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Identifying Gaps in the Protection of Mediterranean Seagrass Habitats Using Network-Based Prioritisation

Damiano Baldan[1,2] | Yohann Chauvier-Mendes[3,4] | Fabrizio Gianni[1,2] | Gianpiero Cossarini[1] | Vinko Bandelj[1,2]

[1]National Institute of Oceanography and Applied Geophysics – OGS, Trieste, Italy | [2]National Biodiversity Future Center – NBFC, Palermo, Italy | [3]Department of Aquatic Ecology, Eawag, Swiss Federal Institute of Aquatic Science and Technology, Dübendorf, Switzerland | [4]Department of Evolutionary Genetics, WSL, Swiss Federal Institute for Forest, Snow and Landscape, Birmensdorf, Switzerland

Correspondence: Damiano Baldan (dbaldan@ogs.it)

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ABSTRACT

Aim: Seagrass meadows represent a key marine ecosystem owing to the significant biodiversity they host. Protection actions are often implemented without considering connectivity between habitats. In this article, we project and prioritise Mediterranean seagrass habitats (*Posidonia oceanica* and *Cymodocea nodosa*) based on their potential as sources/retention and stepping stones for dispersal propagules of the associated biotic communities. We use this information to identify gaps in the protection of highly ranked habitats.

Location: Mediterranean Sea.

Methods: We related seagrass observations with marine environmental predictors to run species distribution models and infer the distribution of Mediterranean seagrasses. We then used a network-based approach (CONEFOR) to rank patches of seagrass suitable areas based on their contribution to the seascape in terms of patch area, potential as source/retention of propagules and stepping stone. Finally, by overlaying our ranking with the spatial distribution of marine protected areas (MPAs), we identified potential gaps in the protection of important seagrass habitats across the Mediterranean and its basins.

Results: Most of the identified patches of seagrass suitable areas are not included in MPAs, only reaching a maximum protection coverage of ~50% in the Northwestern Mediterranean. Relatively few patches contribute disproportionately to connectivity, but top-ranked habitat patches are not included within the existing MPAs network, both at the Mediterranean scale and for most basins. The largest gaps for the source/sink role are in the Aegean and Ionian Sea, and largest gaps for the stepping stone role are in the Adriatic, Ionian and Tyrrhenian Sea.

Main Conclusions: Our results suggest that the current MPAs network fails to protect highly relevant patches of seagrass suitable areas in most of the Mediterranean basins. However, this gap could be filled by a few well-placed MPAs. Overall, we provide novel insights for the identification of key habitats and planning novel coastal MPAs in the region.

1 | Introduction

Seagrass meadows are a key component in coastal ecosystems worldwide (McKenzie et al. 2020), providing important habitats for fish and invertebrates, spawning grounds, shelter, food and also functioning as nursery areas for juveniles of numerous species (Bertness, Gaines, and Hay 2001). Thus, vegetated sites host a significant biodiversity (Calizza et al. 2013; Kalogirou et al. 2010; McHenry et al. 2021; Moranta et al. 2006), supporting local biotic populations and

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communities, with large benefits for fisheries (Unsworth, Nordlund, and Cullen-Unsworth 2019). Furthermore, seagrasses meadows constitute a globally relevant carbon sink (Kennedy et al. 2010). This ecosystem is impacted worldwide by boating activities, coastal development, water quality degradation (De Los Santos et al. 2019; Turschwell et al. 2021) and pressures of climate change (temperature regime shifts, sea-level rise) that are predicted to increase in the future (Chefaoui, Duarte, and Serrão 2018). Such pressures are particularly relevant in the Mediterranean Sea, where a significant contraction of the area occupied by *Posidonia oceanica* and *Cymodocea nodosa* was recorded in the last 150 years (De Los Santos et al. 2019; Marbà, Díaz-Almela, and Duarte 2014; Telesca et al. 2015). Effective protection and restoration measures could reverse this negative trend but are usually performed on a specific-site basis, with limited consideration for the connectivity between habitats (Beger et al. 2022; Bennett et al. 2009) on a sub-regional and regional scale.

At the species level, connectivity is defined as the flow of organisms between habitats and depends on the spatial configuration of the landscape and the ability of organisms to move or disperse between suitable habitats (Beger et al. 2022). Connectivity between habitat patches is relevant for populations and community dynamics, ultimately driving biodiversity distribution (Leibold and Chase 2017). Habitat patches linking distant sections of the landscape can act as stepping stones that connect distant habitats that are not within the dispersal range of species (Saura, Bodin, and Fortin 2014). Habitat patches with many ingoing or outgoing connections can be sources or sinks of propagules for neighbouring habitats (Mari et al. 2020). For instance, isolated habitats typically receive fewer dispersal propagules, leading to their species composition and abundance being influenced by local environmental factors (i.e., species sorting; Economo and Keitt 2010). In comparison, communities located in central habitats are more likely to receive dispersal propagules, exhibit weaker association with local environments and are more prone to hosting a diverse array of species (i.e., mass effects; Borthagaray et al. 2015; Thompson et al. 2020). These communities typically display higher species richness (alpha diversity) and greater similarity between each other (lower beta diversity) relative to communities in more isolated habitats (Engelhard et al. 2017; Gianuca et al. 2017; Suzuki and Economo 2021). Consequently, identifying habitat patches that are disproportionately contributing to landscape connectivity (e.g., stepping stones and sources/sinks sites) is crucial for maximising the design and efficiency of protection actions, especially when the focus is on the protection of biodiversity, rather than single species.

Marine protected areas (MPAs) currently encompass approximately 8% of the Mediterranean Sea (medpan.org), with the goal of safeguarding biodiversity, managing human activities and mitigating their impacts on ecosystems. However, this falls significantly short of the second objective outlined in the 2022 Kunming-Montreal agreement, which targets 30% of marine areas protection and better reserve network connectivity. MPAs have historically been established on a site-specific basis to regulate local human activities. For seagrasses, MPAs have been reported to provide conservation benefits, particularly when stressors (e.g., moorings, anchoring) are removed or reduced (Marbà et al. 2002; Swadling et al. 2023). The need to design a network of ecologically connected MPAs to achieve conservation goals at a large scale started being considered only recently (Balbar and Metaxas 2019; Roberts 2007). However, while the contribution of key habitats to landscape connectivity is rarely considered in marine conservation planning (Balbar and Metaxas 2019), network-based analyses highlighted a general lack of connectivity between European MPAs (Assis et al. 2021). A few studies have integrated connectivity estimates for potential MPAs planning, but only in specific basins of the Mediterranean and for limited spatial extents (Bandelj et al. 2020; Cristiani et al. 2021; Pastor et al. 2023). Mari et al. (2020, 2021) estimated Mediterranean-scale hotspots of *P. oceanica* habitats in terms of seagrass abundances and seeds sink/source potential, highlighting a general lack of protection. These studies focused on the dispersal of propagules of *P. oceanica* or few other species to estimate connectivity, without consideration for the role that seagrass habitats play in regulating connectivity for the associated biodiversity. Further, these studies did not provide any prioritisation of habitats based on their role in supporting connectivity.

Here, we focus on the role of seagrass habitats in regulating connectivity at the Mediterranean scale, addressing potential gaps in the protection of high potential seagrass habitats using network prioritisation and overlap analyses. First, we employed species distribution models (SDMs) to project the potential habitat suitability of two seagrass species (*P. oceanica* and *C. nodosa*). Based on the model's outputs, we defined patches of seagrass suitable areas (hereafter: patches) as a continuous groups of cells identified as suitable by the SDMs. Second, we employed a graph theoretic approach to prioritise and rank habitat patches based on their importance for seascape connectivity. Finally, we conducted a gap analysis to identify seagrass habitats of high ecological importance in terms of connectivity not considered in existing MPAs.

2 | Methods

2.1 | Species Distribution Models

We used the package 'biomod2' (Thuiller et al. 2009) in the R v4.3.1 computing environment (R Core Team 2022) to train SDMs, produce ensembles and predict habitat suitability distributions for *P. oceanica* and *C. nodosa* in the Mediterranean Sea.

2.1.1 | Environmental Data

Most of the environmental predictors used to fit SDMs were obtained from the re-analysis of the Mediterranean Sea physics (Escudier et al. 2020, 2021), biogeochemistry (Cossarini et al. 2021; Teruzzi et al. 2021) and sea waves (Korres et al. 2021) provided by the Copernicus Marine Service (CMS; Le Traon et al. 2019). The physics and biogeochemistry re-analysis products have a resolution of ~4.5×4.5 km and 125 unevenly spaced active vertical layers (thickness ranging between 2 and 100 m, increasing with depth). We downloaded the data with a monthly resolution for the period 2000–2020. The extracted physical variables included sea water velocity (Vm), potential temperature (T) and salinity concentration (SAL). The extracted biogeochemical variables included pH (pH),

concentrations of ammonium (NH_4), nitrate (NO_3), phosphate (PO_4), dissolved oxygen (O_2), chlorophyll (CHL) and phytoplankton expressed as carbon (PHY). The extracted sea waves variables included the wave significant height (VHM0) and the wave mean period from variance spectral density second frequency moment (VTM02). For all physical and biogeochemical variables, we selected the physicochemical conditions of the vertical layer just above sea bottom. Finally, for all variables, we calculated the cell by cell median, maximum, minimum and range of their physicochemical conditions over the 240 monthly maps covering the 20-year period and used those statistics as predictors for the models (Table S1).

Additionally, we used the high-resolution GEBCO bathymetric map (0.5×0.5 km; Weatherall et al. 2015) to calculate the average depth (DEPTH) and slope (SLOPE) of each 4.5×4.5 km grid cell. Finally, to account for human impacts, we considered the EMODnet vessel density (Falco et al. 2019) and used the: total density (VDTOT), fishing boats (VDFI), sailing boats (VDSA) and leisure boats (VDLE). A preliminary analysis showed that both *P. oceanica* and *C. nodosa* have higher occurrence probabilities in areas with intermediate vessel densities (Figure S1). We interpreted this pattern as a spatial correlation without causality, and therefore we dropped the vessel density from the predictor's list.

To retain a parsimonious subset of predictors for fitting the model and avoid overfitting, we performed a hierarchical cluster analysis based on a distance matrix, where we used 1 minus the absolute value of Spearman's correlation coefficient ($1-|r|$) as a measure of predictor's dissimilarity. We used the threshold of $r=0.7$ to identify 17 clusters of predictors and retained one predictor for each cluster (Figure S2; Table S1). Finally, we assessed the multicollinearity of the retained predictors with the variance inflation factor (VIF, function 'vifstep' in the package 'usdm'), resulting in a shorter list of 12 predictors used to fit the models (Table 1).

2.1.2 | Species Observations

Occurrence points for *P. oceanica* and *C. nodosa* data were retrieved from Chefaoui, Duarte, and Serrão (2017) and Chefaoui, Duarte, and Serrão (2018) respectively. The datasets reported a total of 1140 points for *P. oceanica* and 300 points for *C. nodosa*. Considering the spatial resolution of CMS Mediterranean products, we rarefied the data retaining only one occurrence point per 4.5×4.5 km grid cell, resulting in 640 points for *P. oceanica* and 127 points for *C. nodosa* used to fit the models (Figure 1).

