



Identification of Ecological Hotspots for the Seagrass *Posidonia oceanica* via Metapopulation Modeling

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The seagrass *Posidonia oceanica* is a benthic foundation species endemic to the Mediterranean Sea. It is a key component of coastal seascapes across the Mediterranean large marine ecosystem, where it plays fundamental ecological, physical, and economic roles. Despite the importance of this iconic seagrass species, a quantitative assessment of the interplay between local dynamics and basin-wide dispersal patterns is still lacking. Here we propose a Mediterranean-scale metapopulation model for *P. oceanica*, accounting for both demographic processes (inter-annual survival, vegetative growth, fruit production, seed establishment) and the spatial connectivity provided by current-driven dispersal of seagrass fruits. Model simulations are used to identify hotspots of seagrass population abundance, realized connectivity, and long-distance dispersal. Our results indicate that *P. oceanica* multi-functional hotspots, defined as species-suitable areas that rank high in all of the considered functional roles, are unevenly distributed in the four main sub-basins of the Mediterranean Sea, and along both the European and the African coastline. Our analysis also allows us to outline a remarkable geographical gap in protection: in fact, while many of the hotspots located along European coasts occur close to protected sites, the great majority of the hotspots lying on African coasts lack any form of protection. The identification of hotspots of *P. oceanica* metapopulation dynamics can thus help select regions that may serve as priority candidates for focusing conservation efforts.

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1. INTRODUCTION

Posidonia oceanica is a flowering plant endemic to the Mediterranean Sea, where it is the most abundant seagrass and a pivotal foundation species (Ellison, 2019). *P. oceanica* forms large, mono-specific underwater meadows that provide favorable conditions for the assembly of the rich and diverse coastal communities of the Mediterranean basin (Gobert et al., 2006), one of the most important and iconic biodiversity hotspots worldwide (Myers et al., 2000). Despite being often underrepresented in both scientific research and public attention (Duarte et al., 2008), seagrasses play a crucial role in the functioning of aquatic ecosystems, which in turn produce substantial benefits to the human society (Nordlund et al., 2016). *P. oceanica* makes no exception in this regard. It does in fact contribute supporting (nutrient cycling, primary production), provisioning (raw materials, bioindicators, animal feed), regulating (water purification and oxygenation, protection

from coastal erosion and sediment deposition, carbon sequestration, limitation of invasive species, and habitat provisioning for local ones—including many endemic and/or of commercial interest), and cultural (tourism, recreational fishing, knowledge contribution, intrinsic value) ecosystem services (Campagne et al., 2015).

The status of *P. oceanica* is declining in many coastal Mediterranean regions, with a recent report estimating a one-third decrease in areal distribution over the past 50 years (Telesca et al., 2015), adding to the global crisis of seagrass ecosystems (Waycott et al., 2009). Threats to *P. oceanica* include eutrophication and pollution (caused by chemical discharges from farming, aquaculture and urban waste), coastal development (shoreline hardening, coastal infrastructure development, sand mining), mechanical damage (trawling and boat anchoring), alien species, and climate change (Pergent et al., 2016). Because of its importance for coastal Mediterranean ecosystems, coupled with a decreasing population trend and a continuing regression in habitat extent and quality, *P. oceanica* has been a protection target under European (Habitat Directive, Barcelona, and Bern conventions) and national laws since the 1990s (Boudouresque et al., 2012).

P. oceanica is a long-lived, slow-growing seagrass characterized by high productivity (Hemminga and Duarte, 2000). Recruitment occurs *via* both vegetative growth and sexual reproduction, with the former mechanism being preponderant for the maintenance and expansion of existing seagrass beds as compared to the latter (Gobert et al., 2006), which is reportedly sporadic (Balestri and Cinelli, 2003). However, sexual reproduction is essential for colonization dynamics and the preservation of genetic diversity, which is often observed to be rather low (Procaccini et al., 2001). Sexual reproduction entails the production of flowers and fruits, which occurs with considerable spatiotemporal heterogeneity (Balestri and Vallerini, 2003). Fruits are positively buoyant and can be dispersed by surface marine currents, while seeds released by fruits are negatively buoyant and cannot travel far after being released (McMahon et al., 2014). Seedling establishment has also been often reported as quite episodic, although recent investigations have suggested that sexual reproduction could be more relevant for this species than previously thought (Balestri et al., 2017).

All these observations indicate that the population dynamics of *P. oceanica* should be seen as a dynamical balance between processes occurring at local vs. basin spatial scales. For instance, inter-annual shoot survival is eminently a local process, whereas the implications of sexual reproduction are better understood if put in a spatial perspective (Serra et al., 2010; Jahnke et al., 2017). Vegetative growth lays somewhat between these two extremes, because it may certainly contribute to meadow expansion, albeit at rates and distances that are not comparable with those achieved through sexual reproduction and subsequent propagule dispersal (McMahon et al., 2014). In other words, the dynamics of *P. oceanica* in the Mediterranean should be usefully framed in a metapopulation approach (Hanski, 1999). Although not quite common yet in the study of seagrass population dynamics (Bell, 2006), the metapopulation concept has already been evoked

for *P. oceanica* (Rozenfeld et al., 2008), but mainly concerning the assessment of potential and realized connectivity patterns at various spatial scales (Jahnke et al., 2017; Mari et al., 2020). By contrast, no studies have yet attempted a full coupling of demographic and dispersal processes in the analysis of large-scale dynamics of *P. oceanica* in the Mediterranean Sea.

Similarly, no studies have yet been carried out that can guide the modeling of the effects of shoot density on *P. oceanica* vegetative growth, survival, sexual reproduction, seed germination, and/or seedling mortality at a whole-Mediterranean and multi-decadal scale. Density-dependence has been proposed as a factor regulating the vegetative growth of *P. oceanica*, possibly leading to the formation of three-dimensional, topographically complex seagrass structures within local meadows (Kendrick et al., 2005). Density-dependent shading is another process that is thought to limit vegetative growth and recruitment (Duarte et al., 2006). Although not specifically developed for this seagrass species, theoretical models of colony growth have often assumed density-dependent shoot mortality (Sintes et al., 2005; Ruiz-Reynés et al., 2017). For *P. oceanica*, little is known also about the possible effects of shoot density on seed germination and seedling mortality (Balestri and Lardicci, 2008). In seagrass species other than *P. oceanica*, the former process is generally not considered density-dependent (Orth et al., 2003), and the evidence on density dependence negatively affecting the latter is also quite scarce (Statton et al., 2017). In some cases, it has been proposed that positive density dependence may affect the sexual reproduction, patch colonization, and survival of some seagrass species, including *P. oceanica* (Almela et al., 2008; van Katwijk et al., 2016; Valdez et al., 2020). This complicated and somewhat scattered landscape of empirical evidence clearly calls for the development of a quantitative framework allowing the inclusion of simple and testable hypotheses about density dependence.

In this work, we propose a basin-wide metapopulation model for *P. oceanica* that accounts for both local demographic processes and the spatial connectivity provided by current-driven dispersal of seagrass fruits. The model is driven by spatially explicit information on local suitability conditions and marine circulation patterns. Alternative hypotheses concerning density-dependence are tested and compared with each other with respect to their ability to explain presence-absence *P. oceanica* data. The best-performing model is then used to evaluate connectivity and dispersal metrics, as well as their temporal variability. In this way, the different coastal regions inhabited by the seagrass can be assessed according to a recently proposed multi-functional scheme (Melià et al., 2016; Mari et al., 2020) that accounts for both local retention and sink/source dynamics on larger scales. Differently from—and possibly complementary to—other studies, where key conservation areas for *P. oceanica* were proposed based on habitat characteristics (Houngnandan et al., 2020) or spatial connectivity coupled with local suitability conditions (Mari et al., 2020), a full metapopulation approach is used here to suggest a species-specific prioritization strategy to guide large-scale conservation efforts. Specifically, the results obtained from the metapopulation model are used to identify hotspots of various ecological functions for *P. oceanica* at the

scale of the whole Mediterranean Sea basin, as well as to pinpoint possible gaps in protection.

