

Seasonal patterns of biodiversity in Mediterranean coastal lagoons

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Abstract

Aim: Understanding and quantifying the seasonal patterns in biodiversity of phyto-benthos, macro-zoobenthos and fishes in Mediterranean coastal lagoons, and the species dependence upon environmental factors.

Location: The study was carried out in the "Stagnone di Marsala e Saline di Trapani e Paceco," the largest coastal lagoon system in the central Mediterranean Sea (Sicily, Italy), a Special Protection Area located along one of the central ecological corridors joining Africa and Europe.

Methods: The coastal lagoon system was selected as a model ecosystem to investigate the seasonal variations in biodiversity indices and dominance–diversity relationships in phytobenthos, macro-zoobenthos and fishes, and how seasonal variations in temperature, salinity, depth, inorganic and organic suspended matter affect the abundance of the species constituting these communities. Models of ecosystem structure, describing the interactions among functional groups and environmental variables, were also developed using confirmatory path analysis and artificial neural networks to exemplify their application in predicting temperature-driven alterations.

Results: Wide seasonal variations in biodiversity indices and dominance–diversity relationships across the communities of the coastal lagoon system were observed, driven by the dynamics in climate and resource availability. The effects of the environmental variables on taxon abundances varied in relation to the community, with the widest responses elicited in phytobenthos and fishes. Temperature was the main variable affecting taxon abundances in macro-zoobenthos and was also the major driver of shallow water ecosystem structure.

Main conclusions: This research shed light on the seasonal variations in biodiversity of Mediterranean coastal lagoons, elucidating also the tight dependence of phyto-benthos, macro-zoobenthos and fish diversity upon environmental factors. The findings and the methodological approach proposed may be crucial in developing models able to predict future climate-driven alterations in communities inhabiting these important and threatened ecosystems.

KEYWORDS

artificial neural networks, biodiversity, climate change, community structure, confirmatory path analysis, fish, lagoon systems, phytobenthos, ridge regression, zoobenthos

1 | INTRODUCTION

Understanding the effects of climate change on biodiversity is crucial to predict future changes in ecosystem structure and functioning (Bulling et al., 2010; Isbell et al., 2011). However, our ability to predict modifications to community patterns and ecosystem dynamics, in space and/or time, under climate change is still rudimentary owing to the complexity of ecological systems (Thrush et al., 2014). Yet, increasing our predictive ability is crucial to support the development of conservation strategies able to mitigate and counteract the anthropogenic-driven alterations of biodiversity and ecosystem integrity expected in the near future (e.g., Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012; Chapin et al., 2000; Dawson, Jackson, House, Prentice, & Mace, 2011; Hulme, 2005; Sala et al., 2000; Sarà, Gouhier, et al., 2018; Thomas et al., 2004).

Among the emerging global stressors, increasing temperature is expected to have the most pervasive effects on biodiversity (sensu Wang, Brown, Tang, & Fang, 2009). Indeed, temperature drives biological processes in terms of effects on body size and metabolic rates (Brown, Gillooly, Allen, Savage, & West, 2004; Gillooly, Brown, West, Savage, & Charnov, 2001; Worm & Tittensor, 2018), and consequently, it shapes intra- and interspecific ecological interactions and density-dependent processes (Chaparron & Seuront, 2011; Clarke & Gaston, 2006; Sibly, Brown, & Kodric-Brown, 2012; Ockendon et al., 2014; Wang et al., 2009). Future temperature increases are expected to push ecological systems close to their current functional boundaries, beyond which severe effects on communities and ecosystem functioning may occur (Burkett et al., 2005). Most mass mortalities and catastrophic events of the last decade have been driven by sudden changes in weather, such as heat waves (Andréfouët, Dutheil, Menkes, Bador, & Lengaigne, 2015; Frölicher & Laufkötter, 2018; Garrabou et al., 2009; Micheli et al., 2012; Oliver et al., 2018; Pairaud, Bensoussan, Garreau, Faure, & Garrabou, 2014; Vergés et al., 2016; Wernberg et al., 2016). Temperature variations also affect food web structure and energy flows (e.g., Pernet et al., 2014; Tunney, McCann, Lester, & Shuter, 2014) through physiological and behavioural responses of organisms (Kearney & Porter, 2009) and their subsequent effects on trophic interactions (e.g., Best, Stone, & Stachowicz, 2015; Kirby & Beaugrand, 2009; Ockendon et al., 2014; O'Connor, Piehler, Leech, Anton, & Bruno, 2009). Therefore, understanding how organism responses alter food webs, and how ecosystem functioning is affected by food web modifications, still represent crucial requirements in predicting the impacts of climate change on ecosystems (Hansson et al., 2013; Ockendon et al., 2014; Post & Pedersen, 2008; Walther et al., 2002; Woodward et al., 2010).

Shallow water coastal ecosystems are particularly vulnerable to changing environmental conditions (Lloyd, Metaxas, & deYoung,

2012) and are threatened by both local and global factors (Newton & Weichselgartner, 2014; Newton et al., 2014 and references therein; Andréfouët et al., 2015; Parry, Canziani, Palutikof, Linden, & Hanson, 2007). Compared to deeper waters, which are more thermally and chemically stable (e.g., Stefansdottir, Solmundsson, Marteinsdottir, Kristinsson, & Jonasson, 2010), shallow waters such as coastal lagoons and ponds are intrinsically more variable (Pusceddu et al., 2003; Sarà, 2009; Spivak et al., 2017) in their physics and chemistry (e.g., temperature, depth, salinity, inorganic and organic suspended matters). Moreover, due to the physical connections between the benthic layer and the whole water column, the geochemical and biological dynamics are extensively driven by benthic–pelagic interactions (sensu Grenz et al., 2017). Shallow waters are mostly in close proximity to large human populations and are therefore affected by management-induced alterations to physical and chemical conditions (Airoldi & Beck, 2007) that may exacerbate global climate change effects on ecosystems (Anthony et al., 2009).

Easy to reach and rich in biodiversity, shallow waters not only provide a wide range of ecosystem services to citizens but they are also particularly suitable as open-air laboratories to study how biological diversity is affected by changing environmental conditions. Further, shallow waters can be data replete as they easily host large-scale studies measuring community biodiversity (Bintz, Nixon, Buckley, & Granger, 2003; Grenz et al., 2017) and a large number of environmental variables, allowing to investigate the driving processes of biodiversity variations. These systems are thus ideal to develop new avenues for predicting ecosystem responses at scales that are relevant to biodiversity management and conservation in the context of global climate change (Albouy et al., 2015; Petes, Howard, Helmuth, & Fly, 2014).