2.1.3 | Pseudo-Absences

For each species, we used occurrence and pseudo-absence (P-Abs) data to fit the models. We combined two different sampling strategies to generate our P-Abs ($n=10{,}000$): 'density dependent' and 'environmentally stratified'. The first half of the P-Abs ($n=5000$) was generated according to the density-dependent strategy because occurrences of our two species displayed a strong sampling bias towards the north-western part of the Mediterranean (Figure 1). To correct this bias, we inferred the P-Abs based on the kernel smoothing intensity of all occurrence points (functions 'rSSI' and 'density.ppp' in the 'spatstat' package, setting the smoothing bandwidth parameter to 3). This method generated a higher density of P-Abs closer to species observations, mimicking the same sampling effort distribution (Descombes et al. 2022; Righetti et al. 2019). The second half of the P-Abs ($n=5000$) was generated based on a stratified subdivision of the environmental range. For this, we classified both the median temperature and salinity predictor rasters into three bins (splitting data at the 0.3 and 0.6 quantiles) of continuous values, re-grouped them into unique categories of temperature salinity ($n=9$) and sampled an equal number of P-Abs for each combination (Figure S3). This method guarantees that all environmental strata were represented in the training dataset and reduces extrapolation errors at the edge of the species' environmental niche (Da Re et al. 2023; Descombes et al. 2022). Finally, we replicated the above procedure three times for each species to account for the variability in the P-Abs generation.

2.1.4 | Model Calibration

We fitted four types of models: a generalised linear model (GLM), a generalised additive model (GAM), a random forest (RF) and an artificial neural network (ANN). We fitted intermediate complexity models to balance the fitting capacity with the ability to extrapolate to un-sampled environmental conditions, that is, to prevent overfitting following the guidelines in Brun et al. (2020). We fitted GLMs with linear and quadratic terms; set the regularisation in the GAM smooth term to 3; set a minimum size of 40 for terminal nodes and a number of 1000 trees for RF. We trained ANN models with three hidden layers and a decay of 0.1, which we found appropriate to avoid overfitting for the specific datasets.

Finally, we used the biomod2 default setting of equal prevalence to presences and P-Abs (i.e., the sum of the presences weights equals the sum of P-Abs weights). This way, the influence of P-Abs in the calibration of each single model was kept constant, regardless of the number of presence points used for fitting.

2.1.5 | Model Evaluation and Ensemble

To assess model performances, we employed fivefold cross validation (80% of the data for calibration, 20% for validation) and repeated it three times, thus yielding a total amount of 180 models (5 cross-validation folds × 3 repetitions × 3 PA datasets × 4 models) for each species. We used the area under the receiving operating curve (AUC) and the true skill statistics (TSS, Allouche, Tsoar, and Kadmon 2006) to evaluate the performance metrics of each model for both the validation and calibration datasets. Additionally, we assessed the model's performance using the Boyce's index, a presence-only metric (Hirzel et al. 2006). We used the validation AUC and TSS to assess the single models' performance. Additionally, we compared both validation and calibration AUC and TSS and checked how they differed to assess model's overfitting (Radosavljevic and Anderson 2014).

After discarding models with AUC < 0.7, we generated for each species a model ensemble by weight averaging each model based on its AUC score. We assessed the importance of

TABLE 1 | Descriptions and means (25th–75th percentiles) of predictors used in the models over the studied domain, and for the points where species occurrences are available.

Predictor name	Units	Description	Mediterranean	*Posidonia oceanica*	*Cymodocea nodosa*
CHL_{median}	$mg\,m^{-3}$	Concentration of chlorophyll-a close to the seafloor, median of monthly means	0.14 (0.1–0.25)	0.12 (0.09–0.17)	0.14 (0.1–0.22)
DEPTH	m	Median cell depth based on GEBCO bathymetry	23 (16–31)	20 (15–26)	19 (13.5–24.5)
$NO_{3\,median}$	$mmol\,m^{-3}$	Concentration of nitrate close to the seafloor, median of monthly means	0.8 (0.4–1.7)	0.8 (0.6–1.5)	0.7 (0.5–1.2)
$O_{2\,median}$	$mmol\,m^{-3}$	Concentration of dissolved oxygen close to the seafloor, median of monthly means	237.6 (226.1–245.4)	239.1 (229.7–243.8)	241.7 (236.7–245.8)
pH_{median}	—	Sea water pH close to the seafloor, median of monthly means	8.11 (8.08–8.13)	8.11 (8.1–8.13)	8.1 (8.09–8.12)
$PO_{4\,median}$	$mmol\,m^{-3}$	Concentration of orthophosphate close to the seafloor, median of monthly means	0.1 (0.1–0.3)	0.2 (0.1–0.6)	0.2 (0.1–0.5)
SAL_{median}	psu	Sea water salinity close to the seafloor, median of monthly means	38.2 (37.8–38.7)	38.1 (37.9–38.7)	37.8 (37.4–38.1)
SLOPE	$m\,m^{-1}$	Median cell slope based on GEBCo bathymetry	0.3 (0.1–0.7)	0.7 (0.4–1.1)	0.6 (0.3–1)
T_{median}	°C	Sea water potential temperature close to the seafloor, median of monthly means	17.3 (15.8–20.4)	16.3 (15.0–17.6)	16.8 (15.9–17.7)
T_{min}	°C	Sea water potential temperature close to the seafloor, minimum of monthly means	13.1 (11.7–14.6)	13.1 (12.5–13.7)	12.9 (11.7–13.4)
$VHM0_{median}$	m	Sea wave significant height, median of monthly means	0.6 (0.5–0.8)	0.5 (0.4–0.9)	0.5 (0.4–0.6)
Vm_{max}	$m\,s^{-1}$	Sea water velocity close to the bottom, maximum of monthly means	0.05 (0.04–0.07)	0.05 (0.03–0.07)	0.04 (0.03–0.07)

Note: See Table S1 for the full list of predictors extracted from CMS data. All predictors' statistics are calculated over a period of 20 years (2000–2020).

predictors in the final ensemble using a permutation approach. Following this method, each predictor was randomly permuted one at a time and model predictions made accordingly. Each prediction was then compared with and without permutation using Pearson's correlation coefficient (ρ). Predictor importance was determined as $1-\rho$. This process was repeated three times for each predictor, and the average variable importance was considered.

2.1.6 | Model Projection

The ensemble models (one for each species) were used to spatially predict species' habitat suitability over the study area. To binarise the habitat suitability score to suitable and unsuitable habitats, we used a threshold that balances omission and commission errors (Guisan, Thuiller, and Zimmermann 2017). Since both *P. oceanica* and *C. nodosa* are coastal organisms strongly

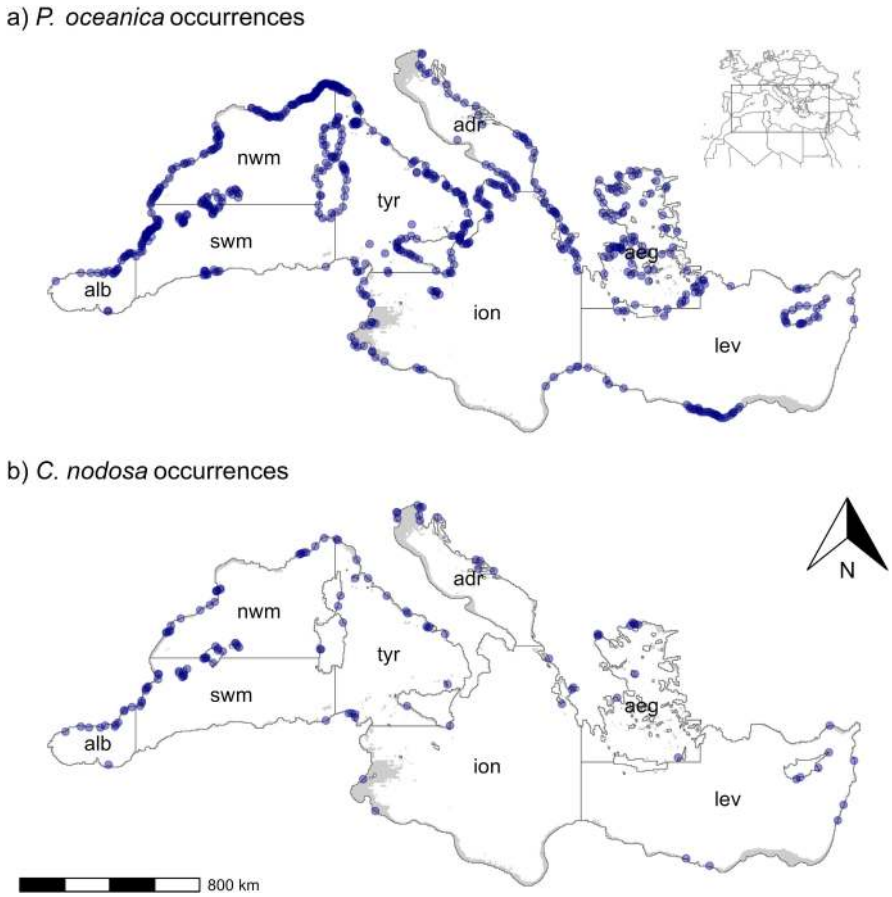

FIGURE 1 | Distribution of thinned (a) *Posidonia oceanica* and (b) *Cymodocea nodosa* occurrence points used to fit the models. The insert on the top-right represents the position of the study area. The shaded area represents the area where models were calibrated, validated and projected (<40 m of depth). The labels represent the Mediterranean basins used in the article: adr, Adriatic Sea; aeg, Aegean Sea; alb, Alborean Sea; ion, Ionian Sea; lev, Levantine Sea; nwm, north-west Mediterranean; swm, south-west Mediterranean; tyr, Tyrrhenian Sea.

limited by depth (Duarte 1991), we only retained in the projection suitable cells where the bottom layer's average depth is <40 m (Figure 1).

2.2 | Network-Based Connectivity Assessment

We used a network theory-based approach to uncover single seagrass habitat contributions to the landscape connectivity of the Mediterranean Sea based on SDM projection of suitable and unsuitable habitats.

First, we defined patches as a continuous group of SDMs suitable 4.5×4.5 km cells ('patches' function in the 'terra' package; Figure S4). Each patch was assigned a habitat weight based on its bathymetric configuration. For this, we used the GEBCO bathymetric map to calculate the fraction of each 4.5×4.5 km model cell that has a depth <40 m (Figure S5), that is, the fraction of the cell potentially occupied by seagrasses. After multiplying each cell fraction by their area, we then summed them all up in each patch to obtain patch-specific weights per patch representing the total area of potential seagrasses. Cells where both *C. nodosa* and *P. oceanica* were predicted to be present were counted twice to account for the increased habitat complexity given by the presence of both species (Figure S6).

Second, using the software CONEFOR (Saura and Torné 2009), we calculated indices of the probability of connectivity (PC) family to estimate the relevance of patches for the regional connectivity. The landscape (i.e., the spatial arrangement of suitable and unsuitable patches) is conceptualised as a graph where nodes are patches and links are all the possible connections between them. Graph nodes were weighted with the habitat weight calculated in the first step and graph links with inter-patch distances. The PC index is defined as the weighted sum of all dispersal probabilities (both direct and indirect, where indirect means through a sequence of stepping stones) between the nodes of the graph (Saura and Pascual-Hortal 2007). The dispersal probability between two adjacent patches is calculated based on the inter-patch (edge-to-edge) distance through a negative exponential probability density function (Table 2). The contribution of each habitat patch (graph node) to landscape connectivity is expressed with the dPC index, which indicates the change in relative PC when a habitat patch is removed. The dPC index is further decomposed into three components: dPC = dPCintra + dPCflux + dPCconnector (Table 2; Saura and Rubio 2010). The first component (dPCintra) depends only on patch attributes (here: patch area); the second (dPCflux) depends on the potential of each patch to act as starting or ending point of a connection (i.e., source/sink patch); the third (dPCconnector) on the relevance of a patch as a stepping stone. The dPCconnector

TABLE 2 | Probability of connectivity and its decomposition: Definitions.