2. MATERIALS AND METHODS

2.1. A Metapopulation Model for *P. oceanica*

The geographic domain of interest is divided into n marine sectors, representing the basic spatial units of the metapopulation model. Each sector is characterized by a fraction of suitable area a_i ($0 < a_i \leq 1$, only sectors that include suitable sites for *P. oceanica* are retained for analysis) with an average suitability level s_i ($0 < s_i \leq 1$). The total suitability of each sector can thus be evaluated as $a_i s_i$. Let $x_i(t)$ be the density (shoots m^{-2}) of *P. oceanica* in the suitable area of marine sector i in year t , before sexual reproduction takes place. The basin-wide metapopulation dynamics of *P. oceanica* are determined by the interplay of four different demographic processes, namely year-to-year shoot survival, vegetative growth, fruit production, and propagule establishment. Indeed, the last two processes represent the initial and finale phases, respectively, of the sexual reproduction process, which additionally also includes inter-sector fruit dispersal and the ensuing ecological connectivity.

To prevent an unbounded growth of local population abundances, the metapopulation model must incorporate density dependence. As discussed above, empirical evidence is to date still too scarce to be used for inferring functional relationships that may be applied consistently over the spatial (whole Mediterranean basin) and temporal (multi-decadal) scales of interest. Therefore, to describe each of the above demographic processes, we adopted a simple, saturating functional form inspired by the classic and widely used Beverton-Holt demographic model (Beverton and Holt, 1957), here modified to account also for local suitability conditions. Specifically:

- the survival $S_i(x_i(t))$ of *P. oceanica* shoots is defined as

$$S_i(x_i(t)) = \sigma_i(x_i(t))x_i(t),$$

where the inter-annual survival probability of seagrass shoots, $\sigma_i(x_i(t))$, is assumed to be positively influenced by local average suitability and inversely related to local *P. oceanica* shoot density according to the functional form

$$\sigma_i(x_i(t)) = \frac{\sigma_{\max} s_i}{1 + \delta_{\sigma} x_i(t)},$$

with σ_{\max} and δ_{σ} being, respectively, the maximum survival probability (i.e., obtained with $s_i = 1$ and $x_i(t) \rightarrow 0$) and a parameter setting the intensity of density-dependent effects on shoot survival;

- vegetative growth $G_i(x_i(t))$ is evaluated as

$$G_i(x_i(t)) = g_i(x_i(t))x_i(t),$$

where the rhizome formation rate, $g_i(x_i(t))$, is also assumed to be positively influenced by local average suitability

and inversely related to local *P. oceanica* shoot density according to

$$g_i(x_i(t)) = \frac{g_{\max} s_i}{1 + \delta_g x_i(t)},$$

with g_{\max} being the maximum rhizome formation rate [i.e., with $s_i = 1$ and $x_i(t) \rightarrow 0$] and δ_g setting the intensity of density-dependent effects on vegetative growth. Note that, for the sake of simplicity, vegetative growth is assumed not to result in seagrass bed expansion and the possible colonization of previously unoccupied substrate within the local sector, or even neighboring sectors, which is deemed to be a reasonable hypothesis if the spatial grain of the model is not too fine. This assumption is backed up by a comparative assessment of the role played by different movement processes in *P. oceanica*, which showed that the dispersal of buoyant fruits allows much faster and longer-range colonization dynamics than clonal growth does (McMahon et al., 2014);

- the contribution of sexual reproduction $R_i(x_1(t), x_2(t), \dots, x_n(t))$ is quantified as

$$R_i(x_1(t), x_2(t), \dots, x_n(t)) = r_i(x_1(t), x_2(t), \dots, x_n(t))f_i(x_i(t)),$$

where $r_i(x_1(t), x_2(t), \dots, x_n(t))$ is the density of *P. oceanica* fruits arriving to sector i after having been sexually produced in any sector j ($j = 1, 2, \dots, n$, including $j = i$) and transported by marine currents, while $f_i(x_i(t))$ is the probability of successful fruit settlement (accounting for fruit germination and seedling survival). In particular, fruit production and transport are described as

$$r_i(x_1(t), x_2(t), \dots, x_n(t)) = \frac{1}{a_i} \sum_{j=1}^n C_{ji}(t) a_j h_j(x_j(t)) x_j(t),$$

where

$$h_j(x_j(t)) = \frac{h_{\max} s_j}{1 + \delta_h x_j(t)}$$

is the rate of fruit production, assumed to be positively influenced by local average suitability and inversely related to local shoot density, with h_{\max} being the maximum rate of seed production (i.e., with $s_j = 1$ and $x_j(t) \rightarrow 0$) and δ_h setting the intensity of density-dependent effects on sexual reproduction. The quantity $C_{ji}(t)$ is the probability that a *P. oceanica* fruit produced in sector j during the reproductive season of year t eventually ends up in sector i (potential connectivity; Jahnke et al., 2017). As for settling,

$$f_i(x_i(t)) = \frac{f_{\max} s_i}{1 + \delta_f x_i(t)}$$

is defined as the probability of fruit germination and inter-annual seedling survival in sector i , also assumed to be positively influenced by local average suitability and inversely related to local shoot density, with f_{\max} and δ_f being the maximum settling probability (i.e., with $a_i = 1$ and $x_i(t) \rightarrow 0$) and a parameter setting the intensity of density-dependent effects on successful fruit germination and seedling survival, respectively.

Note that, for the sake of model simplicity, shoot age is not considered in any of the above processes. Therefore, possible age-related effects on, e.g., inter-annual survival or sexual reproduction are here neglected. However, this choice does not seem to represent an oversimplification for *P. oceanica*. On the one hand, in fact, observational studies suggest that shoot mortality is not strongly influenced by age (e.g., González-Correa et al., 2007a); on the other, while it is typically found that shoots of all ages (from 6-month-old on) can potentially contribute to sexual reproduction, reports vary on the shape of the relationship between age and flowering rate, with peaks being observed around 6 or 14 years of age (Balestri and Cinelli, 2003; Calvo et al., 2006). Also, no positive density-dependent processes (i.e., intraspecific facilitation) have been accounted for.

Summing up the contributions of shoot survival, vegetative growth, and sexual reproduction to the local densities of *P. oceanica* leads to a set of n coupled difference equations, namely

$$\begin{aligned} x_i(t + 1) &= S(x_i(t)) + G(x_i(t)) + R_i(x_1(t), x_2(t), \dots, x_n(t)) = \\ &= \frac{\sigma_{\max} s_i}{1 + \delta_\sigma x_i(t)} x_i(t) + \frac{g_{\max} s_i}{1 + \delta_g x_i(t)} x_i(t) + \\ &+ \frac{f_{\max} s_i}{1 + \delta_f x_i(t)} \frac{1}{a_i} \sum_{j=1}^n C_{ji}(t) a_j \frac{h_{\max} s_j}{1 + \delta_h x_j(t)} x_j(t), \end{aligned}$$

which can be used to describe *P. oceanica* metapopulation dynamics, once the relevant characteristics of the seascape (distribution of suitable habitat, spatial connectivity) have been evaluated.

2.2. Application of the Model to the Mediterranean Sea

Habitat suitability mapping for *P. oceanica* in the Mediterranean Sea has been made available as an output of the MediSeH project (Giannoulaki et al., 2013). There, observations of *P. oceanica* presence/absence and a set of 36 predictor variables (of which nitrate and silicate concentrations, average depth, sea surface temperature and salinity were found to be the most important) were used to train a random forest algorithm (Breiman, 2001) estimating the probability of species occurrence throughout the whole Mediterranean Sea basin at a high spatial resolution (1/240°, corresponding to a regular mesh with an ~460 m-long step). At that spatial scale, about 685,000 individual sites were characterized by positive values of habitat suitability.

