon submerged habitats, and to explore the linkages between these patterns and the ecological status defined in compliance to the WFD. In particular, the specific objectives are: (i) to analyse the spatial patterns of the lagoon's submerged habitats by applying a set of seascape metrics; (ii) to analyse the scale effect, by comparing the results obtained at different spatial extents (whole lagoon scale, lagoon basins' scale and water bodies' scale, i.e. the spatial units identified within in the context of the WFD); (iii) to assess the possible relationships between spatial patterns and the biological quality elements (BQEs), at the water bodies' scale.

2. Materials and methods

2.1. The venice lagoon study area

The Venice lagoon is a shallow coastal lagoon in the northern Adriatic coast. It has a surface area of 550 km^2, and a watershed of about 1800 km^2. The lagoon is protected from the action of the sea by sandbars: Cavallino, Lido and Pellestrina, which are interrupted by three inlets named, from north to south, Lido, Malamocco and Chioggia. The lagoon morphology reflects a sea–land gradient of submerged and intertidal habitats (subtidal flats, intertidal mudflats, salt marshes), interrupted by channels and many islands constantly emerged (Solidoro et al., 2010). The characteristics of the lagoon's habitats are mainly related to gradients of water residence time and salinity, which are driven by the water exchanges between the lagoon and the sea, and by the freshwater inputs from the watershed.

The centuries-old interactions between humans and the lagoon have resulted in profound ecological and morphological modifications of the ecosystem. In particular, interventions such as the diversion of rivers, the construction of jetties at the inlets, the dredging of navigable channels and, in very recent times, the commercial dredging for clams, have led to the progressive deepening of the lagoon and the flattening of its morphology, with a loss of more than 50% of salt marshes' surface in the past century (Pranovi et al., 2004; Sarretta et al., 2010).

2.2. Habitats mapping

Four main types of submerged habitats were identified, considering their potential influence on the structure and functioning of the whole community (Anelli Monti et al., 2021):

(1) tidal flats dominated by seagrass beds, mainly composed by *Zostera marina*, *Cymodocea nodos*a and other species. Seagrass beds host peculiar fish assemblages (Franco et al., 2006a) and provide relevant ecosystem services, such as carbon sequestration and attenuation of erosion (Rova et al., 2015, 2019, 2022). This habitat was mapped using the extension of seagrasses from the 2010 monitoring of the former Venice Water Authority (Magistrato alle Acque) (Comune di Venezia et al., 2018), considering all seagrass species together.

(2) mudflats surrounding the salt marshes, corresponding to the submerged areas that are found in proximity to salt marshes. The presence of salt marshes strongly influences the characteristics of these habitats, which function as nursery areas for several marine migrant fish species (Franco et al., 2006b). This habitat was mapped taking into consideration a 500 m buffer around salt marshes areas, this buffer being considered representative of the area within which mudflat habitat is influenced by nearby salt marshes. The map of natural saltmarsh from the 2013 monitoring of the former Venice Water Authority (Magistrato alle Acque) (Comune di Venezia et al., 2018) was adopted.

(3) tidal flats colonized by the Manila clam *Ruditapes philippinarum*, corresponding mainly to bare and flat sediment bottom where this species is potentially abundant. Both the presence of this invasive species, introduced in the lagoon in 1983, and the harvesting activities that exploit it, have important effects on the functioning of the ecosystem, especially concerning the structure of the benthic community and the benthic-pelagic coupling (Pranovi et al., 2003, 2004, 2006). This habitat was mapped according to the spatial distribution of the potential yield of this species, as modelled by Vincenzi et al. (2011).

(4) tidal flats covered by macroalgae, mainly *Ulvaceae* and *Gracilariaceae*. This habitat was defined as a functional cover for those areas that were not covered by any of the other habitats, and includes also deeper areas, such as the navigable channels, where human pressures related to maritime traffic are particularly high.

Mapping were performed at a spatial resolution of 250 m, using the free software QGIS. The resulting habitat mapping is shown in Fig. 1A.

2.3. Scales of analysis

In order to evaluate how the characteristics of habitats' spatial pattern change across different scales, the study area was analysed according to three spatial extents: whole lagoon, basins (Solidoro et al., 2004) and water bodies (ARPAV, 2016) (Fig. 1B).

The whole lagoon scale gives information at the ecosystem level, and it includes all the submerged areas of the lagoon.

The basin scale divides the lagoon into four basins identified according to the main circulation patterns (Solidoro et al., 2004): the Southern basin, driven mainly by the water flowing through Chioggia inlet, the Central basin, driven mainly by water from the Malamocco inlet, and the Northern basin, driven mainly by flows from the Lido inlet, further subdivided into Far-Northern and Northern-Central, reflecting the bifurcation of the Lido inlet into a channel to the north (Treporti channel), and one to the south (S. Nicolò channel) (Fig. 1B).