Quantity	Formulation	Details
Probability of connectivity index	$PC = \sum_{i=1}^{n} \sum_{j=1}^{n} \frac{a_i \times a_j \times p_{ij}^*}{A^2}$	a_i and a_j are the habitat weights of the patches i and j; A is sum of the weights across the landscape; p_{ij}^* is the dispersal probability between i and j
Dispersal probability	$p_{ij}^* = \exp(-\alpha d_{ij})$	$\alpha = ln2 / d_{50}$; d_{ij} is the distance between patches i and j d_{50} is the dispersal distance at which $p_{ij}^* = 0.5$
dPC index (relative importance of patch k for landscape connectivity)	$dPC_k = \frac{(PC - PC_{remove,k})}{PC} \times 100$	$PC_{remove,k}$ is the PC index of the landscape when the patch k is removed
dPC decomposition	$dPC_k = dPC\ intra_k + dPCflux_k + dPCconnector_k$	
dPCintra (habitat surface area provided by patch k)	$dPCintra_k = dPC_k = a_k^2$ when PC is calculated with the constrain: $i = j = k$	Depends only on the habitat weights (i.e., patch area)
dPCflux (weighted potential dispersal flux of patch k)	$dPCflux_k = dPC_k$ when PC is calculated with the constrain $i = k$ or $j = k$ and $i \neq j$	It defines the number of incoming/outgoing connections and the weights of the nodes, and thus represents the ability of the patch to act as a source or sink for connectivity. It depends on the position of the patch in the network topology
dPCconnector (importance of patch k as stepping stone)	$dPCconnector_k = dPC_k$ when PC is calculated with the constrain $i \neq k, j \neq k$	It defines the irreplaceability of a patch as a link between nodes. It depends on the position of the patch in the network topology

index can be considered a centrality metric and correlates well with other centrality metrics such as betweenness centrality (Figure S7).

We generated the habitat network using a dispersal distance of 60 km. This distance is representative of the dispersal potential of crustaceans, polychaetes and fish whose propagules duration time is between several weeks and few months (Shanks 2009; Shanks, Grantham, and Carr 2003). As a sensitivity analysis, we calculated the indices also for two additional network configurations: (a) a network with a dispersal distance of 10 km, representative of relative short distances that can be covered by the seagrass resident *Sarpa salpa* (Pagès et al. 2013) or other short-range dispersers; (b) a network with a dispersal distance of 150 km, representative of long-range dispersers (Shanks 2009; Shanks, Grantham, and Carr 2003). The indices calculated over these two additional configurations were highly correlated with those resulting from the 60 km network (Spearman's rank correlation = 0.85–0.97 for dPCflux and 0.88–0.97 for dPCconnector; Figure S7), thus here we report only the results from the 60-km network.

2.3 | Gap Analysis Based on MPAs

We overlaid the patch-based connectivity assessment to the Mediterranean MPAs map obtained from the database of MPAs in the Mediterranean (SPA/RAC and MedPAN 2019). We removed cetacean protection areas from the list since their main conservation goal is to protect individual pelagic species. We considered a seagrass patch to be included in the MPAs network if at least 75% of its area falls inside a protected area. We conducted the gap analysis for the Mediterranean and separately for its different basins: Alboran Sea, Northwest Mediterranean, Southwest Mediterranean, Tyrrhenian Sea, Adriatic Sea, Ionian Sea, Aegean Sea and Levantine Sea (Figure 1). First, we compared the number of patches included and excluded from MPAs. Second, we ranked patches based on their relative importance for landscape connectivity at the Mediterranean and at the basin scales and checked the number of protected patches within the high-ranked ones. We considered three MPA categories designed under three different types of legislation: (a) International (e.g., Natura 2000 sites), (b) National and (c) Regional since they generally show a different level of protection and enforcement (National > Regional > International). MPAs established within national jurisdiction often guarantee higher protection and are considered 'fully' or 'strongly protected areas' due to the presence of 'no-take zones', implemented management plans, operational management bodies, regulation of most human activities and periodic monitoring activities (Claudet et al. 2020; Sala et al. 2018). On the contrary, Regional and International MPAs usually lack effective management, surveillance, knowledge on the conservation status of target species inside their borders and stated conservation objectives (Fraschetti et al. 2022; Gianni et al. 2022; Guidetti et al. 2019). A similar ranking was also adopted recently for a North Adriatic MPAs prioritisation according to the level of protection for assessing coastal vulnerability

to oil spill (Bandelj et al. 2024). In the case of spatial overlap between MPAs belonging to different categories, we considered the MPA that conferred the highest level of protection.

3 | Results

The individual models were fitted with acceptable performances (Table 3). The overfitting was limited, with the difference between calibration and validation AUC below than 0.1, and the difference between calibration and validation TSS being lower than 0.2 for most models (Figures S8 and S9). The ensembles used for the habitat projections also had good performances, with an AUC of 0.80 for *P. oceanica* and 0.84 for *C. nodosa*, a TSS of 0.47 for *P. oceanica* and 0.59 for *C. nodosa* and a Boyce index of 0.90 for *P. oceanica* and 0.92 for *C. nodosa* (Table 3). The most important predictors for *P. oceanica* were the median temperature (T_{median}, $1-\rho=0.25$), the seafloor slope (SLOPE, $1-\rho=0.20$), the seafloor depth (DEPTH, $1-\rho=0.17$) and the nitrate concentration ($NO_{3\ median}$; $1-\rho=0.13$), with an optimal species response at lower $NO_{3\ median}$ ($\leq 2.0\,mmol\,m^{-3}$) and intermediate temperature ($\leq 17°C$). The most important predictors for *C. nodosa* were the seafloor slope (SLOPE, $1-\rho=0.24$), the oxygen dissolved at the seafloor ($O_{2\ median}$, $1-\rho=0.20$), the nitrate concentration ($NO_{3\ median}$, $1-\rho=0.17$) and the phosphate concentration ($PO_{4\ median}$, $1-\rho=0.15$; Figure 2). The ensemble model for *P. oceanica* predicted a widespread distribution, with absences in the western Adriatic Sea, in some areas of the eastern Mediterranean and across most part of the Libyan coast (Figure 3a). The ensemble model for *C. nodosa* predicted a smaller extent of suitable habitats in the Eastern Mediterranean, with some habitats in the Aegean Sea and some suitable habitat in the northern Adriatic, where *P. oceanica* was predicted to be absent (Figure 3b).

Based on the habitat projections, we identified 351 *P. oceanica* patches (mean area: $35\,km^2$, maximum area $956\,km^2$) and 232 *C. nodosa* patches (mean area: $41\,km^2$, maximum area: $1329\,km^2$). The union of the two habitat layers resulted in a total number of 383 patches (mean area: $59\,km^2$, maximum area: $1673\,km^2$), which constituted the nodes of the habitat network (Figure 4 and Figure S4).

The identified habitat patches (union of *P. oceanica* and *C. nodosa* habitats) had highly skewed values of dPC indices (Figure 4). The dPCintra, dPCflux and dPCconnector indices had a mean value of 0.03 (range: 0–2.23), 0.46 (range: 0.02–6.13) and 0.09 (range: 0–2.88) respectively. The five patches with higher dPCintra were located along the northern Spanish coast (patch ID: 351 and 285), in the northern Adriatic Sea (1) and in the Thyrrenean Sea (50 and 179; Figure 4a). The five patches with higher dPCflux were located along the Northern Spanish coast (351 and 285), in the western side of the Sardinian coast (388), along the Tyrrhenian coast of Italy (50) and in the northern Adriatic Sea (1; Figure 4b). The five patches with higher dPCconnector were in the Aegean Sea (461 and 263), in the eastern side of the Adriatic Sea (61 and 60) and in the Balearic Islands (361; Figure 4c).

The overlay between identified patches and MPA borders showed many unprotected patches (294 over 383, Figure 5). However, the level of protection exclusion strongly varied between basins. While the highest number of protected patches in relation to unprotected was in the northwest Mediterranean (27 protected vs. 18 unprotected), most patches in the other basins remained unprotected. For instance, in the Aegean Sea, 16 patches were protected against 68 unprotected; and in the Tyrrhenian Sea, 14 patches were protected versus 47 unprotected.

The overlay of the dPC prioritisation with the MPA borders showed that of the most relevant 20 patches, only four were protected in the dPCintra ranking (Regional and International MPAs), five in the dPCflux ranking (Regional and International MPAs) and five in the dPCconnector ranking (only Regional MPAs; Figure 6). The 20 top contributing patches of each index, accounting for 71%, 33% and 57% of all the dPCintra, dPCflux and dPCconnector cumulated values, only 10%, <10% and 13% of dPCintra, dPCflux and dPCconnector were included in some MPAs respectively (Figure 6).

The overlay of the dPC prioritisation with the MPA borders for the different basins also showed differences in the levels of protection (Figure 7). For instance, in the Northwest Mediterranean, the top 20 patches contributed to 96% (89% protected), 99% (76% protected) and 78% (61% protected) of dPCintra, dPCflux and dPCconnector respectively. Here, National MPAs covered several high-ranked patches. On the contrary, for the Aegean Sea,

TABLE 3 | Individual models mean (range) performances.

Species	Algorithm	AUC	TSS	Boyce's index
Posidonia oceanica	ANN	0.76 (0.74, 0.78)	0.41 (0.37, 0.43)	0.94 (0.93, 0.96)
	GAM	0.77 (0.76, 0.78)	0.4 (0.38, 0.43)	0.95 (0.94, 0.96)
	GLM	0.77 (0.75, 0.78)	0.4 (0.38, 0.43)	0.95 (0.94, 0.96)
	RF	0.78 (0.76, 0.79)	0.4 (0.36, 0.42)	0.91 (0.91, 0.92)
	Ensemble	0.8	0.47	0.90
Cymodocea nodosa	ANN	0.75 (0.73, 0.77)	0.38 (0.31, 0.43)	0.92 (0.9, 0.94)
	GAM	0.78 (0.75, 0.8)	0.43 (0.37, 0.47)	0.94 (0.93, 0.95)
	GLM	0.78 (0.76, 0.81)	0.43 (0.37, 0.48)	0.94 (0.93, 0.95)
	RF	0.76 (0.74, 0.8)	0.38 (0.34, 0.46)	0.88 (0.87, 0.89)
	Ensemble	0.84	0.59	0.92