Basin-wide spatial connectivity for *P. oceanica* in the Mediterranean Sea has already been estimated within the ECOPotential project (<https://cordis.europa.eu/project/id/641762/it>) through a biophysical approach (Mari et al., 2020). In that study, more than 30 billion Lagrangian particles, representing free-floating *P. oceanica* fruits, were tracked over a time span of $n_y = 30$ years (1987–2016). Particles were released from suitable sites matching the reproductive season of the seagrass (typically, January throughout April) and the duration of their floating phase (at most 1 month). The transport of *P. oceanica* fruits was driven by surface circulation fields

(daily averages at 1/16° resolution, corresponding to a regular grid with an approximate mesh size of 6.9 km) obtained from a Mediterranean-wide physical reanalysis (Lecci et al., 2017). In the present study, potential connectivity between any two marine sectors during a given season, say sectors i and j in year t , $C_{ij}(t)$, is defined as the fraction of particles released during year t from suitable sites within sector i that reach suitable sites within sector j at the end of the dispersing phase. **Supplementary Figure 1** displays some synthetic metrics of potential connectivity (average values and temporal variability over the 1987–2016 period), namely self-retention (quantifying how many *P. oceanica* fruits both are released and settle in the same marine sector), indegree (indicating the tendency of a sector to function as a potential sink of *P. oceanica* fruits), and outdegree (indicating the tendency of a sector to function as a potential source of *P. oceanica* fruits). Potential connectivity scores can also be used to evaluate metrics pertaining to the average distance traveled by dispersing fruits. In this respect, **Supplementary Figure 2** reports the displacement of dispersing fruits either incoming to or outgoing from each marine sector (again, average values and temporal variability over the 1987–2016 period), where the distance d_{ij} between the centroids of any two sectors i and j , has been evaluated according to the great-circle formula.

Applying the metapopulation model at the fine spatial resolution of the suitability map would likely allow a more detailed description of local-scale demographic dynamics, but would also make it hard to obtain a robust parameterization and perform efficient simulations. Therefore, as a trade-off between accuracy, on the one hand, and robustness and applicability, on the other, the coarser spatial resolution of the circulation fields has been chosen as a reference for the application of the metapopulation model. Coherently, the suitability map has been up-scaled to the spatial resolution of the circulation fields used here. In this way, $n = 9,648$ suitable marine sectors were identified (**Supplementary Figure 3**), each of which covers an area of ~48 km² along the Mediterranean coastline.

Most of the other biological parameters of the metapopulation model described above can be evaluated from available observational studies on the ecology of *P. oceanica*. Specifically, the maximum values of inter-annual shoot survival, σ_{\max} , and of the vegetative growth (rhizome formation) rate, g_{\max} , are taken from studies on the demography and dynamics of seagrass colonies (Marbà et al., 1996, 2005; Badalamenti et al., 2006; González-Correa et al., 2007a; Marbà and Duarte, 2010). The reference values for these parameters are evaluated as the average of the maximum figures reported by each study, under the assumption that the reported values of population recruitment were reflective of vegetative growth alone, i.e., neglecting sexual reproduction—a reasonable hypothesis, considering that flowering is considered to be episodic in *P. oceanica* (e.g., Balestri and Cinelli, 2003; Calvo et al., 2006). The maximum rate of fruit production, h_{\max} , is obtained from one of the few empirical studies on the reproductive success of *P. oceanica* (Balestri and Cinelli, 2003). The reference value for this parameter is selected as the maximum figure reported in that study. The maximum settling probability of dispersing fruits, f_{\max} , is estimated from studies on germination (Balestri et al., 1998a; Balestri and Bertini,

TABLE 1 | Reference parameter values for the *P. oceanica* metapopulation model in the Mediterranean Sea.

Parameter	Value	Range	References
σ_{max}	0.94	0.86–0.98	Marbà et al., 1996, 2005; Badalamenti et al., 2006; González-Correa et al., 2007a; Marbà and Duarte, 2010
g_{max}	1.3	1.1–1.6	Marbà et al., 1996, 2005; Badalamenti et al., 2006; González-Correa et al., 2007a; Marbà and Duarte, 2010
h_{max}	0.099	±50%*	Balestri and Cinelli, 2003
f_{max}	0.70	0.49–0.84	Balestri et al., 1998a,b; Piazzzi et al., 1999; Balestri and Bertini, 2003; Fernández-Torquemada and Sánchez-Lizaso, 2013
δ_{σ}	Calibrated	±50%**	
δ_g	Calibrated	±50%**	
δ_h	Calibrated	±50%**	
δ_f	Calibrated	±50%**	

When available, plausible ranges are taken from the literature; when not, because either a single reference was found * or the parameter is subject to calibration **, a ±50% variation range with respect to the reference value is assumed.

2003; Fernández-Torquemada and Sánchez-Lizaso, 2013) and long-term seedling survival (Balestri et al., 1998b; Piazzzi et al., 1999). The reference value for f_{max} is in fact obtained as the average of the products of the maximum germination and seedling survival probabilities reported in each study. A study providing figures for overall settling probability (Balestri et al., 1998a, maximum reported value 75%) is used to validate the estimate obtained from the combination of multiple reports. Parameter values and relevant references are provided in **Table 1**.

2.3. Model Calibration

To understand which of the processes describing large-scale *P. oceanica* metapopulation dynamics may be influenced by density-dependent effects, a model selection exercise is run to compare the performances of several candidate model structures characterized by alternative hypotheses concerning density dependence. Vegetative growth has always been considered as density-dependent to avoid unbounded growth of local population densities (because, according to the literature, $g_{max} > 1$, see again **Table 1**). Conversely, each of the other three processes (adult shoot survival, sexual reproduction, and post-dispersal settlement) is alternatively considered either density-dependent (and the corresponding δ_q parameter, with $q \in \{\sigma, g, f, h\}$, calibrated) or not (and the corresponding δ_q parameter set to zero). For the sake of model parsimony, we also consider simplified cases in which two or more of the parameters setting the intensity of density dependence are constrained so that they take the same numerical value(s).

For each candidate model, calibration is performed as follows: models are simulated for a period of 100 years from random initial conditions to allow the dynamics of the system to settle to a stationary state. The temporally averaged connectivity scores

$\langle C_{ij} \rangle = \frac{1}{n_y} \sum_{t=1}^{n_y} C_{ij}(t)$ are used to describe propagule dispersal in this phase of the simulation, as preliminary analyses of the metapopulation model showed *P. oceanica* densities to be scarcely influenced by the temporal fluctuations of potential connectivity (as somewhat expected, because vegetative growth reportedly outweighs sexual reproduction in *P. oceanica*, as discussed above). The spatial distribution of shoot densities projected by the model at the equilibrium is compared with the binary observations of *P. oceanica* presence/absence collected in Telesca et al. (2015), suitably up-scaled to the spatial scale of marine sectors. Specifically, *P. oceanica* is assumed to be present in a sector if the majority of the available local observations reports seagrass presence and, vice-versa, absent if the majority of the observations reports absence. Simulated *P. oceanica* densities are used to fit a generalized linear model with a logit link (function `fitglm` in Matlab R2019a). The log-likelihood value (LLV) of the model given the observations is used as the objective function to maximize. The exploration of the parameter space is performed with a genetic algorithm (function `ga` in Matlab R2019a) to maximize each candidate model's ability to explain seagrass presence/absence patterns. For each parameter, the search region is limited to the interval 10^{-4} – 10^4 (shoots m^{-2})⁻¹. To make sure that modeled densities are in line with field observations, parameter search is also constrained so that the 99th percentile of the simulated density distribution corresponds to $1,000 \pm 50$ shoot m^{-2} , consistent with the maximum values reported in current guidelines for *P. oceanica* monitoring (Pergent-Martini, 2015). The whole procedure is repeated 10 times for each candidate model starting from randomly extracted initial parameter sets to improve the exploration of the calibration region.

As the various candidate models are endowed with a different number of calibration parameters (n_p , from one to four), their performances are ranked through the Akaike information criterion (AIC), so as to reveal possible trade-offs between model accuracy and parsimony. Specifically, for each model we evaluate AIC as

$$AIC = 2(n_p - LLV_{max}),$$

where LLV_{max} is the maximum value of LLV found over the 10 independent runs of the calibration procedure. Then, Akaike differences (Δ_{AIC}) are evaluated between the AIC scores of the various candidate models and the AIC score of the best supported model (the one with the lowest AIC score).

2.4. Performance Evaluation of the Selected Model

Once the best supported model according to AIC scoring has been selected, it may be useful to evaluate its actual explanatory power against the actual distribution of *P. oceanica* in the Mediterranean Sea. To that end, a receiver operating characteristic (ROC) curve can be used to evaluate the diagnostic ability of the selected model (which produces a projection of continuous local population density values) as a binary classifier of *P. oceanica* presence/absence data. The ROC curve is obtained by plotting the true positive rate, defined as the ratio between

the number of correctly identified presences and the number of total presence data, against the false positive rate, defined as the number of observations incorrectly classified as presences divided by the number of total absence data, for different values of the discrimination threshold. In ROC analysis, a random classifier would have a value of the area below the ROC curve of 0.5, while a perfect classifier would have a value of 1. A simplistic, yet widely used metric to summarize the performances of a binary classifier is Youden's *J* statistics (Baker and Kramer, 2007), defined as

$$J = \text{sensitivity} + \text{specificity} - 1,$$

where sensitivity is the true positive rate and specificity is the true negative rate, defined as the number of observations correctly classified as absences divided by the number of total absence data. The discrimination threshold that yields the maximum value of Youden's *J* can be used to select the optimal cut-point of the classifier (Schisterman et al., 2005).