The water body scale corresponds to the spatial units defined in compliance with the WFD (Autorità di bacino dell'Adige et al., 2010), and thus reflects the spatial scale at which management actions should be defined and implemented. Within the context of the WFD, the

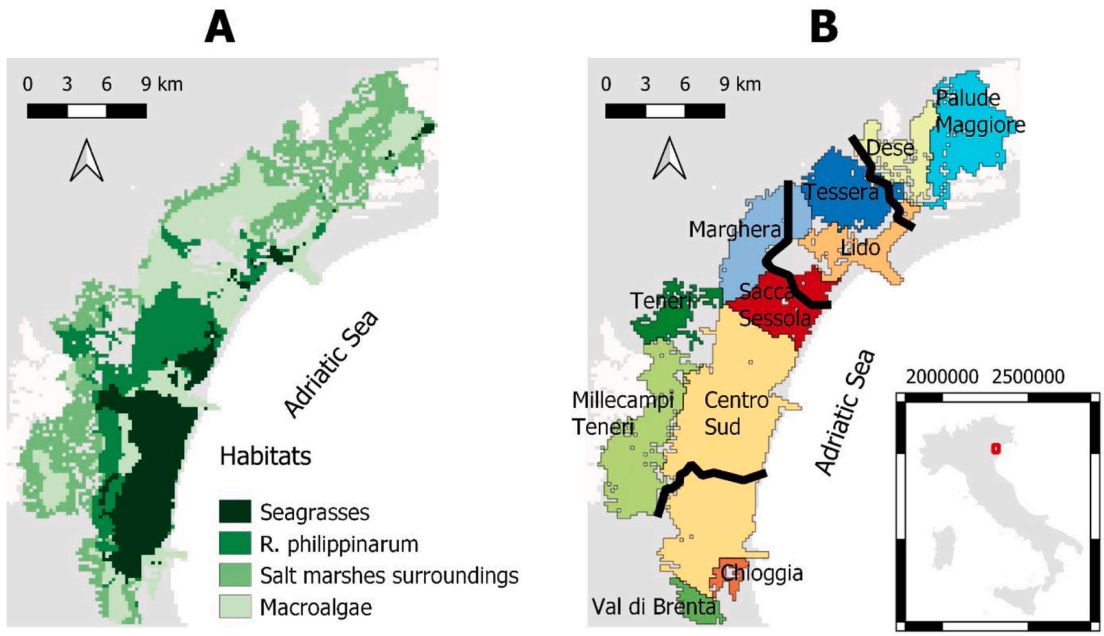

Fig. 1. (A) Spatial distribution of submerged habitats in the Venice lagoon: tidal flats dominated by seagrasses beds ("seagrasses"), tidal flats colonized by the clam *Ruditapes philippinarum* ("*R. philippinarum*"), mudflats surrounding the salt marshes ("salt marshes surroundings"), and tidal flats covered by macroalgae ("macroalgae"); (B) partition of the Venice lagoon into four basins (delimited by bold black lines, from north to south: Far-Northern, Northern-Central, Central, Southern, from Solidoro et al., 2004) and into 11 water bodies defined in compliance with the EU Water Framework Directive 2000/60/EC.

identification of the water bodies inside the lagoon reflects two main characteristics, degree of confinement (confined/unconfined) and salinity (euhaline/polyhaline, within the range 30–40 psu and 20–30 psu, respectively). These attributes, along with existing pressures, resulted in a partition into 14 water bodies. Three of them are "heavily modified water bodies", and were not considered in this study because left out from the ecological status reports. Therefore, we take into consideration a total of 11 water bodies: Palude Maggiore (Euhaline Confined), Centro Sud, Chioggia, Lido, Sacca Sessola (Euhaline Unconfined), Dese, Millecampi Teneri, Teneri, Val di Brenta (Polyhaline Confined), Marghera and Tessera (Polyhalilne Unconfined) (Fig. 1B).

2.4. Biological quality elements

According to the WFD, the ecological status assessment of the EU water bodies is defined through a set of biological quality elements (BQEs), by applying the "one out-all out" scheme (Voulvoulis et al., 2017).