While our ability to provide future predictions is increasing at functional levels with the recent introduction of mechanistic individual trait-based bioenergetic models (e.g., Kearney & Porter, 2009; Sarà, Palmeri, Rinaldi, Montalto, & Helmuth, 2013; Sarà, Rinaldi, & Montalto, 2014; Sarà, Mangano, Johnson, & Mazzola, 2018), quantifying changes in community structure and biodiversity is more complex and challenging (Bellard et al., 2012; Best et al., 2015). On the one hand, machine-learning or deep-learning algorithms may provide a mathematical framework to model complex dynamics, although they may lack ecological realism. On the other hand, process-based models may provide exceptional realism, but the complexity required to model individual populations in complex communities may be overwhelming. Causal network techniques such as Bayesian graphical models, structural equation models or path analysis bridge the gap between the two approaches, providing ecological realism without the

complexity of process-based models, but they are not particularly suited to model complex communities either. These models have been used, for example, to examine the relative weight of environmental factors and anthropogenic disturbances (Schoolmaster, Grace, Schweiger, Mitchell, & Guntenspergen, 2013), and the role of carnivore (Calcagno, Sun, Schmitz, & Loreau, 2011) or alien species on local community structure (McMahon, 2005). In marine systems, causal analysis has been used to model trophic web responses to sea surface temperature in the North Sea (Kirby & Beaugrand, 2009).

The “Stagnone di Marsala e Saline di Trapani e Paceco” is the largest coastal lagoon system in Sicily (Italy) and represents one of the central ecological corridors joining Africa and Europe, housing the largest stop-over sites for migrating avifauna in the central Mediterranean (Special Protection Area; EU Birds Directive 79/409/EEC). Here, we quantify biodiversity in different communities along the lagoon food web and clarify how their species respond to environmental factors. Specifically, we aimed at evaluating the seasonal variations in biodiversity and at modelling the responses of individual species belonging

to phyto-benthic, zoobenthic and fish communities, to temperature, salinity, depth, organic and inorganic suspended matters. Finally, we exemplify a possible modelling approach, based on the relationships among communities and environmental variables, developing also future scenarios for the changes in coastal lagoon ecosystems driven by the environmental conditions expected under climate change.

2 | METHODS

2.1 | Study area

The study was carried out in Western Sicily (Southern Italy) in the “Stagnone di Marsala e Saline di Trapani e Paceco,” one of the most important coastal lagoon systems of central Mediterranean Sea, encompassing 25 water bodies and representing an important hot spot of biodiversity for the Mediterranean Sea (Mannino, 2010; Mannino & Graziano, 2016; Mannino & Sarà, 2006; Mazzola et al., 2010; Vizzini, Sarà, Mateo, & Mazzola, 2003). The site, recognized as Special Protection Area since 2005 (ITA010028, EU Birds

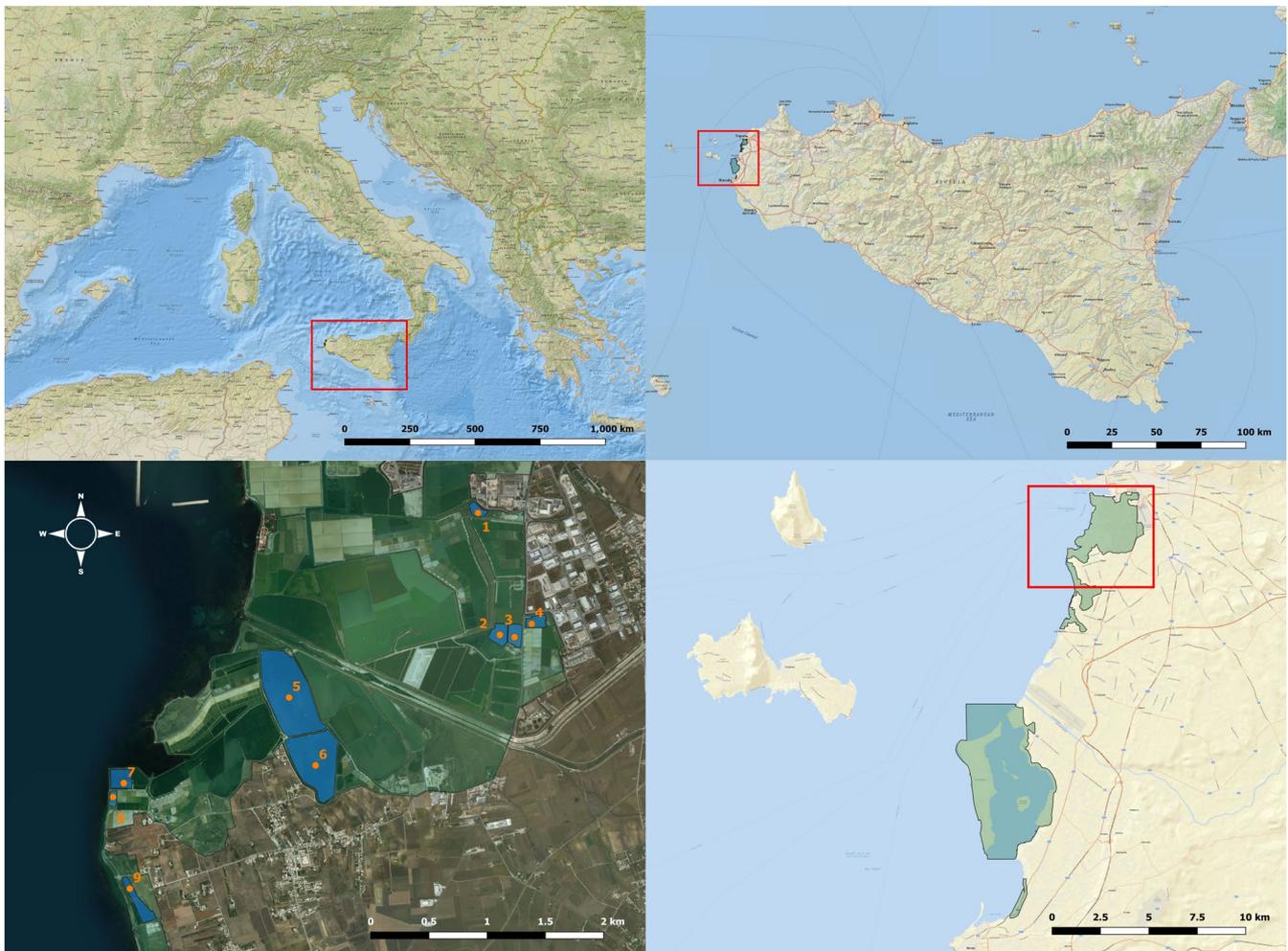


FIGURE 1 The “Stagnone di Marsala e Saline di Trapani e Paceco” lagoon system (green polygons) in Sicily, Italy, shown at different scales. The nine studied coastal ponds (blue polygons) are indicated by orange dots, labelled using Arabic numerals: 1 = Reda (1.2 ha), 2 = Bella I (2.3 ha), 3 = Bella II (2.1 ha), 4 = Maria Stella (1.6 ha), 5 = Morana (25.3 ha), 6 = Moranella (18.0 ha), 7 = Culcasi I (2.9 ha), 8 = Culcasi II (0.8 ha), and 9 = Anselmo (3.1 ha)