2.5. Spatiotemporal Variability and Metapopulation Dynamics

To assess the effect of the temporal variability of marine currents on the metapopulation dynamics of *P. oceanica*, the best-performing metapopulation model selected according to the procedure described in the previous section is simulated again starting from the steady-state solution, corresponding to a spatial distribution of seagrass shoot densities in suitable areas—this time with time-varying connectivity. Specifically, the model is run for a time span of 200 years, for each of which a connectivity matrix $C_{ij}(t)$ is randomly selected from the $n_y = 30$ available. In this way, any possible multi-annual trends in potential connectivity are clearly destroyed. However, previous work (Mari et al., 2020) has shown that trends in *P. oceanica* connectivity can be detected in just a minority of suitable marine sectors (a fraction $\leq 5\%$ in each potential connectivity metric considered). The first 100 years of the simulation are used as a spin-up period; afterwards, six quantities are evaluated for each marine sector over the last 100 years of the simulation, namely:

1. Total *P. oceanica* shoot density (shoots m^{-2})

$$TD_i(t) = x_i(t)a_i;$$

2. Realized self-retention (shoots $m^{-2} \text{ year}^{-1}$)

$$SR_i(t) = TD_i(t)h_i(x_i(t))C_{ii}(t)f_i(x_i(t));$$

3. Realized indegree (shoots $m^{-2} \text{ year}^{-1}$)

$$ID_i(t) = \left[\sum_{j \neq i}^n TD_j(t)h_j(x_j(t))C_{ji}(t) \right] f_i(x_i(t));$$

4. Realized outdegree (shoots $m^{-2} \text{ year}^{-1}$)

$$OD_i(t) = TD_i(t)h_i(x_i(t))a_i \sum_{j \neq i}^n C_{ij}(t) \frac{1}{a_j} f_j(x_j(t));$$

5. Realized inbound displacement (km)

$$IM_i(t) = \frac{1}{ID_i(t)} \left[\sum_{j \neq i}^n TD_j(t)h_j(x_j(t)) (C_{ji}(t)d_{ji}) \right] f_i(x_i(t));$$

6. Realized outbound displacement (km)

$$OM_i(t) = \frac{1}{OD_i(t)} TD_i(t)h_i(x_i(t))a_i \sum_{j \neq i}^n (C_{ij}(t)d_{ij}) \frac{1}{a_j} f_j(x_j(t)).$$

Quantity 1 refers to *P. oceanica* population density, while quantities 2–6 describe realized propagule dispersal, in terms of either connectivity intensity (2–4) or displacement distance (5–6). Quantities 2–6 account for the exchange of fruits that are produced at an origin sector and transported by currents to a destination sector where they actually germinate and survive into seagrass shoots, according to the local demographic and environmental conditions of the origin and destination sectors. Note that all these quantities need a fully dynamic and spatially explicit metapopulation framework to be evaluated. For each sector, the temporal average and variance of each quantity are recorded. The time-varying simulation with randomly extracted connectivity matrices is replicated n_r times, and pooled mean and variance values are evaluated for each sector and quantity.

2.6. Identification of *P. oceanica* Hotspots

Ecological hotspots for *P. oceanica* can be identified following the methodological framework proposed by Melià et al. (2016), in which potential connectivity metrics were used to define a synthetic score recapitulating the capacity of different local populations to simultaneously act as retainers, sinks and sources. The same framework was used in Mari et al. (2020) for a Mediterranean-wide assessment of *P. oceanica* ecological connectivity. Here, we take advantage of the metapopulation model and expand the range of possible ecological functions played by local seagrass populations, namely by including metrics related to population density, realized connectivity, and displacement patterns. For each quantity *Q* defined above (with $Q \in \{TD, SR, ID, OD, IM, OM\}$) and each marine sector *i*, two percentile scores are computed:

- $P_i^{Q,Ave}$, defined as the percentage of sectors $j = 1 \dots n$ characterized by values of $E_p[Q_j]$ not larger than $E_p[Q_i]$, where $E_p[Q_i]$ is the pooled mean of quantity *Q* in sector *i*;
- $P_i^{Q,CV}$, defined as the percentage of sectors $j = 1 \dots n$ characterized by values of $CV_p[Q_j]$ not lower than $CV_p[Q_i]$, where $CV_p[Q_i] = \sqrt{\text{Var}_p[Q_i]} / E_p[Q_i]$ is the pooled coefficient of variation of quantity *Q* in sector *i*, as obtained by dividing the square root of the pooled variance by the pooled mean (note that sectors for which $E_p[Q_i] = 0$, so that $CV_p[Q_i]$ would not be defined, are attributed to the lowest percentile class).

Afterwards, for each quantity *Q* and sector *i*, the two percentiles scores are aggregated

conservatively to form a synthetic percentile index P_i^Q defined as

$$P_i^Q = \min(P_i^{Q,Ave}, P_i^{Q,CV}).$$

Sectors where P_i^Q is highest can be considered as hotspots for quantity Q, because they are endowed with both large average intensity and low temporal variability of the signal associated with Q. Following Melià et al. (2016) and Mari et al. (2020), the six percentile scores can be further aggregated to identify multi-functional hotspots for *P. oceanica* dynamics. For instance, a multi-functional percentile index P_i^{MF} can be defined as

$$P_i^{MF} = \min(P_i^{TD}, P_i^{SR}, P_i^{ID}, P_i^{OD}, P_i^{IM}, P_i^{OM}).$$

Note that this is, again, a conservative aggregation rule, in that sectors are evaluated according to the percentile index in which they are weakest. For this reason, sectors where P_i^{MF} is highest can be considered as multi-functional hotspots, because the seagrass populations they host are the most effective (or the least constrained) at providing simultaneously multiple ecological functions—thus arguably qualifying as possible priority candidates for protection (Orth et al., 2006).

2.7. Sensitivity Analysis

To assess the robustness of the hotspot identification procedure outlined above, two different types of sensitivity analysis are carried out, one related to geographic resolution and the other to model parameterization. In the former, robustness against the spatial grain of the model is tested, specifically concerning the evaluation of realized connectivity and displacement metrics. To that end, the hotspot identification procedure is repeated assuming that connectivity occurring between sectors located at distance $d_{ij} < d^*$ from each other contributes to self-retention of the originating sector (hence, it does not count toward in/outdegree or in/outbound displacement). In the latter, robustness against parameter uncertainty is assessed, namely by repeating n_s times the simulation algorithm with time-varying connectivity, each time with parameter values randomly and independently drawn from uniform distributions with supports defined within the ranges reported in **Table 1**. When possible (parameters σ_{max} , g_{max} , and f_{max}), plausible ranges of variation are obtained from the studies used to estimate the reference value of each parameter; when not, plausible ranges are defined as $\pm 50\%$ variations of the reference (or calibrated) values.

3. RESULTS

The lowest AIC score is attained by a model describing shoot survival, vegetative growth, and post-dispersal settlement as density-dependent processes ($\delta_\sigma > 0$, $\delta_g > 0$, $\delta_f > 0$), and density-independent fruit production ($\delta_h = 0$; **Table 2**). The model is parsimonious in that the calibrated intensities of the density feedback are the same for all selected processes

($\delta_g = \delta_\sigma = \delta_f = \delta$). The best-supported model can thus be rewritten as

$$x_i(t+1) = \frac{s_i}{1 + \delta x_i(t)} \left[(\sigma_{max} + g_{max})x_i(t) + \frac{f_{max}h_{max}}{a_i} \sum_{j=1}^n C_{ji}(t)a_j s_j x_j(t) \right].$$

With an area under the ROC curve of 0.926 (**Figure 1**), this model has a good ability to separate *P. oceanica* presence/absence data. As a matter of fact, at the discrimination threshold of the logit link that maximizes Youden's J statistics the model correctly identifies 90.7% of true absences and 80.3% of true presences.