In the case of the Venice lagoon, the ecological status depends upon the BQEs macrophytes (macroalgae and phanerogams) and benthic macroinvertebrates (ISPRA-ARPAV, 2021). Two additional BQEs, ichthyofauna and phytoplankton, are also monitored to provide supporting information. For the scope of this work, the data concerning the individual BQEs in the water bodies were retrieved from the monitoring implemented in the Venice lagoon in compliance with the WFD, for the period 2013–2015 (ISPRA-ARPAV, 2016). This period was chosen because of its good time alignment with the data used for habitat mapping. The numerical data of the indexes used to assess the individual BQE (all ranging between 0 and 1) were used in the analysis. Macrophytes are assessed through the MaQI index (Macrophyte Quality Index, Sfriso et al., 2009), which is a specific index proposed for the evaluation of the transitional environments in the Mediterranean eco-region and it is based on the composition of macrophyte assemblages (Sfriso et al., 2009). According to this BQE, the water bodies Palude Maggiore, Lido and Centro Sud are in good status, all the others being in moderate or poor status (ISPRA-ARPAV, 2016). Benthic macroinvertebrates are assessed through the M-AMBI index (Multivariate-AZTI Marine Biotic Index, Muxika et al., 2007). M-AMBI is a multivariate index based on the benthic community, which integrates the Shannon-Weiner diversity index and the number of species with the AMBI score (Borja et al., 2000), and requires a previous classification of reference conditions (Muxika et al., 2007; Borja et al., 2009). According to this BQE, only the water body Val di Brenta is in good status, all the other being in moderate or poor status (ISPRA-ARPAV, 2016). Therefore, none of the water bodies achieves an overall good ecological status, according to the "one out-all out" scheme required by the Directive (ISPRA-ARPAV, 2016). The additional BQE ichthyofauna is assessed through the HFBI index (Habitat Fish Bioindicator Index), which is specific for the fish fauna of lagoon environments and combines the total biomass density, the number of resident lagoon species, the average individual biomass of benthivores species, and Margalef's species richness of different feeding guilds (ISPRA-ARPAV, 2016). Unfortunately, the overall assessment of phytoplankton status (Multimetric Phytoplankton Index, Facca et al., 2014) is not available for this monitoring period (ISPRA-ARPAV, 2016) and thus this BQE was not included in this work.

2.5. Calculation of seascape metrics and statistical analysis

The spatial patterns of the lagoon's submerged habitats have been analysed through a set of seascape ecology metrics, selected based on Scapin et al. (2018). The selected metrics, described in Table 1, have been calculated using the Fragstats software (McGarigal et al., 2012) for the three scales of analysis (lagoon, basins and water bodies). The metrics measure different aspects of the submerged habitats' spatial patterns, that are area and edge, diversity, interspersion (spatial intermixing of different patch types), shape and subdivision. In this analysis, each spatial unit at the three different spatial scales (the whole lagoon, the four basins, and the 11 water bodies) was considered as a separate seascape, and the metrics were computed at the "seascape level", that is, for the whole mosaic of habitats in the seascape itself, following the patch-mosaic approach. The metrics selected are not dependent on the overall size of the seascape, therefore allow the comparison of seascapes of different extents. Overall, this allowed to compare the habitats' spatial configuration both within the same spatial scale and across the three spatial scales.

The values assumed by the selected metrics in the whole lagoon, the four basins and the 11 water bodies, are visualized using star plots (Pebesma, 2022), which represent the values of all the selected metrics normalized on a 0-1 scale. The similarities among the spatial patterns were analysed through a hierarchical cluster analysis based on Euclidean distance (group average clustering method), after fourth root transformation of dataset.

The relationships between the habitat spatial patterns and the BQEs (as described by M-AMBI, MaQI and HFBI) have been explored using two approaches : (i) the analysis of the linear relationships between each seascape metric and each BQE, through the use of generalized linear models, and (ii) a principal component analysis (PCA) performed using all the selected seascape metrics, after fourth-root transformation, and the subsequent analysis of how the BQEs are correlated with the PCA axes (Spearman's rho). These two approaches allow to evaluate whether the ecological status can be linked with the individual seascape metrics or with a combination of them, respectively. To characterize the distribution of the water bodies in the PCA multidimensional space, we tested whether the principal components' (PCs) scores differ between confined and unconfined water bodies, and between euhaline and polyhaline ones (Student's t-test). Generalized linear models, PCA and t-tests were calculated in R statistical software (Hadley Wickham, 2016; R Core Team, 2022; Urbanek and Horner, 2022; Wickham et al., 2022; Robinson et al., 2023), focusing on the water bodies scale, that is the scale at which BQE data are available.

Table 1
Description of the seascape metrics used to characterize the spatial patterns of the Venice lagoon submerged habitats, selected after Scapin et al. (2018). Please refer to McGarigal (2015) for a full description of the metrics.

Aspect of landscape pattern measured	Metric	Abbreviation	Description
Area and edge	Largest patch index	LPI	Area of the largest patch in the landscape, expressed as percentage of the total landscape area.
Area and edge	Landscape shape index	LSI	A standardized measure of total edge that adjusts for the size of the landscape. It can be interpreted as a measure of the overall geometric complexity of the landscape. It is calculated as a perimeter-to-area ratio for the landscape as a whole, where the perimeter includes the entire landscape boundary and all edge segments within the landscape boundary.
Area and edge	Mean patch area as fraction of total area	AREA_MN/ Area	Average area of all patches, divided by the total landscape area.
Diversity	Shannon's diversity index	SHDI	Diversity of patch types in the landscape, expressed as the Shannon's index calculated based on the proportion of landscape occupied by each habitat type.
Diversity	Shannon's Evenness Index	SHEI	Evenness of patch types in the landscape, expressed as Pielou's index calculated based on the proportion of landscape occupied by each habitat type and on the total number of patches.
Diversity	Patch richness	PR	Number of habitat types in the landscape.
Interspersion	Patch cohesion index	COHESION	Patch cohesion index reflects the physical connectedness of the different habitat types.
Shape	Fractal index distribution	FRAC_MN	Mean fractal dimension index of the patches of the landscape. This index reflects the patches' shape complexity: it ranges between 1 for shapes with very simple perimeters, such as squares, and 2 for shapes with highly convoluted perimeters.
Subdivision	Patch density	PD	Number of patches divided by the total landscape area.