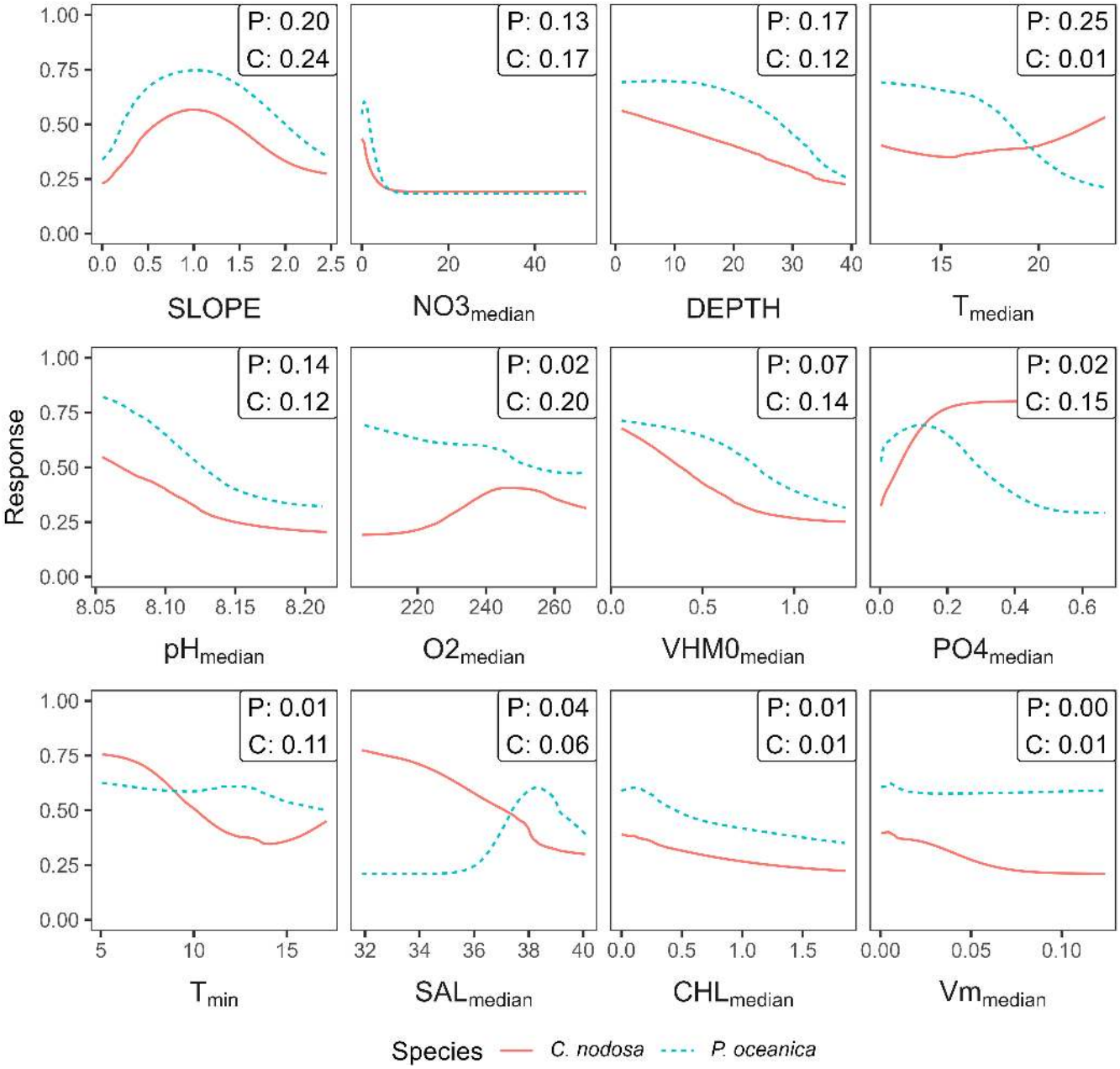

FIGURE 2 | Partial dependency plots for *Posidonia oceanica* and *Cymodocea nodosa*. The inserts on the graphs are the variable importance (see Section 2).

the top 20 patches contributed to 87% (<5% protected), 90% (26% protected) and 60% (5% protected) of dPCintra, dPCflux and dPCconnector respectively. Here, Regional MPAs covered only a few patches, and only two patches relevant for dPCconnector was protected by a National MPA, but not among the top ranked. In the Ionian Sea, almost no patches were protected, with <10% of dPCintra and dPCflux, and dPCconnector protected. In the Thyrrenian sea, despite the existence of several patches included in MPAs, only <10% of dPCintra and dPCflux, and 30% of dPCconnector was protected. Here, a National MPAs covers a patch that is not top-ranked for dPCflux, but the fourth top-ranked patch for dPConnector. In the Adriatic Sea, one National MPA covers a patch that is relevant for dPCintra and dPCconnector, but not top ranked, while dPCflux patches are not covered by National MPAs. For most of the basins, the values of dPCintra, dPCflux and dPC connector of protected patches were not significantly different than those of unprotected patches, except for dPCintra in the Northwest Mediterranean and dPCconnector for the Aegean Sea and the Alboran Sea (Mann–Whitney *U* test; Table S2).

4 | Discussion

4.1 | Environmental Drivers of Seagrasses Distribution

Our analyses identify seafloor slope and depth, water quality (prominently nitrate concentration and pH), temperature and waves as being the most relevant predictors for *P. oceanica* and *C. nodosa*. Seafloor depth is directly related to the quantity of

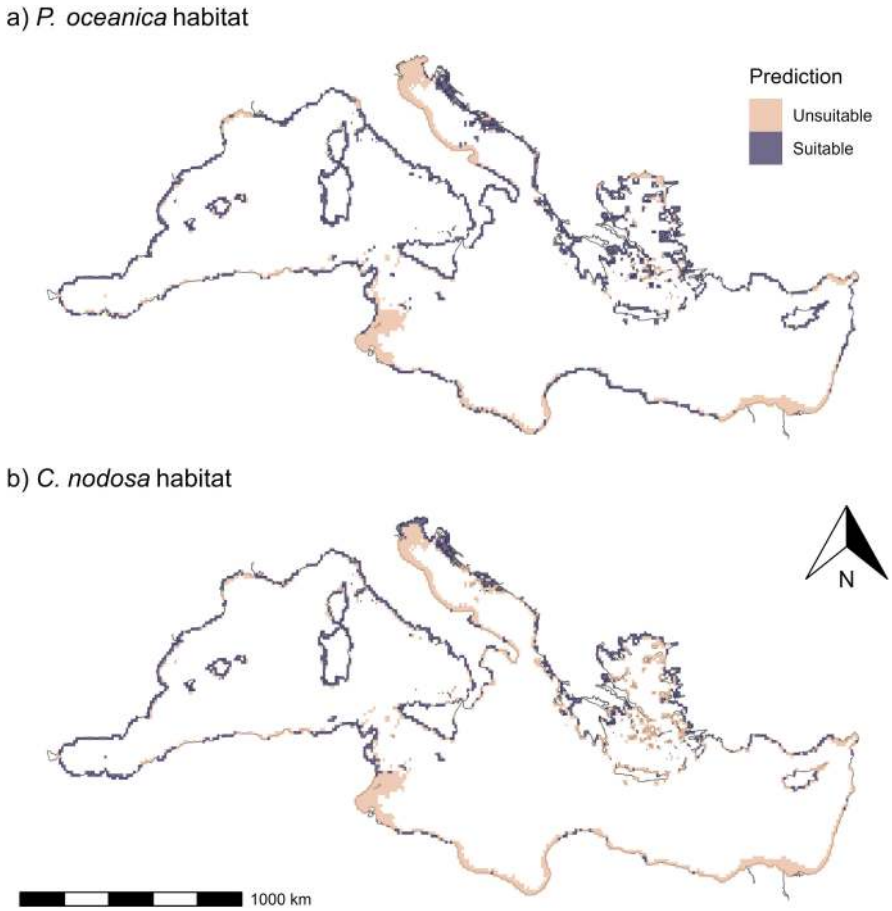

FIGURE 3 | Projected occurrence for (a) *Posidonia oceanica* and (b) *Cymodocea nodosa*. To improve visualisation, the indices are displayed with an artificially coarser resolution (13.5 × 13.5 km, three times the original grid resolution; see Figures A1–A9 in the Appendix A for the zoomed maps at the native resolution).

light available and was also recorded as the most influential variable in other modelling studies (Catucci and Scardi 2020). Further, low nitrate concentrations and temperatures were found to be highly suitable conditions for seagrasses, following previous experimental studies that found detrimental effects of high temperature and nitrate concentration at the individual level (e.g., growth rate, leaf formation, leaf biomass; Olsen et al. 2012). Particularly, seagrass dependency to low levels of nitrogen and phosphorous could reflect the known positive effects of small quantities of nutrients in the context of nutrient limitation (Alcoverro et al. 1997), and the negative effects of increasing grazing pressure due to changes in epiphytic assemblages (Balata et al. 2010). Furthermore, modelling studies in the Mediterranean found similar dependencies for temperature and salinity (a proxy for nutrients; Chefaoui et al. 2016; Chefaoui, Duarte, and Serrão 2018). The preference of *C. nodosa* for sites with low wave significant height was also recorded in other modelling studies (Chefaoui et al. 2016). Overall, our models confirmed the known major expert-based distributional patterns of seagrasses such as their presence in the western Mediterranean coast and the Aegean Sea and absence in the western side of the Adriatic Sea and in most of the eastern coast of the Mediterranean (Telesca et al. 2015). Our results are also in agreement with the large-scale patterns detected in a study that employed satellite mapping to reconstruct the distribution of *P. oceanica* (Traganos et al. 2022).

4.2 | Gaps in the Protection of Connectivity Between Seagrasses Habitats

Building on the projected habitat distribution, our network analysis ranks the patches based on their contribution to landscape connectivity. Our results show significant gaps in the protection of both seagrass habitats (dPCintra index) and inter-patch connectivity (dPCflux and dPCconnector indices), both at the Mediterranean scale and for a large majority of the basins. This result comes as no surprise, since only a low percentage of the Mediterranean is protected: according to Claudet et al. (2020), 6% of the basin is protected, of which 0.23% can be categorised under 'highly protected' and 'fully protected' areas. Moreover, a single patch that is ranked high for all the three indices does not exist for the whole Mediterranean Sea nor for single basins.

The lack of protection of patches relevant for connectivity is probably because historically, MPAs have been established to regulate local human activities on a site-specific basis. As a result, connectivity aspects have been systematically disregarded (Balbar and Metaxas 2019). This is true in the Mediterranean Sea, where a systematic lack of connectivity between no-take reserves was already pointed out (Assis et al. 2021), but also at smaller spatial scales (basins), where protection planning should be less complex. For instance, current protected