Other two models reach a similar level of statistical support as the first one ($\Delta_{AIC} < 2$). The second-ranked model according to AIC has the same density-dependence structure as the best one with two free calibration parameters instead of just one. The similarity of the calibrated parameter values provides further support for the parsimony of the top-ranked model. The third-ranked candidate is also another parsimonious model with one free parameter, but with vegetative growth and shoot survival as the only density-dependent processes. Not surprisingly, given the models' structure and parameter similarities, the shoot densities projected by the three top models appear to be very similar to each other (**Supplementary Figure 4**), and pairwise two-sample Kolmogorov-Smirnov testing does not reject the hypothesis that three samples of simulated total density obtained with the three top-ranked models come from the same underlying distribution at significance $p \ll 10^{-4}$. Four other models turn out to be somewhat supported ($2 < \Delta_{AIC} < 4$): two of them have the same structure of the two best-ranked models (with two free parameters), one also includes density-dependent sexual reproduction (although with a value of δ_h close to the lower bound of the search interval, which makes the process practically ineffective), and another with the same structure as the third-ranked model (but with two free parameters instead of one). All other models are considerably less supported by the data ($\Delta_{AIC} > 4$). Among these, the candidates not accounting for density-dependent shoot survival perform very poorly in terms of AIC ($\Delta_{AIC} > 100$). For all these reasons, no candidates other than the best-performing model are retained for further analysis.

With the only purpose of evaluating the role of dispersal in the overall dynamics of the metapopulation, a simulation is performed with the parameter set of the best-performing model but no connectivity, i.e., with the identity matrix of size n replacing the average connectivity scores $\langle C_{ij} \rangle$ (**Supplementary Figure 5**). This exercise shows that 63.6% of suitable marine sectors are characterized by larger total shoot density in the presence of connectivity than in the absence thereof, while 19.7% of sectors have smaller population density when dispersal is operating. Positive variations are typically small in absolute magnitude (+0.98 shoots m^{-2} on average), but quite large in relative terms, e.g., if compared with the model simulation shown in **Figure 1** (+96.6% on average), indicating that dispersal may be instrumental to maintaining local populations (albeit at low shoot densities) in places that

TABLE 2 | Model calibration and selection results.

$\log_{10}(\delta_r)$	$\log_{10}(\delta_g)$	$\log_{10}(\delta_f)$	$\log_{10}(\delta_h)$	n_p	LLV	Δ_{AIC}
-2.95*	-2.95*	-2.95*	—	1	-1966.92	0
-2.94	-2.94*	-2.94*	—	2	-1966.41	0.97
-2.95*	-2.95*	—	—	1	-1967.82	1.80
-2.97*	-2.97*	-2.87	—	2	-1966.93	2.02
-2.94*	-2.95	-2.94*	—	2	-1966.94	2.04
-2.95*	-2.95*	-2.95*	-3.97	2	-1967.50	3.14
-2.96	-2.95	—	—	2	-1967.82	3.79
-2.93*	-2.93*	-3.99†	-3.99†	2	-1967.93	4.01
-2.96	-2.96	-2.89	—	3	-1966.93	4.01
-2.94*	-2.94*	—	-3.99	2	-1968.24	4.62
-2.94*	-2.94*	-2.86	-3.96	3	-1967.36	4.88
-2.94	-2.95*	-2.95*	-3.99	3	-1967.46	5.08
-2.93*	-2.94	-2.93*	-3.99	3	-1967.47	5.08
-2.93	-2.93	-3.99*	-3.99*	3	-1968.04	6.22
-2.93	-2.92	—	-3.99	3	-1968.19	6.52
-2.94	-2.95	-3.00	-4.00	4	-1967.48	7.11
-2.98*	-2.98*	-2.98*	-2.98*	1	-1970.78	7.71
-2.94*	-2.94*	—	-2.94*	1	-1971.06	8.27
-2.98*	-2.91	-2.98*	-2.98*	2	-1970.66	9.47
-3.00*	-2.93†	-2.93†	-3.00*	2	-1970.68	9.52
-2.96	-2.99*	-2.99*	-2.99*	2	-1970.72	9.60
-2.96*	-2.99†	-2.96*	-2.99†	2	-1970.73	9.60
-2.94*	-2.94*	-2.99	-2.94*	2	-1970.78	9.70
-2.96*	-2.91	—	-2.96*	2	-1970.97	10.09
-2.92	-2.97*	—	-2.97*	2	-1970.98	10.11
-3.01*	-2.95	-3.01	-3.01*	3	-1970.67	11.48
-2.94	-2.98*	-2.97	-2.98*	3	-1970.73	11.60
—	-1.96*	-1.96*	—	1	-2045.03	156.21
—	-1.93	-2.02	—	2	-2045.00	158.14
—	-1.93*	-1.93*	-4.00	2	-2045.59	159.33
—	-1.92	-2.03	-4.00	3	-2045.52	161.19
—	-1.93	-2.70*	-2.70*	2	-2050.56	169.27
—	-1.96*	-1.96*	-1.96*	1	-2053.78	173.71
—	-1.96*	-2.30	-1.96*	2	-2053.42	175.00
—	-1.96*	—	-1.96*	1	-2054.63	175.42
—	-1.89	—	-2.33	2	-2053.98	176.11
—	-1.65	—	—	1	-2063.34	192.84

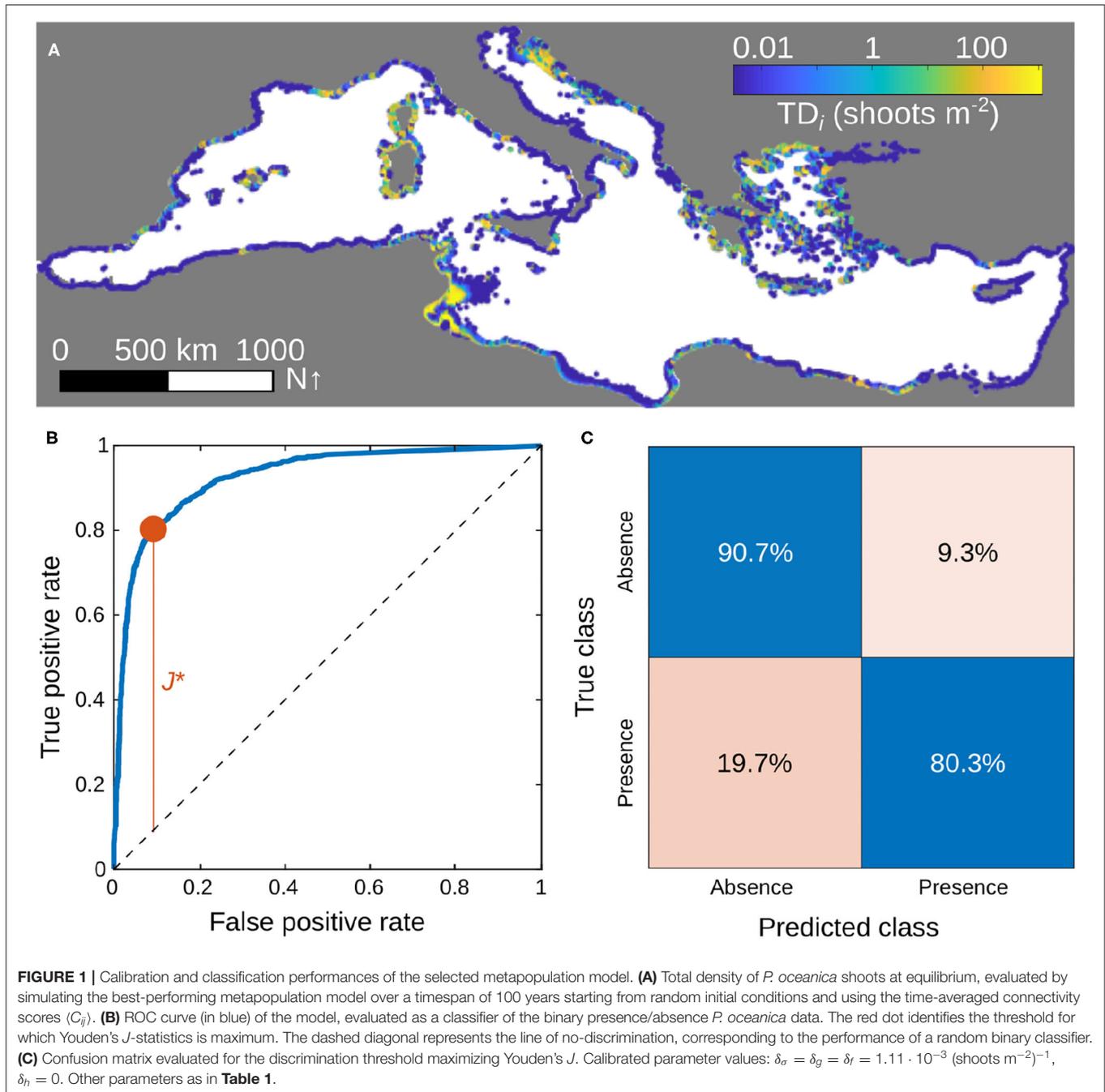
Models are sorted from most to least supported, i.e., according to increasing Δ_{AIC} scores ($\Delta_{AIC} = 0$ refers to the best candidate model). Parameters whose values have been constrained to be equal in the calibration process are marked with the same superscript symbol, while “—” indicates parameters that are set to zero (no density dependence for that model component). All δ 's are in units of (shoots m^{-2})⁻¹.