TABLE 1 Minimum and maximum values of the variables studied during the year in the nine ponds, as well as the mean squares statistics based on the variances among ponds (MS_p) and among seasons (MS_s)

Variable	Winter	Spring	Summer	Autumn	MS_p	MS_s
Temperature– T (°C)	14.08–17.93	18.16–21.10	27.23–31.72	20.49–22.92	0.3×10^1	3.2×10^2
Salinity– S (‰)	24.06–36.60	19.75–29.80	28.31–46.67	27.23–33.29	1.8×10^1	1.6×10^2
Depth– W (m)	0.12–0.76	0.25–0.73	0.13–0.65	0.17–0.78	1.2×10^{-1}	3.0×10^{-2}
Inorganic suspended matter–ISM (mg/L)	7.00–212.22	8.01–115.67	8.21–99.75	2.05–159.80	2.8×10^3	1.3×10^3
Organic suspended matter–OSM (mg/L)	8.42–77.78	6.25–703.03	3.58–394.33	3.72–54.58	1.7×10^4	6.7×10^4

Directive 79/409/EEC), lies on one of the most important migratory corridors and represents a stop-over site for avifauna coming from Africa to Europe and *vice versa* (Figure 1). The area, described in detail in Sarà, Leonardi, and Mazzola (1999), covers a total of 3,742 ha and includes both a large coastal pond system (“Saline di Trapani e Paceco”) and the largest coastal lagoon in Southern Italy: the “Stagnone di Marsala” (Site of Community Importance since 1995, ITA010026, EU Habitat Directive 92/43/EEC). The entire area is subjected to a Mediterranean climate, with mild winters and the highest temperatures in summer, associated with the lowest precipitations.

2.2 | Field surveys and data collection

Sampling surveys were carried out in each season, during 2011–2012, in nine coastal ponds (Figure 1, Table 1), representing more than 75% of the area covered by water bodies in the “Saline di Trapani e Paceco” lagoon system. To study the relationships among biotic and abiotic components, we focused on the major communities (phytobenthos [Pc], macro-zoobenthos [Zc] and fishes [Fc]) and on the main physicochemical variables (water temperature [T], salinity [S], depth [W], organic [OSM] and inorganic [ISM] suspended matters). Pc and Zc communities were sampled manually over three quadrats of 20 cm² per pond in each season, whereas Fc by mean of three seine nets (12 × 1 m; 5 mm wings mesh, 1 mm coded mesh) deployed by hand, per pond in each season. Samples from both quadrats and nets were fixed in 70% ethanol and properly labelled. Once in the laboratory, samples were gently washed over sieves (0.5 mm mesh), and thereafter, Pc and Zc components were sorted. Pc and Zc were identified to the lower taxonomic level possible (Mannino & Sarà, 2006 and references therein; Mangano et al., 2014), and the total number of individuals per species was quantified. Environmental variables included in this study were measured near the bottom in triplicate per pond in each season. T , S and W were measured in the field near each quadrat with a multiprobe gauge (YellowSpring Ysi 556), whereas ISM and OSM were measured on water samples, collected nearby the quadrats using Niskin bottles, through drying and loss-on-ignition (450°C for 4 hr). Further details on the methods employed in environmental analyses can be found in Sarà et al. (1999). Overall, the dataset comprised a number of 108 quadrats, seine nets and measures of each environmental variable (3 replicates × 9 basins × 4 seasons).

2.3 | Data analysis

The number of taxa and the relative abundances of Pc, Zc and Fc were measured and combined using biodiversity indices (Magurran, 2004): estimated species richness (S_{ACE}), Margalef (D_{Mg}), Shannon (H'), Brillouin (HB), Simpson (D) and Pielou (J'). Two indices for each biodiversity measure, that is, species richness (S_{ACE} and D_{Mg}), diversity (H' and HB) and dominance/evenness (D and J') were employed. The S_{ACE} index was derived according to abundance-based coverage estimate (ACE) models. All the indices were calculated based on the absolute abundances, where applicable. Differences in biodiversity among seasons and communities were evaluated through a multivariate analysis of variance (MANOVA) using the biodiversity indices as dependent variables, the season and community variables as fixed factors and Pillai's trace as the test statistics. The differences in each biodiversity index in relation to the seasons and communities were assessed through linear mixed models using the pond as a random factor. The significance of the differences among seasons and among Pc, Zc and Fc was then evaluated using a Kenward–Roger adjusted F test. These analyses were performed using the functions of the “stats” (R Core Team, 2018), “lme4” (Bates, Maechler, Bolker, & Walker, 2015), “emmeans” (Lenth, 2018) and “multcompView” (Graves, Piepho, Selzer, & Dorai-Raj, 2015) packages within the R 3.4.4 programming environment (R Core Team, 2018).

Community structure of Pc, Zc and Fc in each season was evaluated using dominance–diversity curves, described by the broken-stick, niche preemption, lognormal, Zipf or Mandelbrot models of species abundance. The models imply different set of hypotheses about the niche apportionment, from lowest (preemption) to highest (lognormal and broken-stick) niche overlap, or about the relative ecological requirements of species, with species selected by environmental constraints (Zipf and Mandelbrot). Further details about the models can be found in Wilson (1991) and Magurran (2004). The choice of the optimal model was based on Akaike's information criterion (AIC). Index calculation, curve construction and model fitting were performed using the functions of the “vegan” package (Oksanen et al., 2018) within the R 3.4.4 programming environment (R Core Team, 2018).

To estimate the functional dependence of each taxon of Pc, Zc and Fc upon the measured environmental variables, separate ridge regression models were derived for each community using the “glmnet” package (Friedman, Hastie, & Tibshirani, 2010) for the R 3.4.4

programming environment (R Core Team, 2018). Specifically, L_2 penalized generalized linear models (elastic nets with ridge behaviour) were defined, using the Hellinger-transformed abundance data of each taxon as dependent variables and T , S , W , OSM and ISM as predictors. The choice of the optimal penalty parameter (λ) value was based on tenfold cross-validation using a grid of 10^3 λ values in the $[0,1]$ range. The multivariate Gaussian family was employed for all the models.