3. Results

3.1. Spatial patterns at different scales

The values assumed by the selected seascape metrics are shown in Fig. 2A–B for the whole lagoon and the four basins, and in Fig. 2C for the 11 water bodies. These plots summarize the characteristics of habitats' spatial patterns at the three spatial scales of analysis.

The whole lagoon shows high values of Shannon's Diversity Index (SHDI), Shannon's Evenness Index (SHEI), Landscape Shape Index (LSI) and Patch Richness (PR). Moving to the basins scale, some similarities can be identified, as suggested by the cluster analysis (Fig. 3A). The configuration of the Central basin fits well with that at the whole lagoon level. A certain similarity can also be seen between the two basins directly connected and conditioned by the central one (Southern and Northern Central ones). The characteristics of the spatial patterns of the Far Northern basin instead differ from those of the other basins.

Finally, in terms of water bodies, three groupings emerge from the cluster analysis, that include water bodies showing some clear similarity patterns (Fig. 3B): one consisting of Dese, Millecampi Teneri, Palude maggiore and Teneri, corresponding to confined water bodies, with high values of Patch Cohesion Index (COHESION) and Larger Patch Index (LPI); one consisting of Marghera, Sacca Sessola, Tessera and Val di Brenta with generally lower values of most of the metrics; and the last one consisting of Centro Sud and Lido, which are located close to the inlets and present rather marine-like characteristics, with high values of PR, SHEI and SHDI. The water body Chioggia looks different from all the others and is also the only one to present a high value for Patch Density (PD).

3.2. Relationships between spatial patterns and ecological status

Fig. 4 shows the pair-wise relationships between BQEs and seascape metrics. Very few statistically significant relations have been detected, that are, a positive relationship between MaQI and SHDI and between MaQI and PR, and a negative relationship between MaQI and Mean patch area (AREA_MN/ Area). Neither M-AMBI nor HFBI are significantly related with any of the selected metrics.

Moving to the PCA, the first three PCs were selected, which altogether explain 94.7% of variance (56.2%, 22.3% and 16.1%, respectively) (Fig. 5). The PC1 is strongly negatively related with LPI (eigenvector −0.94), and weakly positively related with SHDI and SHEI (eigenvectors 0.21 and 0.20, respectively). The PC2 is positively related with LSI and negatively with PD (eigenvectors 0.44 and −0.83, respectively). The PC3 is positively related with LSI, PD and PR and negatively with AREA_MN/Area (eigenvectors 0.54, 0.45, 0.40 and