would not be colonized by *P. oceanica* meadows otherwise. Conversely, negative variations of population densities are usually larger than positive ones in absolute magnitude (−7.6 shoots m^{-2} on average), but remarkably smaller in relative terms (−9.3% on average).

A simulation of the selected metapopulation model run with the reference parameter set and time-varying connectivity is shown in **Figure 2**, specifically in terms of the pooled temporal average (A) and coefficient of variation (B) of the total density of *P. oceanica* shoots. The simulation converges to a condition

characterized by conspicuous, geographically structured spatial heterogeneity of average shoot density. The highest values are projected to occur in Tunisia, especially in the Gulf of Gabès, and Croatia, as well as in the main islands of the Western Mediterranean basin, namely Sicily and Sardinia (Italy), Corsica (France), and the Balearic archipelago (Spain).

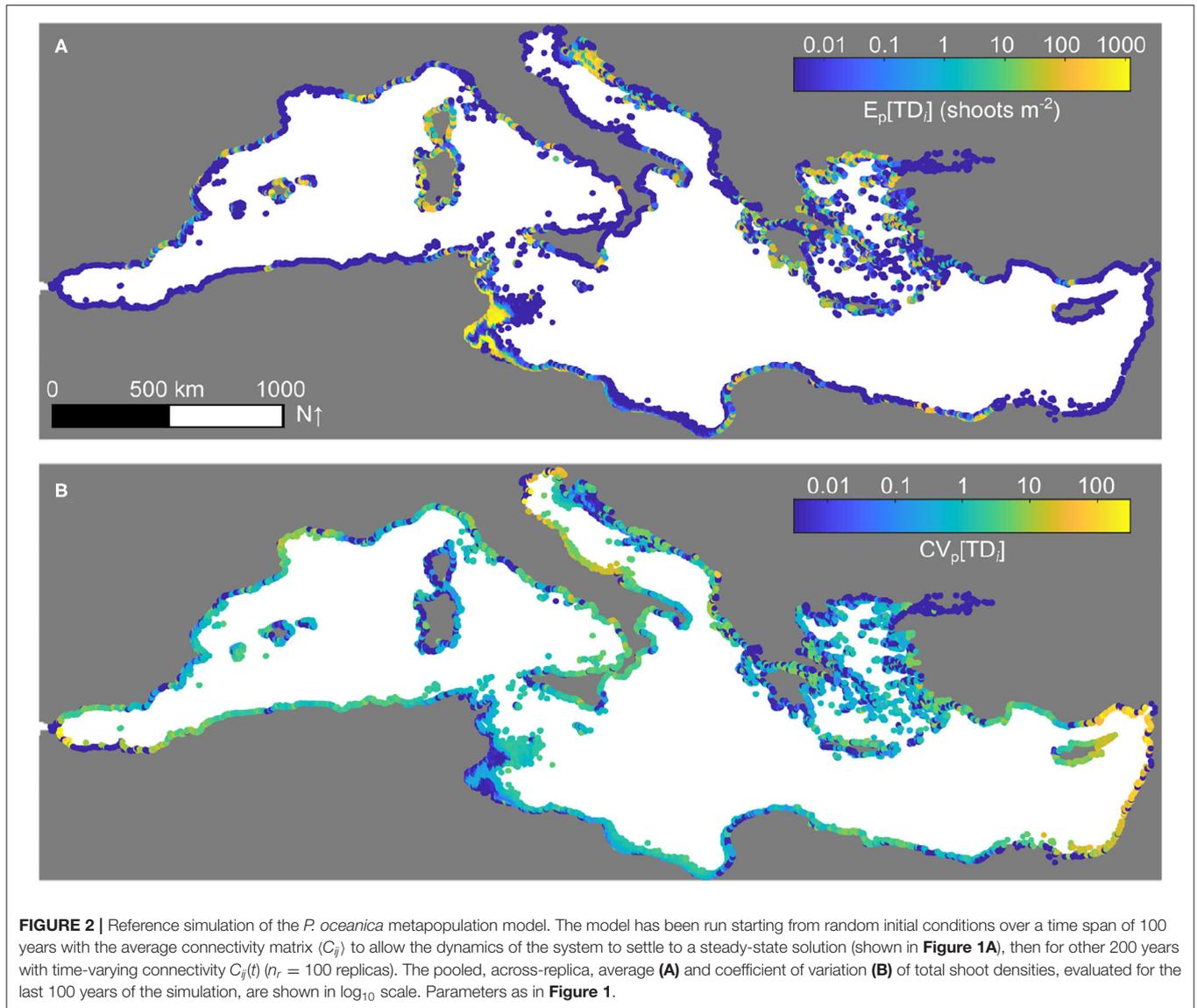
The spatial patterns of realized connectivity for *P. oceanica* evaluated with the top-ranked metapopulation model for the reference simulation of **Figure 2** are shown in **Figure 3**. Because realized connectivity accounts not only for the potential



means of dispersal provided by marine currents but also for the demographic dynamics of the metapopulation and their interactions with the seascape, the resulting spatial patterns turn indeed out to be quite distinct from those of potential connectivity, as it is apparent by contrasting realized (i.e., metapopulation-based) vs. potential (i.e., oceanographic) connectivity metrics (**Figure 3** vs. **Supplementary Figure 1**). From a quantitative perspective, the contribution of average realized connectivity to the spatiotemporal dynamics of *P. oceanica* appears to be quite small compared to that of

local population densities, reflecting the somewhat sporadic nature of sexual reproduction in *P. oceanica*. This observation is also backed up by the estimates of temporal variability in connectivity strength, which are large (e.g., $CV_p \geq 10$) in many sectors throughout the Mediterranean basin. Interestingly, the maximum values of average indegree are in line with reported observations of recruitment by seed in highly suitable locations (around 20–30 seedlings m^{-2} ; Balestri et al., 2017).

The spatial patterns of propagule displacement, i.e., the average distances traveled by *P. oceanica* fruits successfully



dispersing to/from a given marine sector, have also been evaluated for the reference simulation of **Figure 2** and are shown in **Figure 4**. While most connections are local, with average dispersal distances confined to a few kilometers, some sectors appear to be characterized by relatively long-distance dispersal, with average in/outbound successful propagule displacements up to a few hundred kilometers. This is the case, in particular, for the sectors located in the region of the Gulf of Gabès, at the crossroad between the western and eastern basins of the Mediterranean Sea.