Modelling of temperature-driven changes in species richness, through an approach coupling confirmatory path analysis (CPA) and non-linear modelling with artificial neural networks (ANNs), was demonstrated using environmental and D_{Mg} data. D_{Mg} was chosen over S_{ACE} as the response variable in DAGs due to its lower

sensitivity to parameters related to sample size and rarity of the species, upon which the latter is weighted (Magurran, 2004). Specifically, fifteen hypothetical models relating D_{Mg} of Pc , Zc and Fc and all the environmental variables were developed and expressed as directed acyclic graphs (DAGs). Models varied in the degree of connectivity, expressing different hypotheses about the complexity in the relationships among the communities and the environmental variables. Directed acyclic graphs were tested using the "cpa" package (Bellino et al., 2015) in the R 3.4.4 programming environment (R Core Team, 2018), and the best model was selected based on the AIC, in order to take into account model complexity, and on model probability (p), derived from Fisher's C statistics and employed to exclude models with $p < \alpha$ (with

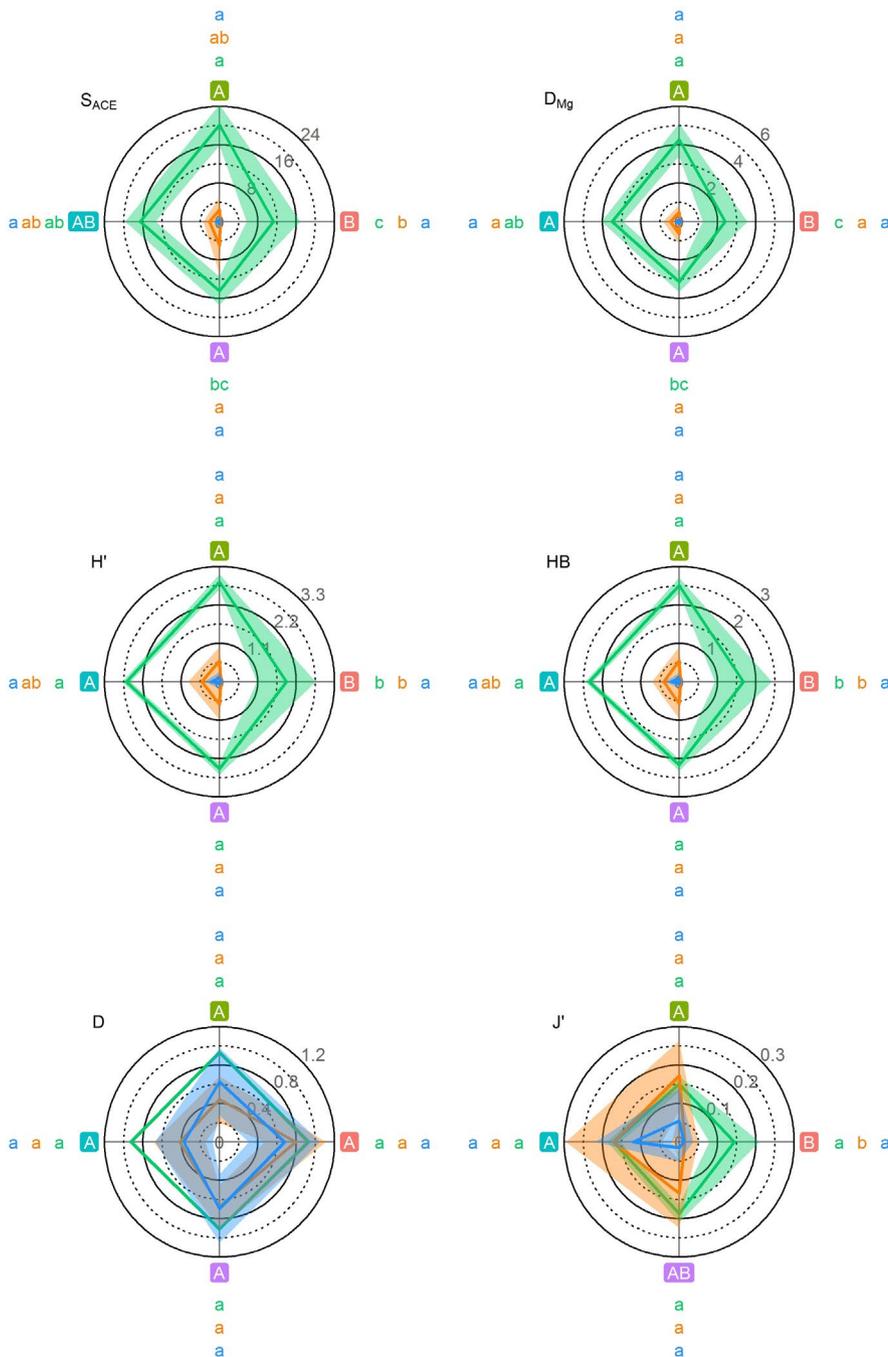
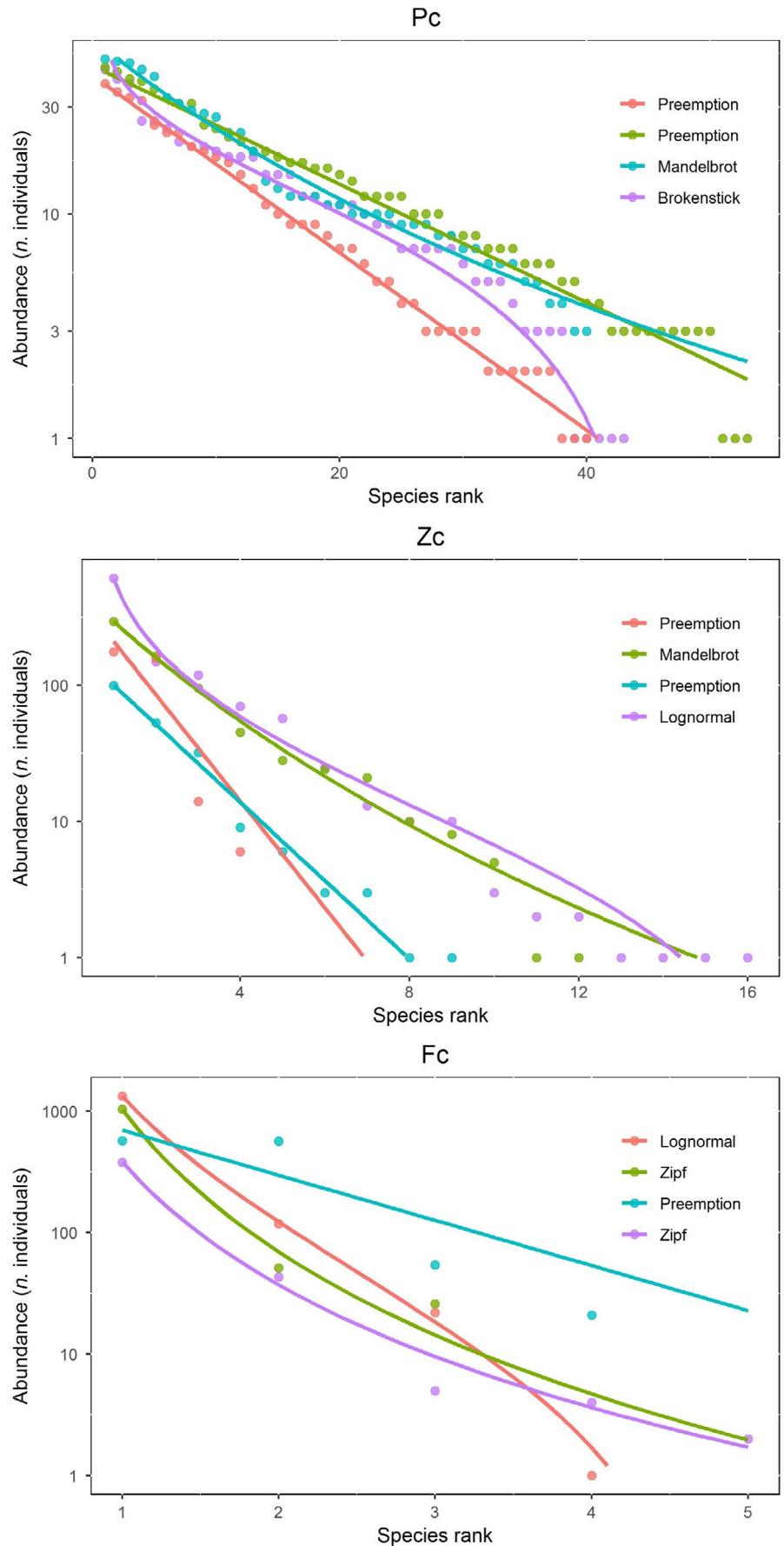