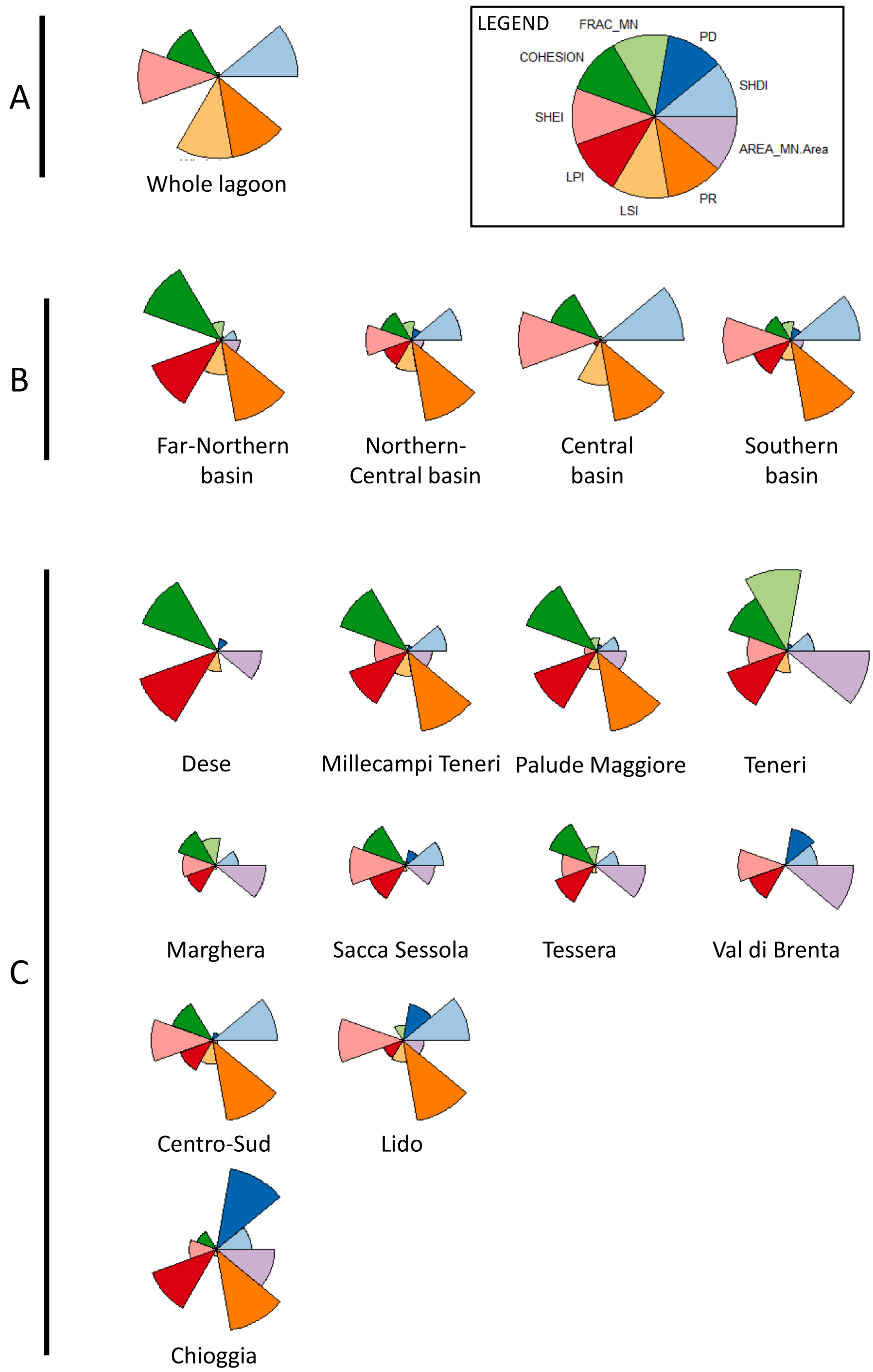

Fig. 2. Starplots representing the values assumed by the selected seascape metrics at the three spatial scales of analysis (whole lagoon (A), basins (B) and water bodies (C)), normalized on a scale from 0 (centre of the star) to 1 (full petals' length in the legend). Water bodies are ordered according to the groupings emerging from the cluster analysis. Please refer to Table 1 for the metrics' abbreviations.

−0.46, respectively). The PC1 and PC3 distinguish between the water bodies' degree of confinement and salinity, respectively. Unconfined water bodies have significantly higher scores of PC1 compared to confined ones ($t = -2.5$, $p<0.05$), while euhaline water bodies have significantly higher scores of PC3 compared to polyhaline ones ($t = 2.6$, $p<0.05$). The blue vectors in Fig. 5 represent the Spearman's correlation between BQEs and PCs. Considering the three-dimensional space defined by the first three axes of the PCA, the vectors of the three BQEs assume different orientations: MaQI is positively correlated with PC1 and PC3 (rho equal to 0.43 and 0.63, respectively), M-AMBI is negatively correlated with PC1 and PC3 (rho equal to −0.34 and −0.29, respectively), and HFBI is negatively correlated with PC2 (rho equal to −0.63).

4. Discussion

The influence of landscape patterns on ecological processes has been the subject of a large variety of studies in terrestrial ecosystems (Turner, 2005). This is only partially reflected in marine and coastal ecosystems (Boström et al., 2011). However, the lower amount of scientific literature available should not lead to think that seascape patterns are less relevant than their terrestrial counterparts. In fact, the spatial patterns of submerged habitats (e.g. seagrass meadows) do play a role in

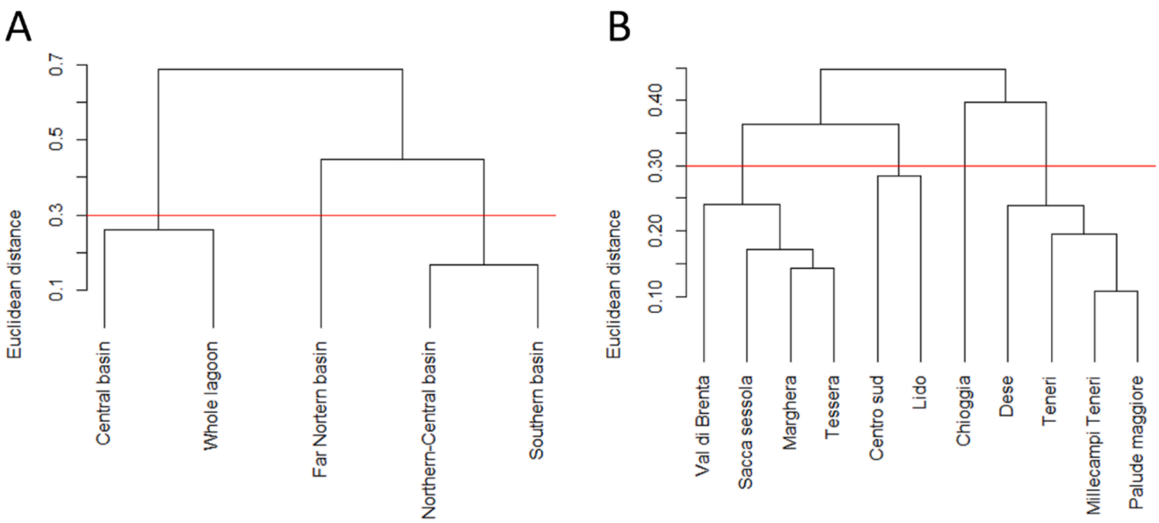

Fig. 3. Dendrogram of the hierarchical cluster analysis referred to lagoon's basins and whole lagoon (A) and to the lagoon's water bodies (B), based on the Euclidean Distance between the values assumed by the selected seascape metrics.