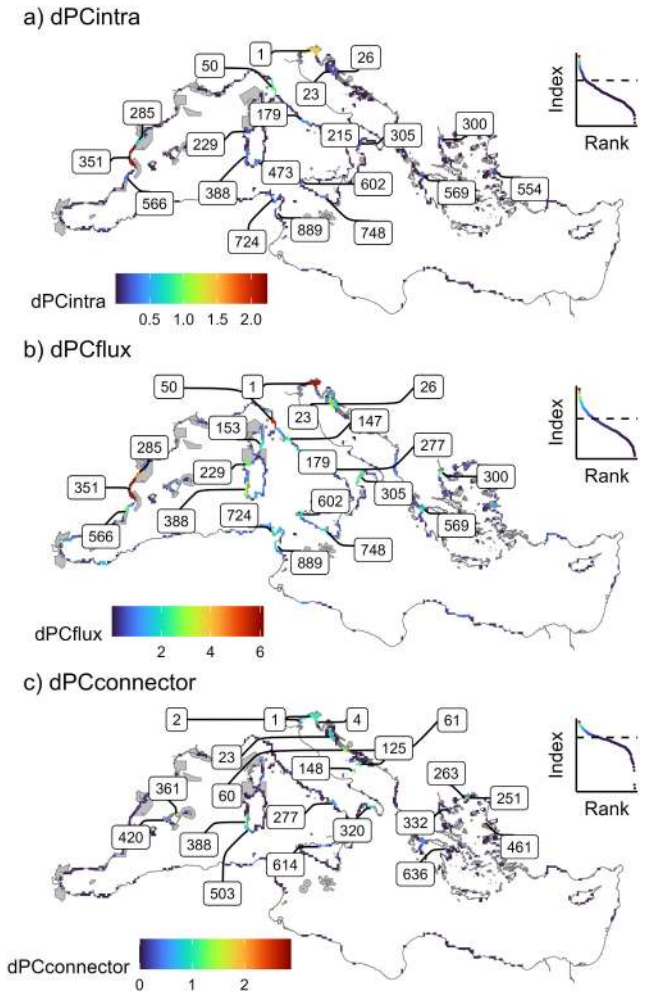

FIGURE 4 | Spatial distribution of the indices (a) dPCintra, (b) dPCflux and (c) dPCconnector for the union of *Posidonia oceanica* and *Cymodocea nodosa* habitats. The grey-shaded polygons show the position of marine protected areas. Labels highlight the 20 patches with the highest indices. The insert on each map shows the indices ordered by their rank (from most to less important); the dashed line represents the index mean value (index is log-transformed, the colour scale is the same as the map). To improve visualisation, the indices are displayed with an artificially coarser resolution (13.5×13.5 km, three times the original grid resolution; see Figures A1–A9 in the Appendix A for the zoomed maps at the native resolution).

areas are insufficient to protect meta-communities living in patchy biogenic habitats in the Northern Adriatic Sea (Bandelj et al. 2020). Only in the recent decades, the idea and need to design a network of ecologically connected MPAs has been stated to achieve conservation goals at a large scale (Balbar and Metaxas 2019; Roberts 2007). An MPA network, if well designed and managed, can theoretically operate more effectively and comprehensively than individual MPA sites or a group of isolated MPAs (McLeod et al. 2009). Well-connected MPAs exchange propagules, increase individual dispersal, genetic diversity and may generate economic and social benefits (Beger et al. 2022; Bennett et al. 2009; Bevilacqua et al. 2023). Connectivity aspects could be included in future MPAs planning by, for example, considering the rankings of dPCflux and dPCconnector in the prioritisation of candidate sites. Since the distribution of such indices is highly skewed, even the inclusion of a few high-ranked patches would be meaningful for keeping the seagrasses landscape connected.

4.3 | Links Between Connectivity Indices and Biodiversity Facets

Organisms' dispersal/movement across the landscape is one of the major factors structuring biodiversity distribution (Leibold and Chase 2017). Since the indices we employed describe the easiness of movement across the patchy landscape, they could be considered as relevant proxies for biodiversity distribution and could relate to different facets of biodiversity that need to be considered in conservation planning (Beger et al. 2022).

The dPCintra index scales with the patch area attribute and can be used to rank patches based on habitat capacity. Sites with higher dPCintra should host a larger number of resident species (a higher alpha diversity; Engelhard et al. 2017). Furthermore, considering sites with higher dPCintra in a MPA maximises the protected seagrasses area, decreasing the habitat destruction risks from localised disturbances (e.g., excessive sedimentation due to extreme storms; Gera et al. 2014). Our analysis shows such sites to be concentrated in the Northwest Mediterranean, in the Tyrrhenian Sea, in the northern Adriatic and in the Sicilian strait. However, only in the Northwestern Mediterranean patches falling within an MPA also have significantly high dPCintra values. Large patches belonging to such basins should therefore be prioritised when the protection of alpha diversity is a priority.

The dPCflux index depends on the patch position in the network in terms of the number of connections it has with other patches, and can be used to rank patches based on the potential to act as a source or a sink of dispersal propagules. Sites with high dPCflux can potentially act as sources of dispersal propagules or retention zones (Melià et al. 2016). In the case of asymmetric dispersal (directed network), the source/sink functions are described by two dPCflux indices, calculated using either inbound or outbound connections. Sites with high dPCflux values and should be prioritised when the goal is the protection of sites that maximise the stability of meta-populations and meta-communities relying on the habitat network. In fact, sites acting as sources of propagules can sustain populations and communities persistence in neighbouring sub-optimal sites, preventing local extinctions via mass effects (Thompson et al. 2020). The source/sink role is particularly relevant for those sites that host valuable populations or endangered organisms, such as the critically threatened fan mussel *Pinna nobilis* (Tatton et al. 2019). Our analysis shows such sites to be concentrated in the northwest Mediterranean, in the Tyrrhenian Sea, in the northern Adriatic Sea and in the Sicilian strait. Patches with high dPCflux should therefore be prioritised when the protection of the source/sink dynamics is a priority.

The dPCconnector index depends on the position of the patch in the network and can be used to rank patches based on

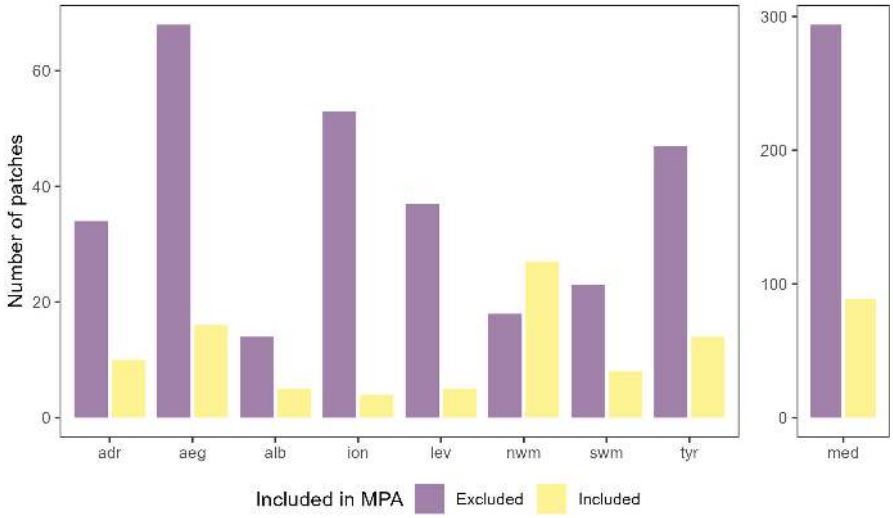

FIGURE 5 | Number of habitat patches included and excluded from MPAs for different basins and for the whole Mediterranean Sea. See Figure 1 for the position of the basins: adr, Adriatic Sea; alb, Alborean Sea; arg, Aegean Sea; ion, Ionian Sea; lev, Levantine Sea; med, Mediterranean Sea; nwm, north-west Mediterranean; swm, south-west Mediterranean; tyr, Tyrrhenian Sea. Habitat patches are defined as a group of adjacent SDM suitable cells, see Section 2.

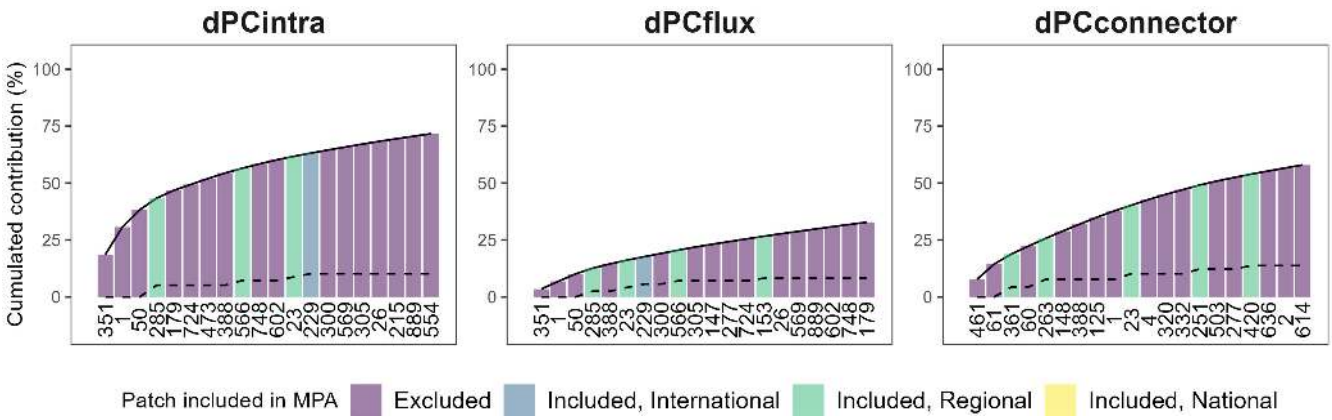

FIGURE 6 | Cumulated contribution of the 20 most relevant habitat patches to the dPCintra, dPCflux and dPCconnector indices for the Mediterranean. The patches are arranged by decreasing importance and the cumulative contribution is normalised to 100. The dashed line represents the cumulative contribution of the patches that are included in marine protected areas. The geographic positions of the five top-contributing patches for each index are represented in Figure 4. See Figure S10 for the plot with all the patches. Excluded: Patches not included in any MPA; Included-International: Patches included in an international MPA; Included-Regional: Patches included in a regional MPA; Included-National: Patches included in a national MPA. Habitat patches are defined as a group of adjacent SDM suitable cells, see Section 2.

their role as bottlenecks, that is, their relevance in connecting distant sections of the habitats network. According to meta-community theory, central habitats, that is, sites with higher dPCconnector are expected to host a larger number of mobile species, since they are more exposed to the arrival of dispersal propagules. Sites with lower dPCflux and dPCconnector, on the other hand, would tend to have a higher beta diversity, that is, to host very different communities (Heino et al. 2015). Sites with higher dPCconnector should be prioritised when the objective is to preserve the long-range connectivity of the patches network. Our analysis shows such sites to be scattered over the whole Mediterranean, often being sites with limited area located in between larger patches. However, only in the Aegean Sea and in the Alboran Sea patches falling within an MPA also have significantly high dPCconnector values. Protecting patches with high dPCconnector should be a priority when the objective is the preservation of landscape integrity with respect to connectivity.

Building on the spatial distribution of the connectivity indices, a final prioritisation for the Mediterranean or for specific basins could be derived using a multi-criteria analysis. Based on the conservation goals described earlier, weights can be assigned to dPCintra, dPCconnector and dPCflux for a final prioritisation. In this regard, tradeoffs between the different indices should be explored before weighting them.