The metapopulation density, connectivity, and displacement patterns projected by the reference model simulation have been used to identify *P. oceanica* hotspots, regions of the Mediterranean Sea that play a key role in the basin-wide metapopulation dynamics of this seagrass species. Visual inspection of the spatial distribution of the hotspots based on the percentiles P_i^Q ($Q \in \{TD, SR, ID, OD, IM, OM\}$, **Figure 5**) reveals

distinctive spatial patterns for the hotspots identified using density (panel A), connectivity (B–D), or displacement-related measures (E–F). The diversity of the hotspots corresponding to specific ecological functions is well-reflected in the identification of multi-functional hotspots, defined according to a conservative aggregation of the performances of each sector in the various percentile scores (**Figure 6A**). The marine sectors identified as multi-functional hotspots (e.g., those with $P_i^{MF} \geq 50$) are mainly located along the coasts of Tunisia and Libya, for Africa, as well as in the Aegean Sea, in Sardinia and along the Spanish coastline—with other, more isolated occurrences in the Balearic Islands, France, and the Adriatic Sea, for Europe. Hotspot identification also helps recognize possible gaps in the protection of this foundation species. Specifically, a clear pattern emerges where European *P. oceanica* multi-functional hotspots are within or close to areas characterized by some form (not necessarily *P. oceanica*-specific) of protection,

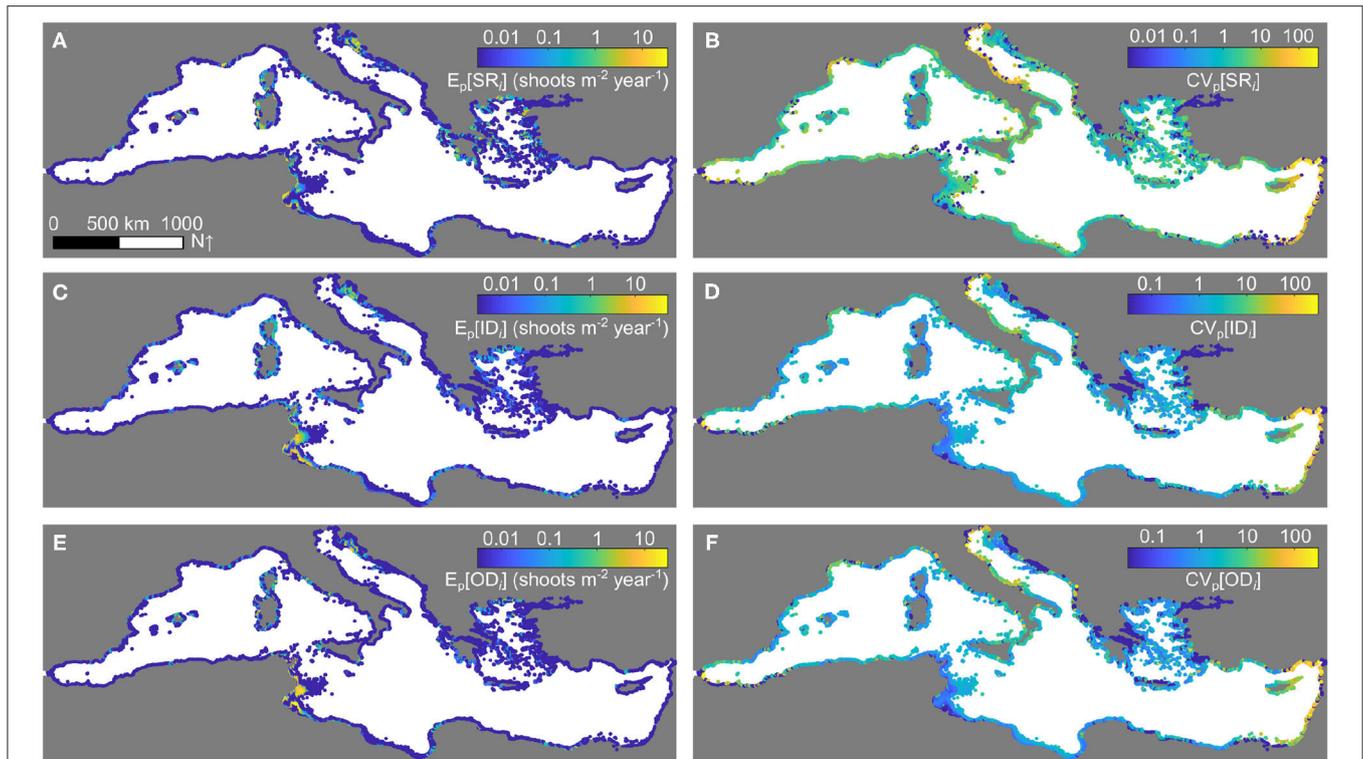


FIGURE 3 | Realized connectivity patterns for *P. oceanica* evaluated from the metapopulation model. **(A)** Pooled average and **(B)** coefficient of variation of self-retention. **(C)** Pooled average and **(D)** coefficient of variation of indegree connectivity. **(E)** Pooled average and **(F)** coefficient of variation of outdegree connectivity. All quantities refer to the simulation of **Figure 2** and are shown in \log_{10} scale.

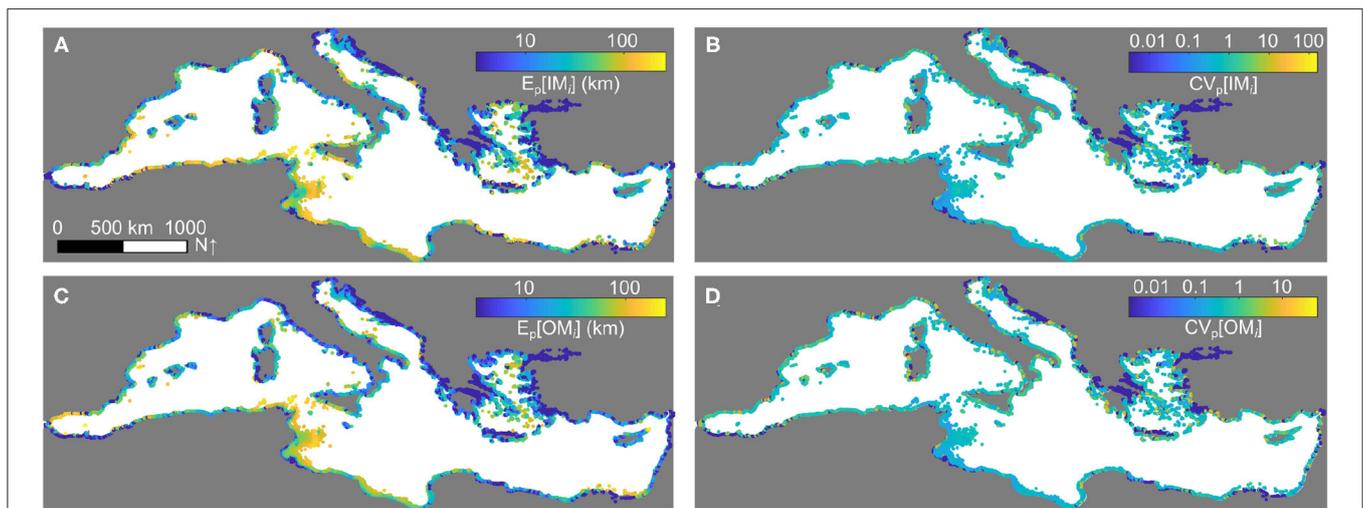
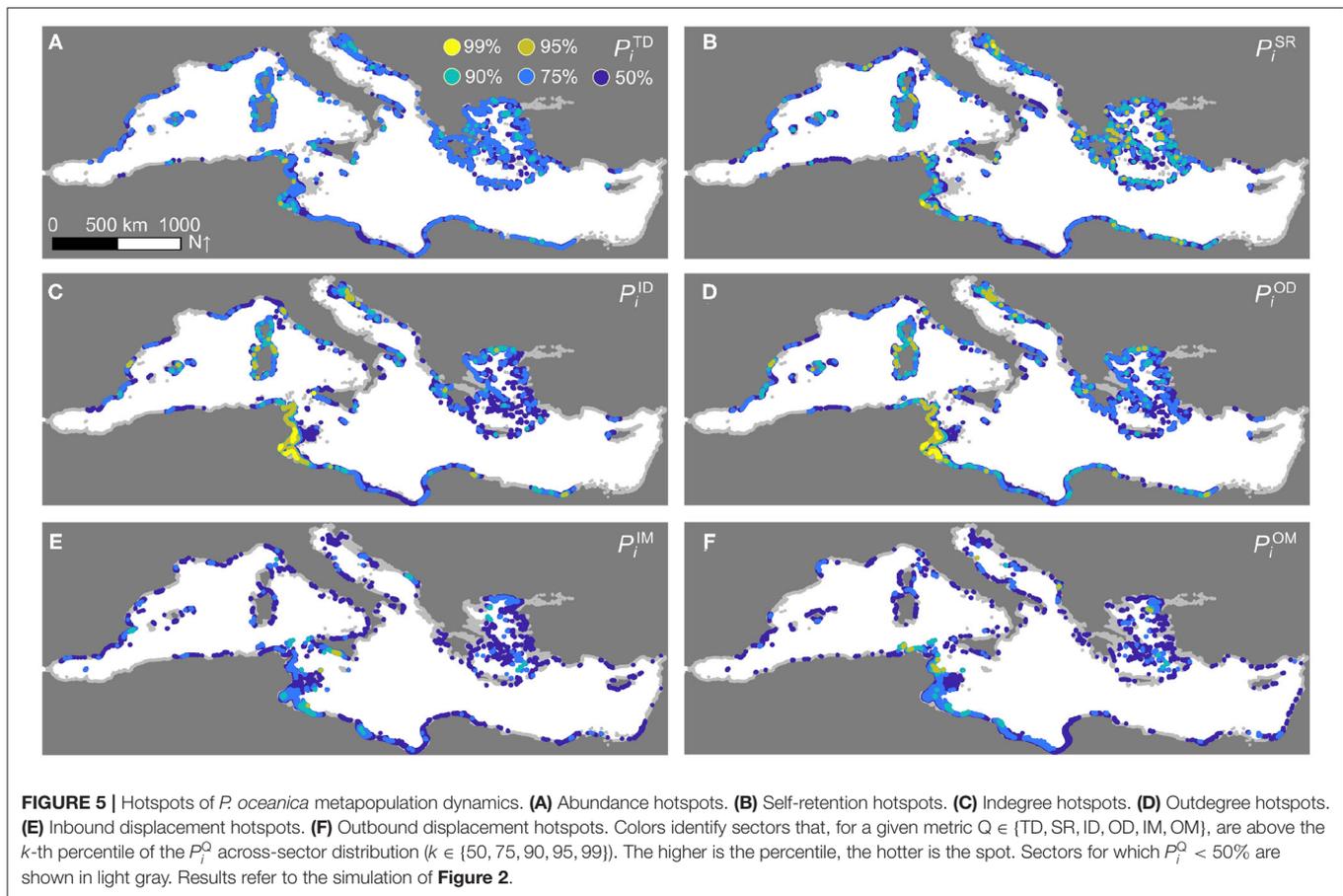