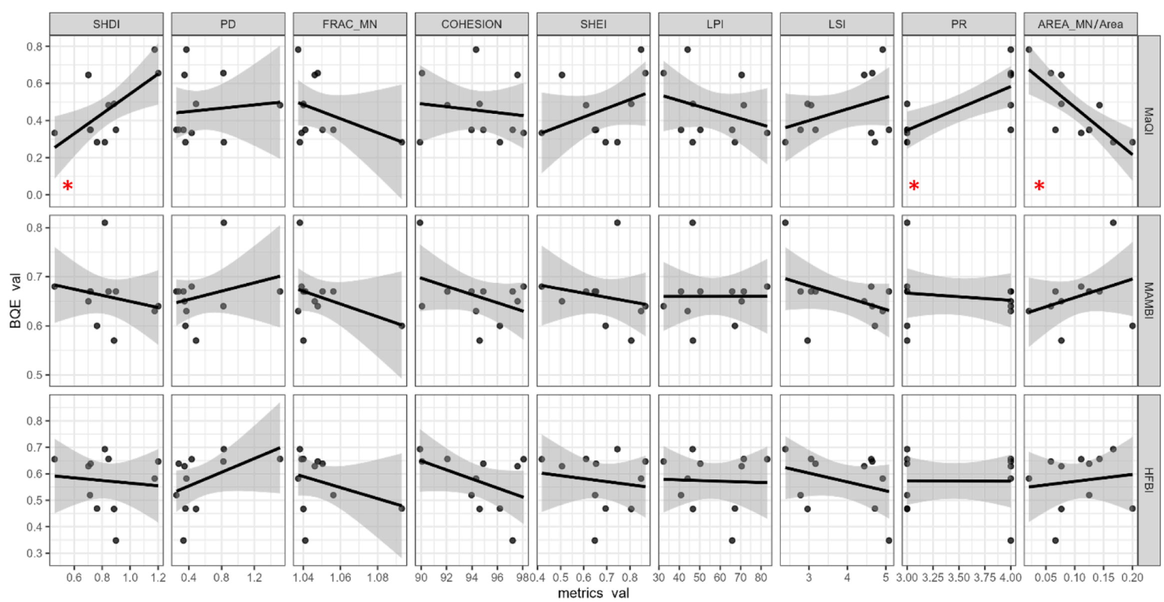

Fig. 4. Generalized linear models showing the linear relationships between the seascape metrics and the biological quality elements (BQE). Significant relationships are marked with an asterisk.

influencing the faunal assemblages and a variety of marine ecological processes (Sekund and Pittman, 2017; Abadie et al., 2018; Santos et al., 2018, 2022; James et al., 2021). The Venice lagoon does not make an exception in this sense: it is poorly studied from a seascape ecology perspective, but first evidences suggest a link between habitats' spatial patterns, fish assemblages and local fisheries (Scapin et al., 2018, 2022). In this context, our study brings a contribution by exploring the spatial characteristics of the submerged habitats at different spatial scales and their link with the ecological status of the lagoon.

In terms of submerged habitats' spatial patterns, we found a strong difference between the Far-Northern basin and the whole lagoon, which instead appears to be much more similar to the Central basin. These results can be interpreted in the light of the conditions of the different areas of the lagoon. According to previous literature, the Northern part of the lagoon still retains more peculiar lagoon characteristics, which are instead getting lost in other parts of the lagoon through a progressive marinization process (Fagherazzi et al., 2006; Solidoro et al., 2010). For example, in the Northern lagoon, if we move from the Lido inlet to the internal margins of the lagoon (in particular towards Dese river mouth) we can still observe a discrete amount of intertidal habitats, which create a gradient of habitats between sea and land, typical of lagoon ecosystems. This is reflected by the bottom elevation distribution, which in the Northern lagoon is still closer to that of the beginning of 20th century (Fagherazzi et al., 2006). Also salinity and water residence time still have marked gradients in this area, gradients that are progressively getting lost in central and southern lagoon (Solidoro et al., 2004). The articulated morphology and the presence of a relatively large surface of salt marshes seems to play a strong influence on the spatial patterns of submerged habitats, which in the Far-Northern basin appear to be strongly dominated by a single patch of salt marshes surroundings (high LPI), highly connected (high COHESION), and with a moderately complex shape (medium LSI). In contrast, the Central basin is characterized by stronger erosive trends that produced a gradual shift towards more marine characteristics: an important loss of salt marshes and a general evolution towards deeper tidal flats (Fagherazzi et al., 2006; Sarretta et al., 2010) resulted in a more "bay-like" ecosystem in which the typical