FIGURE 2 Radar plots of S_{ACE} , D_{Mg} , H' , HB , D and J' indices in relation to the seasons indicated by coloured boxes at the four vertices (red: winter, olive: spring, turquoise: summer, violet: autumn) and the communities (green: Pc , orange: Zc , blue: Fc). Mean values are plotted along with 95% confidence intervals (solid lines and coloured bands, respectively). Different capital letters in coloured boxes indicate overall significant (for $\alpha = 0.05$) differences in each index among seasons, irrespectively of the communities. Different small letters indicate significant differences (for $\alpha = 0.05$) among seasons for each community, according to their colour

FIGURE 3 Dominance–diversity (Whittaker's) plots of P_c , Z_c and F_c in winter (red), spring (olive), summer (turquoise) and autumn (violet) showing the observed (points) and the predicted (lines) abundances based on the theoretical model with the lowest AIC for each community and season (indicated in legends)



$\alpha = 0.05$). Single-hidden layer ANNs, regularized through weight decay using leave-one-out cross-validation, were used to functionalize the relationships implied by the best DAG. The number of hidden units was set to 20 for all the models, whereas the choice of the weight decay parameter was made among 12 candidate values in the range [0,1] differing by half-order of magnitude each other. Artificial neural networks were trained on the data using the “nnet” package (Venables & Ripley, 2002) in the R 3.4.4 programming environment (R Core Team, 2018). Finally, projections of Pc, Zc and Fc diversity changes due to increases in temperature were obtained by running ANN models with temperatures increasing in steps of 0.25°C up to 3°C above those measured, to simulate the high-emission trajectory scenario “business-as-usual” from the IPCC (2014) (+3.2°C until 2,100, Representative Concentration Pathway 8.5, AR5).

3 | RESULTS

All the environmental variables varied more among seasons (MS_s) than among ponds (MS_p), with the only exception of ISM (Table 1). The variations of S_{ACE} , D_{Mg} , H' , HB, D and J' across the four seasons in Pc, Zc and Fc are reported in Figure 2.

Overall, MANOVA highlighted significant differences both among communities (Pillai's trace = 1.044, $p < 0.001$) and seasons (Pillai's trace = 0.415, $p < 0.001$) in relation to biodiversity indices. The same differences among Pc, Zc and Fc (always $p < 0.001$), as well as seasons (S_{ACE} and J' : $p < 0.01$; D_{Mg} , H' and HB: $p < 0.001$), were highlighted by the linear mixed models on individual indices, with the exception of D , for which no difference was observed among seasons. Pc constantly showed the highest values of all the indices, with the exception of J' for which no difference (for $\alpha = 0.05$) was observed between Pc and Zc. Zc and Fc differed in the values of H' , HB and J' , all higher in the former than in the latter, but not in the values of S_{ACE} , D_{Mg} and D .

The models describing the dominance–diversity curves of Pc, Zc and Fc varied across the seasons (Figure 3). In Pc, the dominance–diversity pattern was described better by the niche preemption model in winter and spring, which changed to the Mandelbrot model in summer and then to the McArthur broken-stick model in autumn. The niche preemption model also described the dominance–diversity pattern of Zc in winter and summer, replaced by the Mandelbrot model in spring and by the lognormal model in autumn. The latter model described also the dominance–diversity pattern of Fc in winter and was substituted by the Zipf model in spring and autumn and by the niche preemption model in summer.

The coefficients (β) derived from the ridge regressions relative to T , S , W , ISM and OSM for each taxon, indicating the relative strength of their linear dependence upon the environmental variables, are reported in Figure 4. On average, Zc showed the narrowest β range for all the predictors, especially W , ISM and OSM, whereas Fc showed on average the widest β variations. More than half of Pc taxa showed a negative response to S and, to a lower

extent, to ISM, and positive responses to W and OSM. The responses to T were mixed, with almost half of the taxa increasing in abundance with T and the others decreasing. Similar mixed responses were observed for Fc in relation to all the variables with the exception of OSM, which had a negative effect on all Fc taxa, especially pronounced in *Aphanius fasciatus*.

The fifteen DAGs developed for CPA are shown in Figure 5. Two DAGs, H and L, were rejected ($p < 0.05$) by CPA, making the choice among the others a function of the AIC alone, due to their different complexities. The model C (AIC = 89.28; $p = 0.789$) was thus considered the best representation of the coastal lagoon ecosystem structure. In addition, this model allowed describing the diversity of Pc, Zc and Fc as a function of temperature only, avoiding the need to control other environmental variables during the simulations.

The simulation outcomes varied seasonally (Figure 6), showing either increases or decreases in D_{Mg} due to increasing temperature. Under an increasing temperature scenario, Pc showed the highest richness values and the simplest dynamics, with predicted monotonic decreases in spring and autumn and monotonic increases in summer and winter. Conversely, Zc and Fc showed lower diversity ($Zc > Fc$) and non-linear dynamics. In particular, an inversion in the temperature-driven dynamics of D_{Mg} is recognizable in autumn for Zc and Fc. In spring, summer and winter, Zc richness increased according to increasing temperature, a pattern shared by Fc in summer and winter only. Fc showed a decreasing richness with increasing temperature in spring only. Overall, Zc showed the largest seasonal variations due to the temperature gradient, especially in winter.