4.4 | Limitations and Perspectives

While our models predicted well the general biogeographic patterns of seagrass distribution in the Mediterranean Sea,

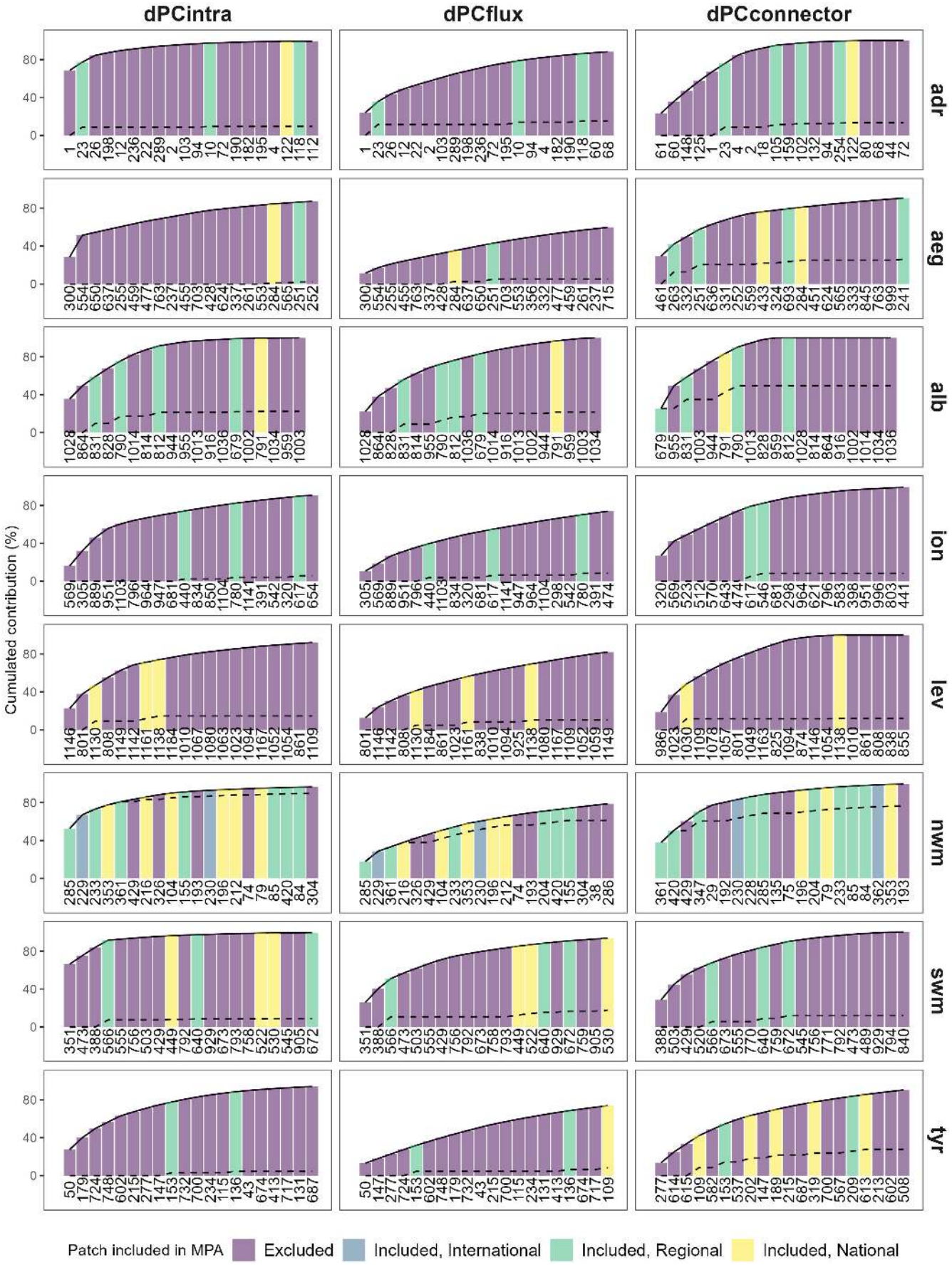

FIGURE 7 | Legend on next page.

FIGURE 7 | Cumulated contribution of the 20 most relevant habitat patches to the dPCintra, dPCflux and dPCconnector indices for different basins. The patches are arranged by decreasing importance and the cumulative contribution is normalised to 100. The dashed line represents the cumulative contribution of the patches that are included in marine protected areas. See Figure 1 for the position of the basins: adr, Adriatic Sea; alb, Alborean Sea; arg, Aegean Sea; ion, Ionian Sea; lev, Levantine Sea; nwm, north-west Mediterranean; swm, south-west Mediterranean; tyr, Tyrrhenian Sea. See Figure S11 for the plot with all the patches. Excluded: Patch not included in any MPA; Included-International: Patch included in an international MPA; Included-Regional: Patch included in a regional MPA; Included-National: Patch included in a national MPA. Habitat patches are defined as a group of adjacent SDM suitable cells, see Section 2.

the distributional range of *C. nodosa* was smaller than expected based on the occurrence data. In fact, almost only absences were predicted in the eastern Mediterranean, where few occurrence points are available. Although the techniques employed for generating P-Abs allow for reducing biases due to uneven sampling efforts across different Mediterranean countries, higher uncertainty is to be expected for predictions in the southern and eastern side of the Mediterranean. More efforts should be made in the future in mapping those under surveyed areas. In any case, the developed habitat suitability models are particularly relevant for two reasons. First, while the same network-based prioritisation of patches could rely on habitat surveys, this information is rarely available when dealing with larger spatial extents, where sampling efforts are hardly evenly distributed. Second, the network-based prioritisation is valid only for present conditions. In the future, climate change could lead to increases in seawater temperature, and to changes in nutrients and salinity regimes due to modified fluvial inputs in the coastal zone. Thus, the developed models can be used to project potential habitat changes and the cascading effects over ecological seagrasses hotspots under future scenarios. In this regard, the limited overfitting of the calibrated models makes them good candidates for extrapolations to potentially different environmental conditions, both for projecting habitat suitability in sites or regions where extensive mapping is not available, or under climate change scenarios (Brun et al. 2020).

Besides the uncertainties related with the SDMs discussed before, another caveat of our network analysis is that in an oceanographic context, movement and dispersal of organisms are influenced by the physical properties of the medium (i.e., velocity field, density, temperature). Recent work addressed this issue by implementing connectivity assessment of *P. oceanica* seeds based on Lagrangian dispersal, but either covering a smaller spatial extent (Cristiani et al. 2021; Grech et al. 2016; Pastor et al. 2023) or using a coarse resolution, which hinders the identification of habitat patches (Mari et al. 2020, 2021). When considering different organisms inhabiting the meadow, several complications arise. For instance, considering a set of organisms would require different parametrisations of the propagule's behaviour in terms of dispersal capacity, further increasing the complexity of the problem. Although in our connectivity analysis we did not consider oceanographic conditions, our approach is flexible. First, potential dispersal could be used as an upper boundary for estimating potential connectivity (Watson et al. 2012). Second, probabilities based on Lagrangian dispersal or individual-based models could be included in a later stage to produce species-specific or basin-specific stochastic connectivity estimates. CONEFOR requires only a definition of a probability of dispersal, dPC indices could be computed also based on such refined connectivity estimates. Finally, we note that the patches prioritisation we obtained is relatively robust with respect to the choice of the dispersal kernel. While larger dispersal kernels would generate networks with different topologies, they would not be representative of organisms inhabiting the seagrass meadows.

The inclusion of directionality in our estimates of dispersal could also affect our results. For instance, it has been shown that betweenness centrality, a metric we found highly correlated with dPCconnector, is highly sensitive to network directionality (Tiwari et al. 2023). Thus, patches prioritisation could also be substantially impacted by the inclusion of asymmetric dispersal due to currents induced directionality. In the Adriatic Sea, the counter-clockwise circulation pattern generates distributions of passively dispersing propagules that are skewed towards the direction of prevailing currents (Melià et al. 2016). A directional network should therefore be used here given passively dispersing organisms will not disperse symmetrically. In this case, indices based on the directional network should be used for the prioritisation. For instance, dPCflux and dPCconnector can still be calculated on a directional network by considering only inbound links or outbound links. The dPCflux is influenced by the number of inbound/outbound links. With inbound links only, patches with high dPCflux would be located more downstream than the non-directional case; while with outbound links, patches with high dPCflux would be located more upstream than the non-directional case. Similarly, the dPCconnector index is related to the number of connections crossing a patch, and an upstream/downstream shift is to be expected when outbound/inbound links only are considered respectively. Thus, an important caveat in our work is that the prioritisation yields only for species whose dispersal is not heavily influenced by currents.

The approach we propose could be validated with biotic data. Network-based indices were successfully related to species richness (Engelhard et al. 2017) and beta-diversity (Bandelj et al. 2020) to prioritise areas to protect. However, so far, such relationships have been developed to smaller spatial extents. Future research could focus on validating such connectivity indices at the Mediterranean or at the sub-basin scale, with the limitation that currently available occurrence data have a strong spatial bias (Coll et al. 2012).

The difficulty of assessing ecological connectivity and how to consider it in practice may also be another reason hindering the use of this criterion in the MPA planning process. In this context, the approach proposed here is a first step towards the inclusion of different facets of connectivity in this process and to identify habitats that are expected to be relevant contributors.

Author Contributions

Damiano Baldan: conceptualization, data curation, methodology, investigation, visualization, writing – original draft, writing – review and editing. **Yohann Chauvier-Mendes:** methodology, writing – review and editing. **Fabrizio Gianni:** data curation, writing – review and editing. **Gianpiero Cossarini:** methodology, funding acquisition, writing – review and editing. **Vinko Bandelj:** conceptualization, methodology, funding acquisition, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data generated in this study are available on Dryad at https://doi.org/10.5061/dryad.nvx0k6f0c.

Peer Review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.13922.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.

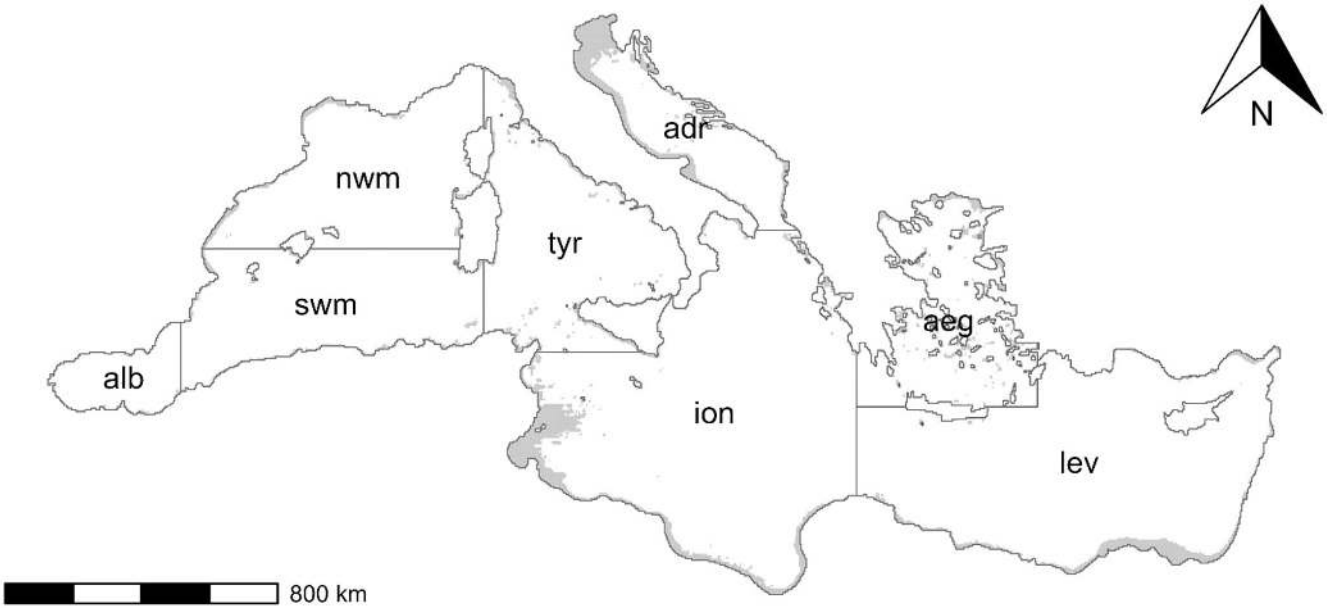

FIGURE A1 | Distribution of basins used in the analysis.