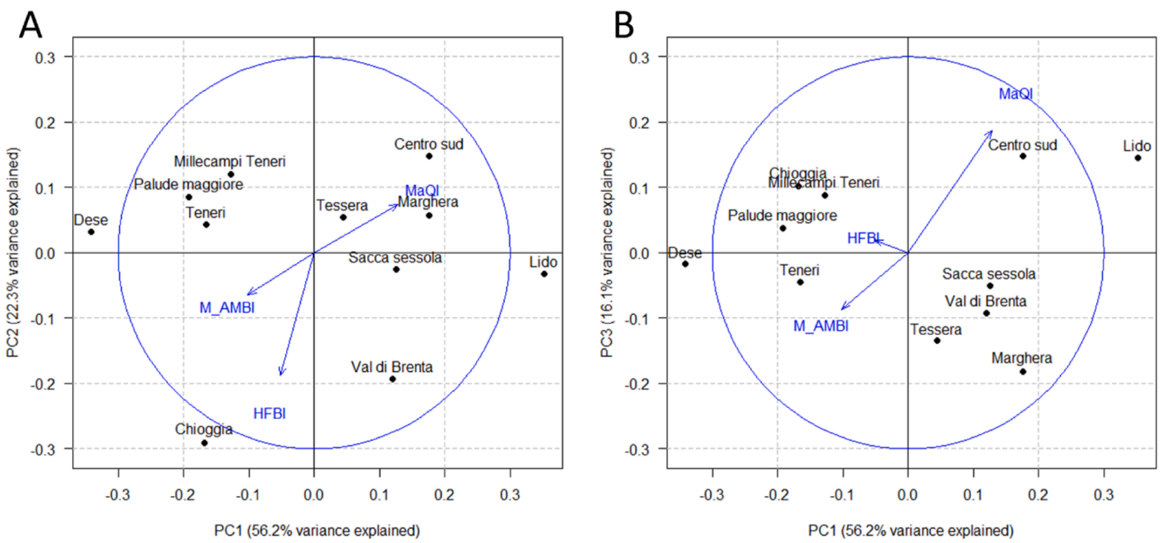

Fig. 5. Plots of the Principal Component Analysis on the seascape metrics. Left: first and second axis; right: first and third axis. The blue vectors represent the correlation (Spearman's rho) between the ordination axes and the biological quality elements, the blue circle representing rho = 1.

lagoon gradients found in the Northern areas are getting lost. The spatial patterns found in this basin suggest that the marinization process brings a greater diversity in the spatial patterns of submerged habitats. This can be explained by the fact that salt marshes surroundings are no longer dominant here (low LPI), whereas seagrass beds tend to have a greater development, increasing the overall diversity (higher SHEI and SHDI). Now, if we look at the configuration observed at the whole lagoon scale, we see that on one hand, it is radically different from that observed in the Far-Northern basin, and on the other hand, it is closer to what found in the Central basin. This suggests that the lagoon characteristics are getting lost at the whole lagoon scale, not only from the morphological point of view, as previously found (Fagherazzi et al., 2006), but also from the point of view of submerged habitats' spatial patterns, which are evolving towards more marine characteristics.

Moving at the water body scale, some links can be drawn between the water body groupings and the basins, although not always corresponding to a geographical overlap. The confined ones (Dese, Millecampi, Palude maggiore and Teneri) showed similarity with the lagoon characteristics of the Far-Northern basin, being characterized by the dominance of a single patch (high LPI) and highly connected (high COHESION). Lido and Centro-Sud are more similar to the Northern-Central and Southern basins, with a high diversity (high SHDI and SHEI) and a moderate dominance (medium LPI). The other water bodies instead do not present particular similarities with basins. The low overall metrics values in Marghera, Sacca Sessola and Tessera could be explained by the greater anthropic pressures to which these water bodies are subjected, such as navigation and clam harvesting. These pressures might have produced a simplification of the submerged habitats, for example through the enhancement of erosive processes (Pranovi et al., 2004).

Concerning the BQEs, no clear pair-wise relationships with the individual indices were detected, with the exception of MaQI. This could be explained by the fact that this BQE strictly depends on the assemblages of macrophytes, particularly seagrass beds (Sfriso et al., 2009), which play a crucial "structural" role with respect to the submerged habitats considered here. The presence of well-structured seagrass beds increases the status of MaQI (Sfriso et al., 2009) as well as the diversity of submerged habitats' mosaic, with respect to the areas where meadows are lacking. At the same time, the presence of seagrass meadows decreases the dominance of salt marshes' surroundings, again increasing the habitat diversity. Moving to the other BQEs, referred to the benthic macroinvertebrates' and ichthyofaunal communities, the lack of relationship could be a matter of spatial scale of analysis. The previous local seascape ecology studies found an influence of seascape patterns on fish assemblages by considering mosaics with extents of tens to hundreds of ha (Scapin et al., 2018, 2022). Conversely, the WFD water bodies have a much greater surface, ranging between 4 and 135 km^2. Perhaps, these BQEs could be linked with seascape metrics applied at smaller spatial scales, an hypothesis that could be investigated by further studies in this field.