4 | DISCUSSION

The present research constitutes the first study encompassing the seasonal variations in biodiversity across phytobenthic, macrozoobenthic and fish communities and the modelling of their responses to several environmental factors in Mediterranean coastal lagoons. The results obtained from 9 of the coastal ponds of the “Stagnone di Marsala e Saline di Trapani e Paceco” lagoon system highlighted uneven seasonal patterns of richness, diversity, dominance/evenness and community structure. The two indices chosen for each biodiversity measure provided similar responses in terms of seasonal variations in the different communities. However, the couple constituted by the Simpson and the Pielou indices, in which the former provides a measure of dominance and the latter a measure of evenness, represents an obvious exception. Species richness, either derived from ACE analysis or normalized to total specimen abundance (Margalef index), showed the widest seasonal variations with a peak in spring and the lowest values in winter. The pattern is mostly determined by the variations in the phytobenthic community, almost doubling the number of taxa from winter to spring. Interestingly, the greater availability of resources occurring in spring under Mediterranean climate, especially light, coupled

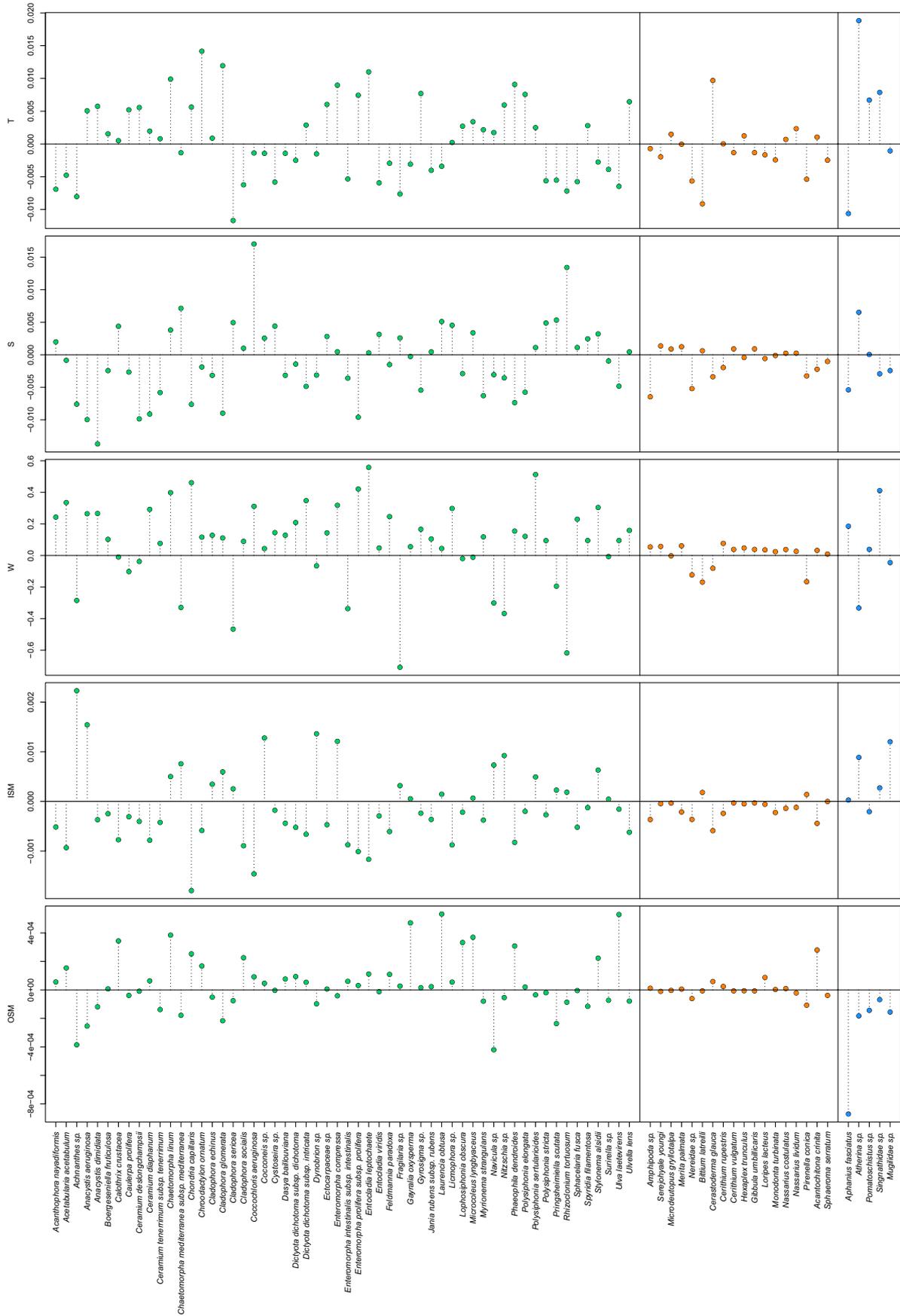


FIGURE 4 Lollipop plots of the elastic net coefficients derived for T, S, W, ISM and OSM relative to the Pc (green), Zc (orange) and Fc (blue) taxa