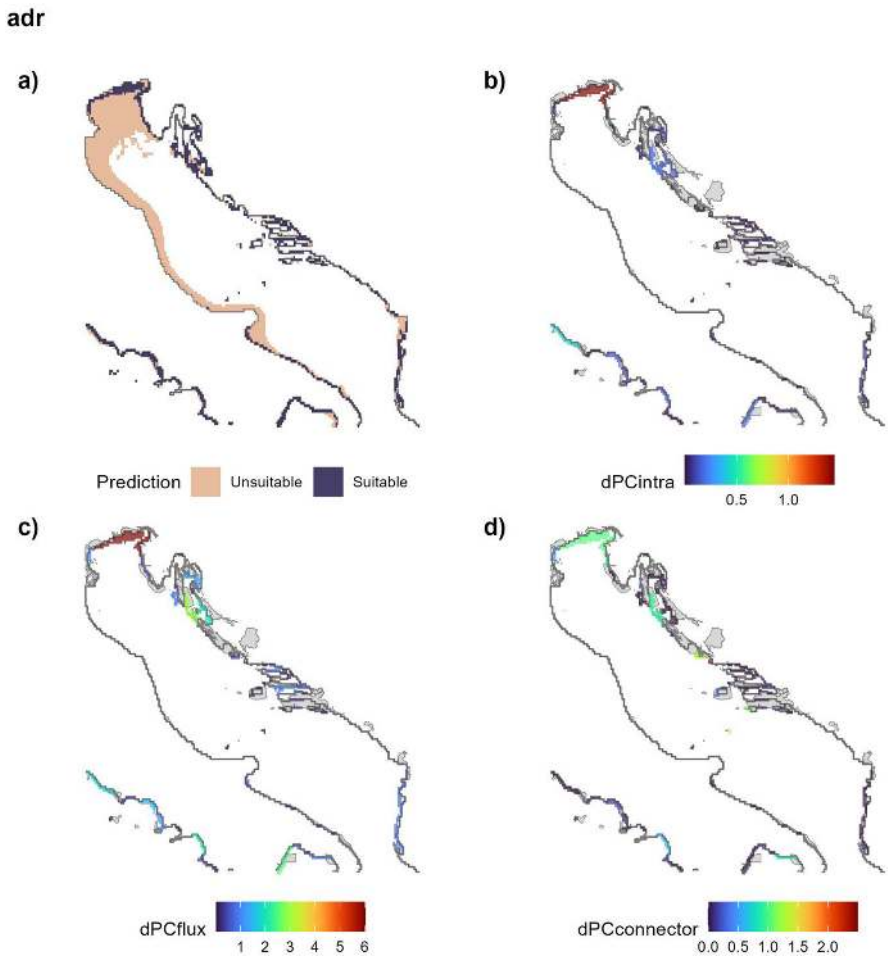

FIGURE A2 | Spatial distribution of suitable and unsuitable sites (a), dPCintra (b), dPCflux (c) and dPCconnector (d) over the Adriatic Sea. See Figure A1 for the position in the Mediterranean Sea. The shaded polygons are the position of the marine protected areas used in the analysis.

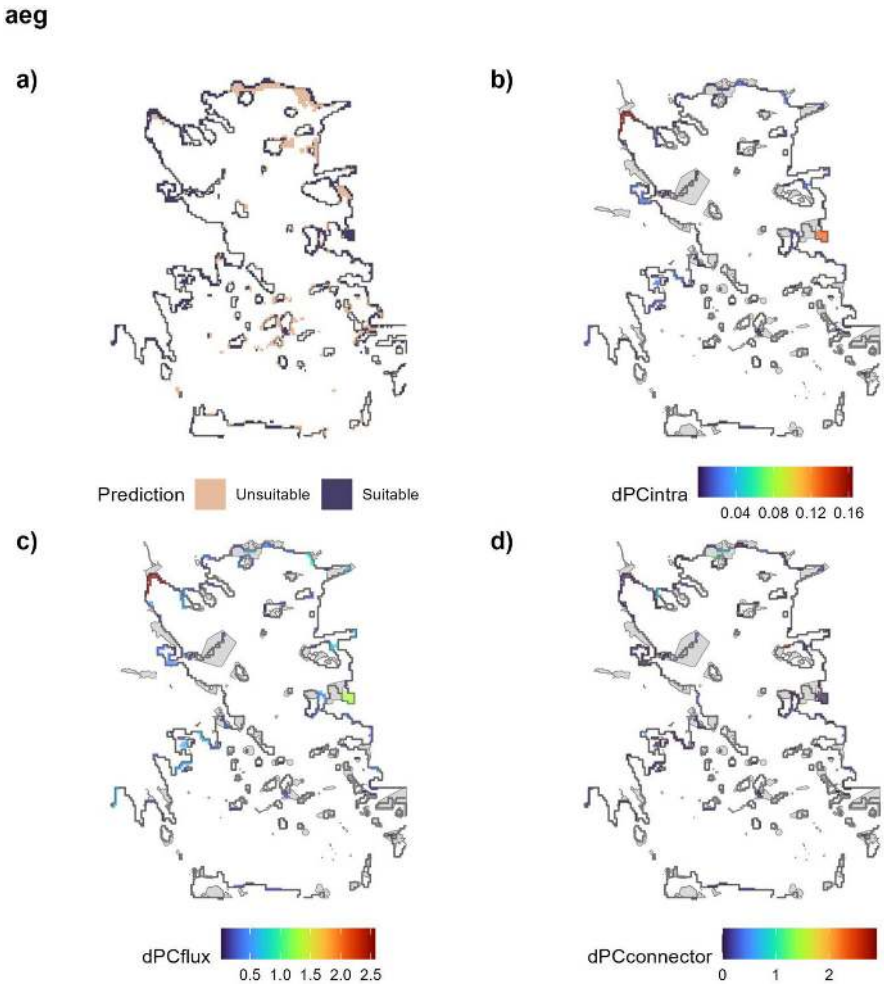

FIGURE A3 | Spatial distribution of suitable and unsuitable sites (a), dPCintra (b), dPCflux (c) and dPCconnector (d) over the Aegean Sea. See Figure A1 for the position in the Mediterranean Sea. The shaded polygons are the position of the marine protected areas used in the analysis.

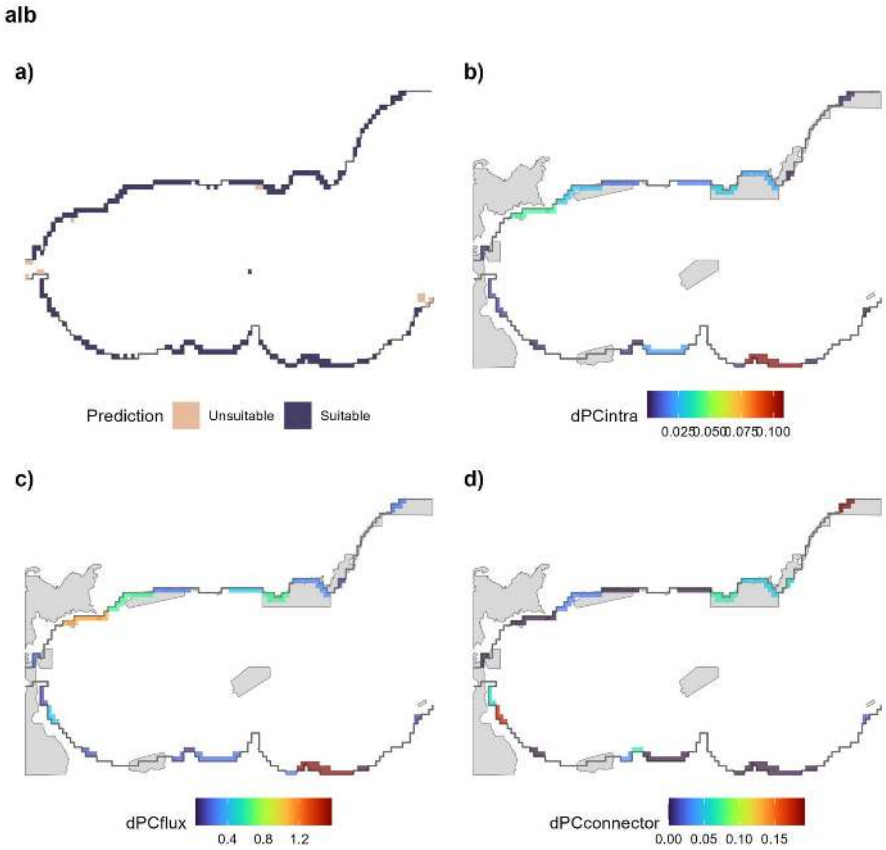

FIGURE A4 | Spatial distribution of suitable and unsuitable sites (a), dPCintra (b), dPCflux (c) and dPCconnector (d) over the Alboran Sea. See Figure A1 for the position in the Mediterranean Sea. The shaded polygons are the position of the marine protected areas used in the analysis.

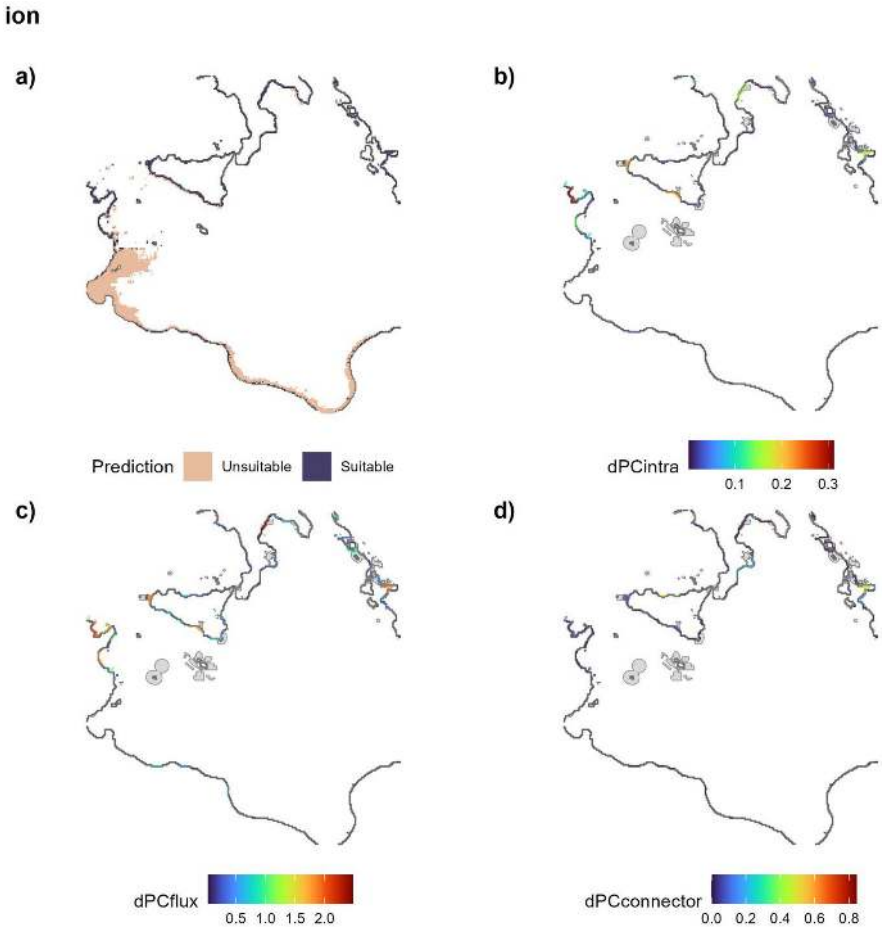

FIGURE A5 | Spatial distribution of suitable and unsuitable sites (a), dPCintra (b), dPCflux (c) and dPCconnector (d) over the Ionian Sea. See Figure A1 for the position in the Mediterranean Sea. The shaded polygons are the position of the marine protected areas used in the analysis.