The multivariate analysis, on the other hand, allows to draw some considerations about the orientation of the BQEs' vectors in the space defined by the PCA axes. The three BQEs in fact point towards different portions of the PCA graph, that means, they tend to be associated with different combinations of seascape metrics. A certain spatial configuration at the water body level could favour the improvement of one BQE, but could not be as favourable with respect to the other BQEs, which could instead decrease. This seems to be the case for M-AMBI and MaQI, whose vectors are nearly opposite. MaQI is associated with a combination of high LSI, PR and PD, and low mean patch area, which are mainly found in euhaline water bodies. M-AMBI, although less strongly, tends to be associated with opposite conditions, more akin to those found in confined and polyhaline water bodies. The issue remains the same if we, as a pure exercise, repeat the same analysis using the most recent WFD monitoring data (period 2017–2019, ISPRA-ARPAV, 2021): also in this case the BQEs' vectors assume contrasting orientations (data not shown). Therefore, from a seascape ecology perspective, the improvement of the overall ecological status in the Venice lagoon seems quite difficult: our results do not identify conditions (and thus management solutions) that favour all BQEs at the same time. This is in line with previous findings that showed that different BQEs tend to be associated with radically different patterns of multiple ecosystem services in the lagoon (Rova et al., 2019), and with different ecosystem functioning indicators (Anelli Monti et al., 2021).

Getting back to the marinization of the lagoon, how do the different BQEs respond to this ongoing process? The BQEs that concur to the definition of the ecological status (MaQI and M-AMBI) have originally been selected because of their sensitivity to the main pressures existing in the lagoon (Autorità di bacino dell'Adige et al. 2010, ISPRA-(ARPAV, 2016)). However, these two BQEs could have a different response to the changes brought by the marinization of the lagoon. This process could increase the presence of seagrasses meadows, thus probably increasing MaQI, but also bringing habitat changes that could instead decrease the status of M-AMBI, as suggested by the opposite directions assumed by the BQEs' vectors in the PCA space. This does not facilitate the achievement of the WFD's objective: the "one out-all out" principle requires that both these BQEs reach at least a good status, a target still very far for the water bodies of the Venice lagoon.

Perhaps, the findings of this work suggest that we should look at the management of the lagoon from a different angle. Concerning the BQEs, if we cannot improve them all, at some point we will probably have to choose which to prioritize. This requires to focus, on a broader perspective, on what kind of lagoon we would like to have, that is, on a shared vision for the future of the lagoon. We should evaluate this vision from a systemic perspective that considers, jointly, the lagoon's ecological status, morphology, seascape structure, ecosystem functioning, ecosystem services and stakeholders' needs. We should critically reflect on the ongoing trends, for example the marinization of the lagoon. Do we welcome or reject this loss of typical lagoon conditions, which, according to our results, emerges also from the configuration of submerged habitats at the whole lagoon scale? Probably, this joint reflection, which involves local decision makers, researchers, citizens, and more generally, the variety of local stakeholders, is a very urgent need, considering the evidence of this trend. Then, more "practical" decisions can be evaluated in the light of this vision and of the available research, knowing that trade-offs will be probably unavoidable, as this study suggests for the case of the BQEs. We are aware that these considerations are very far from being a practical solution, but we believe it is urgent to highlight the need of a systemic vision, knowing that this raises even more questions, given the high level of complexity of the lagoon ecosystem (or, better, social-ecological system). With this, we hope to stimulate new research and reflections on the future of the lagoon and its long term management.

5. Conclusions

Overall, the analysis of the Venice lagoon ecosystem from a seascape ecology perspective allows to draw two main conclusions. First, a shift from lagoon characteristics to marine ones can be detected at the lagoon-wide scale. In fact, the multi-scale analysis shows that the spatial patterns of submerged habitats at the lagoon scale resemble those of the marine-like areas of the lagoon, suggesting that typical lagoon traits are getting lost. Second, at the water body scale, the habitat configuration changes primarily between confined and unconfined water bodies, and, to a smaller extent, between euhaline and polyhaline ones. These different habitat configurations seem to affect, differently, the individual BQEs. Therefore, we cannot identify a spatial configuration that favours the joint improvement of the BQEs, but rather characterize the habitat configurations to which each BQE seems to be associated. If we cannot achieve a joint improvement of the BQEs, as required by the Directive, at some point we will have to choose what to prioritize. On a broader perspective, this highlights the need to identify, in a participated way, a broad systemic vision for the future of the lagoon. A vision that depicts the lagoon we want to pursue, while embracing its complexity, current trends and challenges.

CRediT authorship contribution statement

Silvia Rova: Conceptualization, Methodology, Formal analysis, Writing – original draft, Writing – review & editing. **Marco Anelli Monti:** Conceptualization, Methodology, Formal analysis, Writing – review & editing. **Sara Bergamin:** Conceptualization, Methodology, Formal analysis, Writing – review & editing. **Fabio Pranovi:** Conceptualization, Methodology, Writing – review & editing, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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