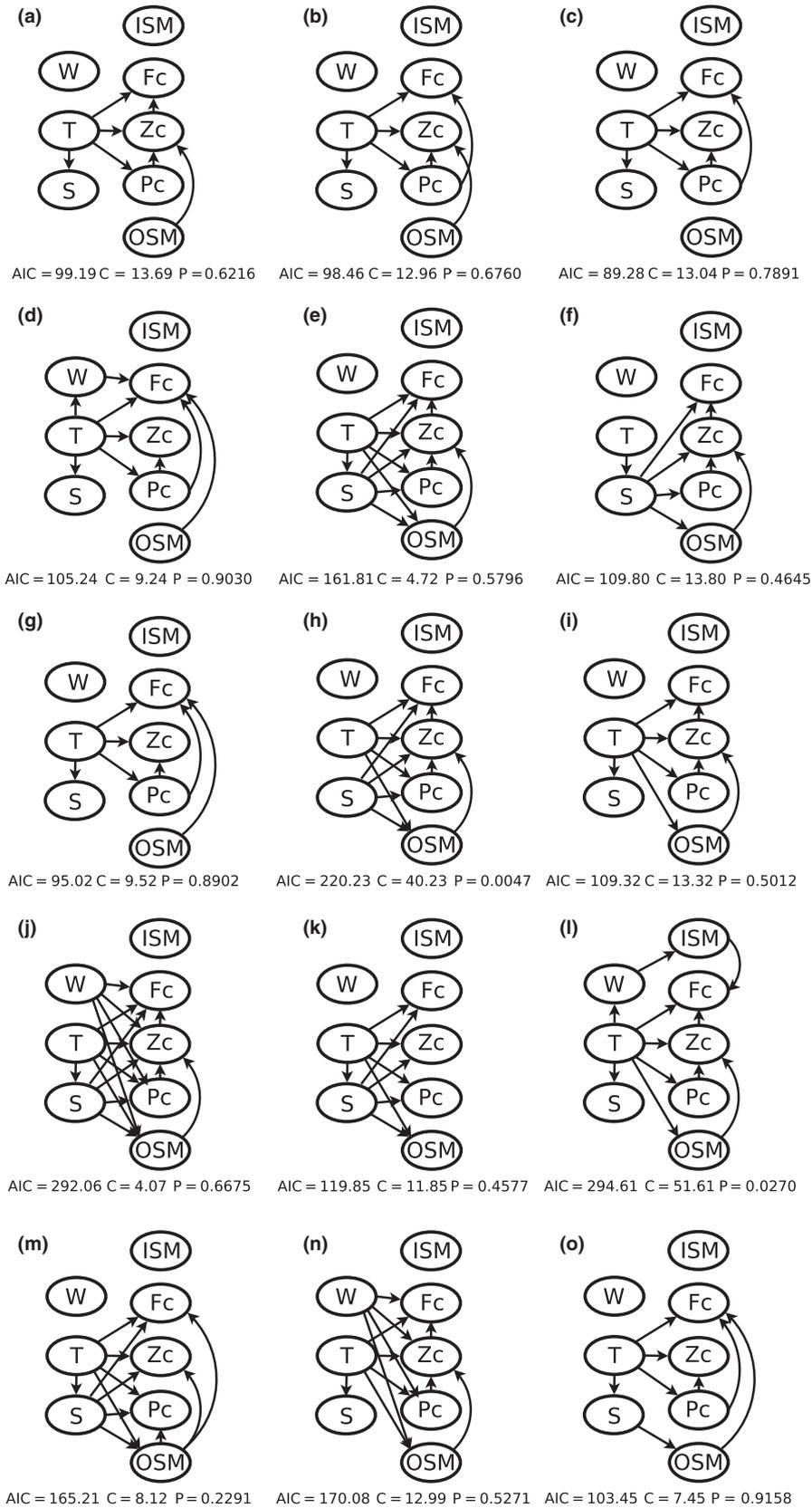


FIGURE 5 Directed acyclic graphs (DAGs) describing the causal relationships among T , S , W , ISM , OSM and D_{Mg} of Pc , Zc and Fc . The AIC, Fisher's C statistic (C) and the probability (p) for each model are also reported. The model with the lowest AIC is highlighted by a black frame

with optimal environmental conditions (Mayot et al., 2017), determined diversification of phytoplankton rather than algal blooms. Although with similar outcomes at the ecosystem level (increase in primary productivity), the processes actually underpin very

different dynamics at the community level. While algal blooms imply increases in dominance, higher slopes of the dominance-diversity relationships and reductions in diversity, eventually determining mono- or oligo-specific assemblages (Gomoiu, 1992;

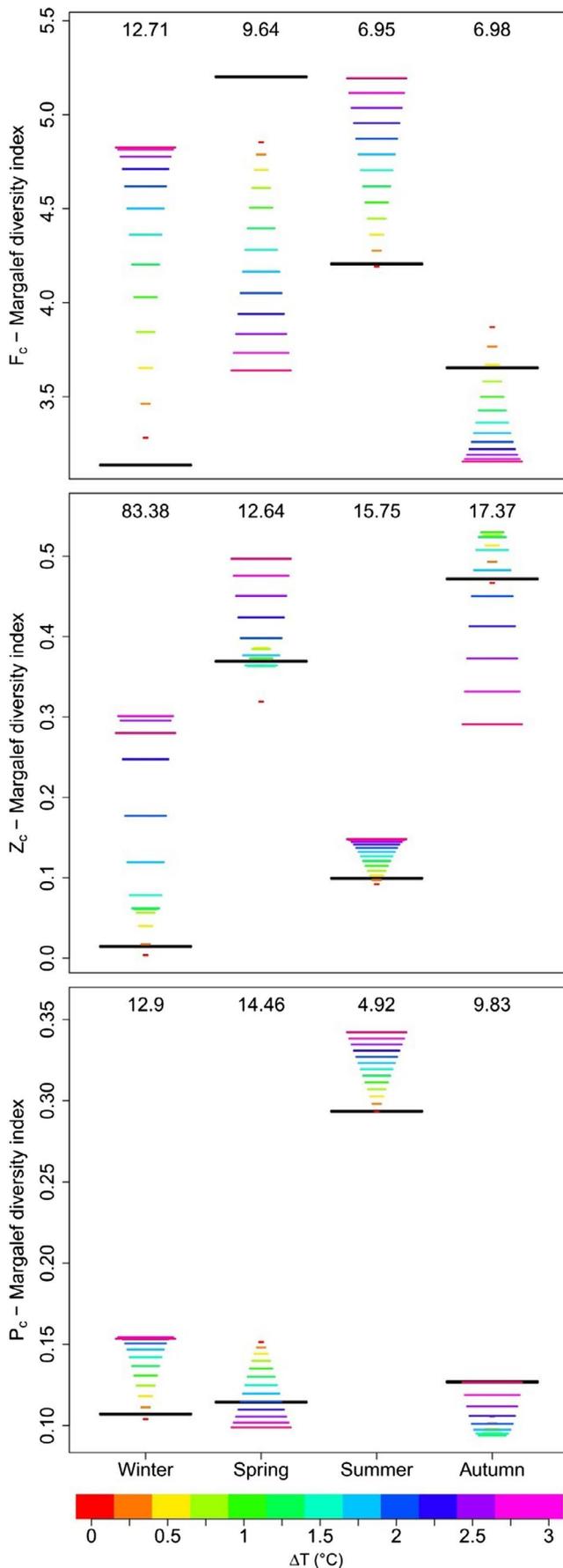


FIGURE 6 Simulated seasonal responses of species richness (D_{Mg}) of Pc, Zc and Fc to increasing temperatures. Black bars indicate the empirical means whereas coloured bars indicate the simulated values according to ANNs; the coefficients of variations for each community in each season are also reported in the upper part of each graph. Bar colour and length indicate the ΔT increase over the measured temperatures

Green-Gavrielidis, MacKechnie, Thornber, & Gomez-Chiari, 2018; Yoshida et al., 2018), the opposite was observed in our coastal lagoon system. Indeed, not only the number of phytobenthic taxa increased during spring, but also the dominance remained substantially the same during the year and the slope of Whittaker's curves actually decreased from winter to spring. In this context, the niche preemption model suggests a sequential build-up of the phytobenthic community, in which the number of species is limited by resource abundance rather than by interspecific competition (Magurran, 2004). This occurrence further supports the hypothesis of a resource-driven diversification of phytobenthos during spring. It is interesting to note how limiting factors or interspecific competition (implied by the Mandelbrot community model; Wilson, 1991) shaped species abundances later, in summer, as expected considering the higher environmental constraints (water temperature, salinity, depth), eventually determining a structure typical of late successional stages in autumn, described by the broken-stick model (Magurran, 2004). A similar pattern of seasonal community development was shared by the macro-zoobenthic community, in which an analogous sigmoid model described the dominance-diversity relationship in autumn. The similarities between the dynamics of the phytobenthos and the macro-zoobenthos also encompassed the presence of two peaks of biodiversity in spring and autumn and, conversely, its decline in winter, indicating a tight dependence of the macro-zoobenthos dynamics upon those of the autotrophic group. Indeed, an increase in phytobenthos diversity would result in a greater availability of trophic and spatial niches for macro-zoobenthos and fishes (Schindler & Scheuerell, 2002; Solomon et al., 2011). However, the variability among ponds in phytobenthos diversity was widest during winter, whereas the opposite occurred in the macro-zoobenthic community, suggesting a variable versus homogeneous occurrence of the environmental constraints for the two communities across the nine coastal ponds of the "Saline di Trapani e Paceco" lagoon system. Albeit with the same seasonal dynamics in phytobenthic and macro-zoobenthic communities, both richness and diversity reached values much lower in the latter than in the former, and even lower in the fish community, indicating a decrease in biodiversity going up the trophic level. Although with some differences, this result agrees with both theoretical (Bastolla, Lässig, Manrubia, & Valleriani, 2005) and field (Cohen, Briand, & Newman, 1990; Lässig, Bastolla, Manrubia, & Valleriani, 2001) studies demonstrating biodiversity declines towards the higher trophic levels. Although seasonal variations in species richness and diversity were also observed in the fish community, with