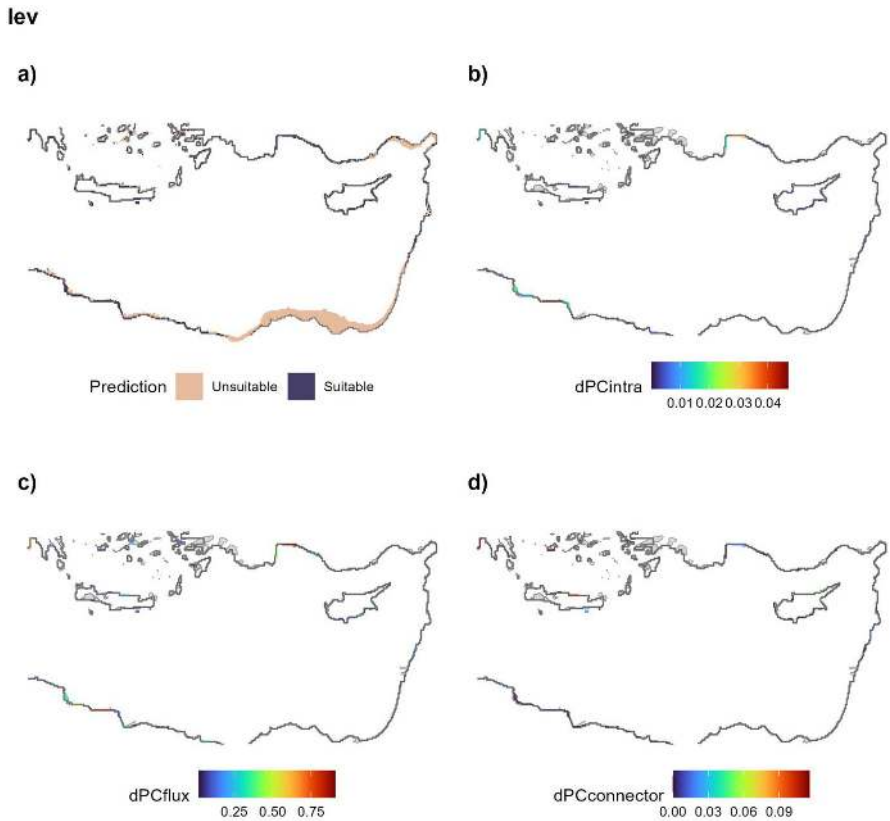

FIGURE A6 | Spatial distribution of suitable and unsuitable sites (a), dPCintra (b), dPCflux (c) and dPCconnector (d) over the Levantine Sea. See Figure A1 for the position in the Mediterranean Sea. The shaded polygons are the position of the marine protected areas used in the analysis.

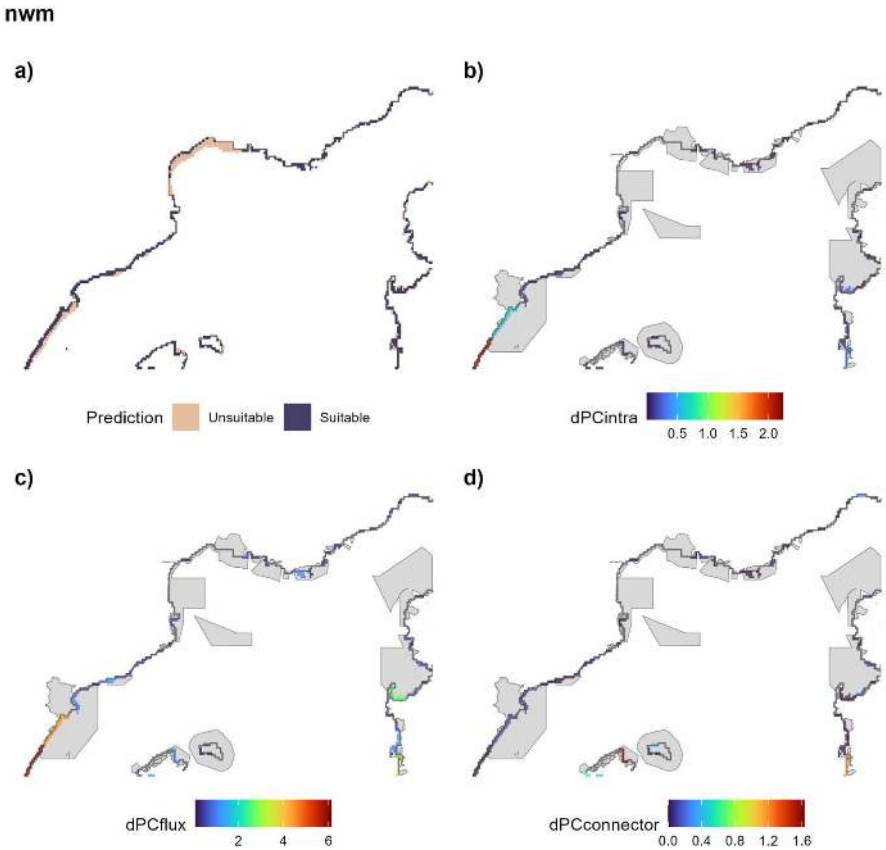

FIGURE A7 | Spatial distribution of suitable and unsuitable sites (a), dPCintra (b), dPCflux (c) and dPCconnector (d) over the Northwestern Mediterranean. See Figure A1 for the position in the Mediterranean Sea. The shaded polygons are the position of the marine protected areas used in the analysis.

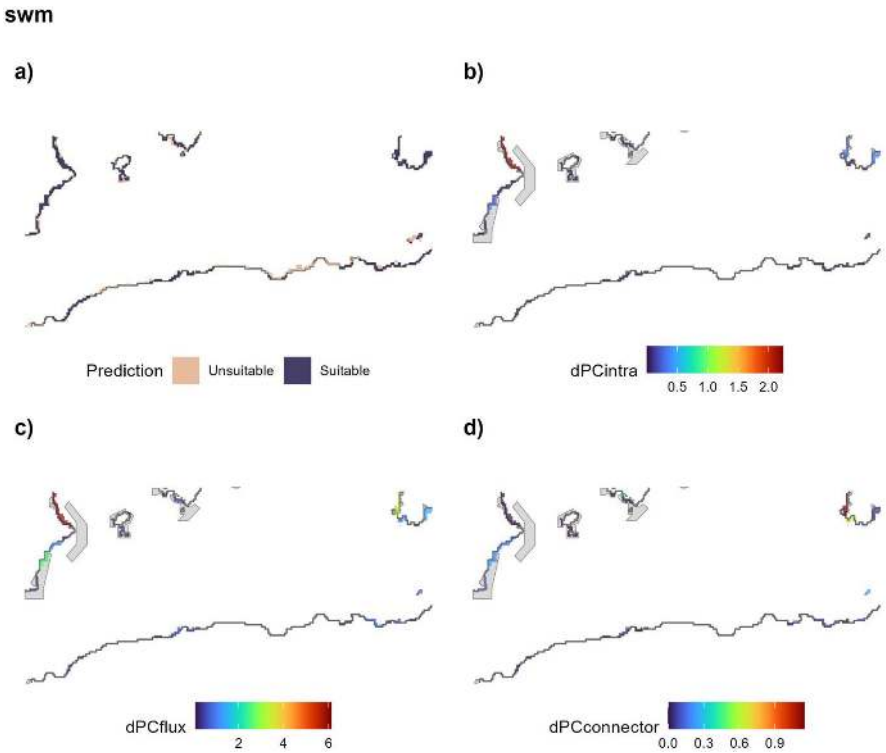

FIGURE A8 | Spatial distribution of suitable and unsuitable sites (a), dPCintra (b), dPCflux (c) and dPCconnector (d) over the Southwestern Mediterranean. See Figure A1 for the position in the Mediterranean Sea. The shaded polygons are the position of the marine protected areas used in the analysis.

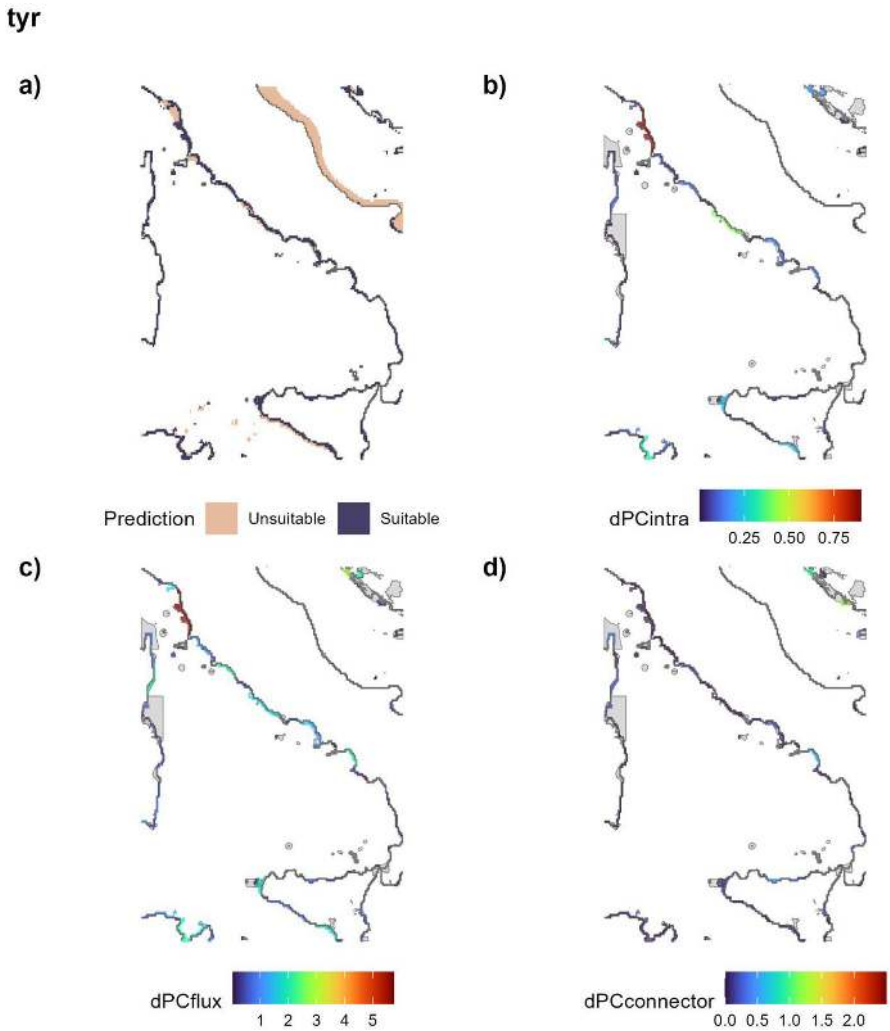

FIGURE A9 | Spatial distribution of suitable and unsuitable sites (a), dPCintra (b), dPCflux (c) and dPCconnector (d) over the Thyrrenean Sea. See Figure A1 for the position in the Mediterranean Sea. The shaded polygons are the position of the marine protected areas used in the analysis.