peaks in summer, the low values (almost one order of magnitude lower than in the phytobenthic community) and the wide variability among coastal ponds hindered the detection of clear seasonal trends. Similarly, the low number of taxa limits the effectiveness of the models in describing the dominance–diversity relationships in the fish community, preventing the proper evaluation of the community structure seasonal variations.

Clear, instead, is the negative effect of the organic suspended matter on the abundance of fishes, especially the killifish *A. fasciatus*, a threatened species (listed in Appendix II—Strictly protected fauna species—and Appendix III—Protected fauna species—of the Bern Convention, and in Annex II of the Habitats Directive CD 92/43/EEC (I) 1992 and CD 97/62/EC 1997; Crivelli, 2006) representing the principal prey for the top predator and migrating bird *Egretta garzetta* in the “Saline di Trapani e Paceco” lagoon system (Piazza, Morganti, Sarà, & Campobello, 2006). Converse to the negative effects on fish abundance, organic suspended matter, as with most of the environmental variables considered in this study, did not affect the macro-zoobenthic taxa (with the exception of *Acanthochitona crinita*). The environmental variable determining the widest responses in the macro-zoobenthic community was temperature, eliciting either increases in species abundance, as in the mollusc gastropod *Cerastoderma glaucum*, or decreases, as in the gastropods *Bittium latrellii* and *Pirenella conica* as well as in the isopod *Sphaeroma serratum* and in polychaetes of the family *Nereidae*. More complex are the responses of the phytobenthic community, exhibiting wide variations in taxon responses, either positive or negative, to the increase in each environmental variable, especially temperature. Although species of high trophic levels are thought to be more sensitive to temperature changes due to their steep increase in growth rate with temperature (Montoya & Raffaelli, 2010; Voigt et al., 2003), the same did not occur in our study system, where many phytobenthic taxa exhibited elastic net coefficients comparable or higher than those of the macro-zoobenthos and fish.

Among the candidate models relating water salinity, temperature, depth and the abundance of phytobenthos, macro-zoobenthos and fish, CPA selected a model indicating that temperature primarily affects the communities directly rather than indirectly (e.g., by changing salinity) and it is one of the main determinants of community diversity. Salinity is related to water temperature (Pawlowicz, 2013), and this variable can be also a primary shaper of marine communities (Lappalainen, Shurukhin, Alekseev, & Rinne, 2000; Williams, 1998), but does not appear to affect species richness in this system, an occurrence likely related to the abundance of euryhaline species in coastal shallow waters (Kennish & Paerl, 2010). Similarly, depth consistently affects phytobenthic taxa, mainly colonizing deeper waters, but was not selected as a driver of species richness in the three communities. Although some of the fish species observed in the lagoon system feed on zoobenthos (e.g., *Pomatoschistus* sp.), the model did not involve a causal relationship between species abundance of macro-zoobenthos

and species abundance of fish, likely in relation to the generalist feeding behaviour of the species. The central role of temperature on species abundances in various trophic levels was already elucidated by Kirby and Beaugrand (2009) in the North Sea, showing how increasing temperature altered ecosystem dynamics, favouring jellyfish, decapod and detritivore communities.

Our study represents the first attempt to model diversity across different communities (phytobenthos, macro-zoobenthos, fish) in relation to water temperature in Mediterranean coastal shallow waters, also employing model testing in the form of Fisher's C statistic and AIC. Moreover, this approach focuses directly on the community level, rather than on the species level, whereas other approaches, from the bioenergetics to the niche models, allow simulation of the responses of single populations or species to changing climate. The niche model, in particular, was employed to predict the dynamics of more than one thousand marine species until the 2050 (Cheung et al., 2009). These approaches, however, cannot model changes in biodiversity across different functional or trophic levels since they would require information rarely available for all the interacting species constituting the communities. Although coarser, our approach may thus allow a more comprehensive view, and possibly projection, of the effects of the dynamic thermal mosaic on aquatic food webs. The projected effects of temperature on diversity varied among the communities and seasons, suggesting shifts in species abundances and community composition that may have relevant effects on ecosystem processes, for example, trophic webs and nutrient cycling (Eviner & Chapin, 2003). Our model implies that the observed relationships between community diversity and temperature will be preserved across the +3°C ΔT above the measured temperatures. This assumption may hold for moderate warming but becomes more uncertain with more extreme increases in ΔT . Moreover, the parameterization based on one year dynamics further contributes to the uncertainty in the projections, which should be viewed as indications of possible system evolution based on its current status and as an illustration of the potential of the modelling approach in Mediterranean coastal lagoons, rather than reliable forecasts.

According to our simulations, richness of phytobenthos will show simple dynamics, with a progressive shift of the springtime peak of biodiversity to winter and the highest increase in biodiversity during summer. The diversity of the macro-zoobenthic and fish communities similarly will increase during winter and summer, an occurrence which can be related either directly to the changes in temperature or indirectly through the increase in phytobenthos diversity. Such patterns can be related to early phytobenthos development and arrival of migratory benthic or pelagic animals or their permanence for prolonged periods. Conversely, decreases in biodiversity can be easily viewed as the result of niche loss and determinants like competition and predation with newly incoming species. Indeed, biotic interactions may be the primary mediators of the impact of climate change on populations in both terrestrial

(Ockendon et al., 2014) and marine ecosystems (Falkenberg, Russell, & Connell, 2012; Ghedini, Russell, & Connell, 2015; Nagelkerken, Russell, Gillanders, & Connell, 2016).

Considering the positive relationship between biodiversity and productivity in many ecosystems (Cardinale, Ives, & Inchausti, 2004; Cardinale, Palmer, & Collins, 2002; Fridley, 2001; Paine, 1966), our modelling approach may allow translating the changes to diversity across different trophic levels to changes in ecosystem productivity (Doney et al., 2012), not traditionally considered in climate change research (Tunney et al., 2014). Longer time series in the future will allow enhancing the accuracy of the model and of projections (e.g., Gauthier et al., 2013) that currently constitute a baseline and a conceptual approach to assess ecosystem structure and predict future evolutionary trajectories under climate change, allowing the development of early warning tools for conservation of entire systems.

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BIOSKETCH

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