FIGURE 4 | Realized displacement patterns for *P. oceanica*. **(A)** Pooled average and **(B)** coefficient of variation of inbound displacement. **(C)** Pooled average and **(D)** coefficient of variation of outbound displacement. All quantities refer to the simulation of **Figure 2** and are shown in \log_{10} scale.

while hotspots located along the African coastline may be hundreds of kilometers away from the closest marine protected area (**Figure 6B**).

Finally, in terms of sensitivity analysis, the hotspot identification procedure produces consistent results when

the spatial grain of the metapopulation model is altered. As an example, **Supplementary Figure 6** shows the computation of density, connectivity and displacement indicators from the output of the model simulation, while **Supplementary Figure 7** reports the evaluation of percentile

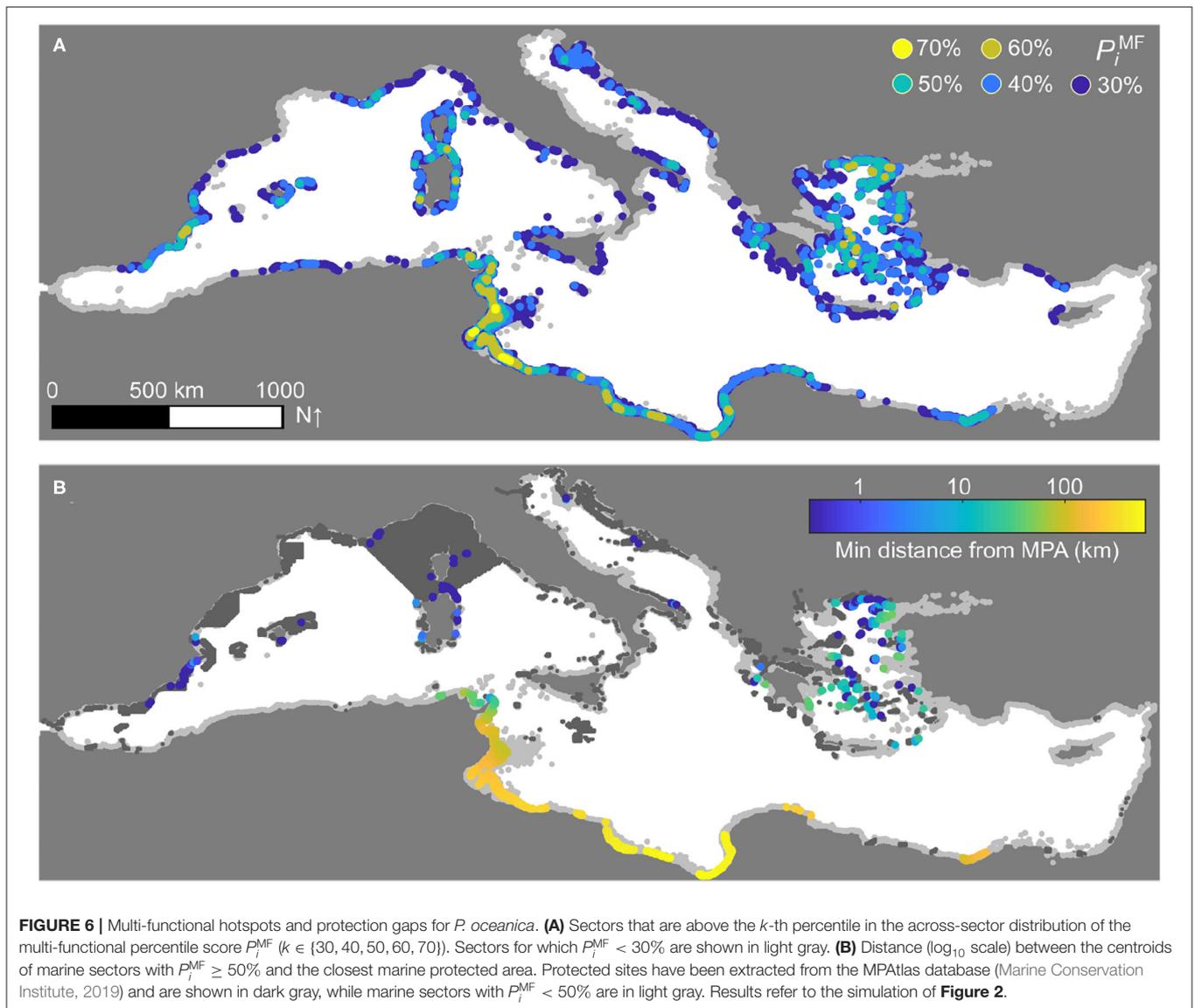


scores and their multi-functional aggregation, both with $d^* = 50$ km. The results show that, despite differences in function-specific indicators (hence, possibly, also in the relevant sector rankings) with respect to the reference case, the same key marine regions tend to emerge. A generalization of these findings to other threshold distances is shown in **Supplementary Figure 8**. A remarkable robustness of model projections is also found when sensitivity analysis is performed with respect to parameter uncertainty. **Supplementary Figure 9** shows what happens to average seagrass densities when the model parameters are varied within biologically plausible ranges (**Table 1**), while **Supplementary Figure 10** reports the evaluation of function-specific indicators. Based on these results, the identification of *P. oceanica* hotspots seems to be quite robust also to changes in the parameterization of the model, in that most of the key areas identified in **Figures 5, 6A** consistently emerge also under parameter uncertainty (**Figure 7**).

4. DISCUSSION

In this work, we have presented a quantitative analysis of the Mediterranean-wide dynamics of an iconic foundation species, the endemic seagrass *P. oceanica*, using a spatially explicit and dynamic metapopulation approach. The model couples local

density-dependent demographic dynamics, driven by spatially explicit information on habitat suitability, with current-driven dispersal of seagrass fruits, informed by data from oceanographic reanalyses. Using a formal model-selection framework, we tested several concurrent hypotheses concerning the role possibly played by density dependence in different phenological processes. We found that a parsimonious approach describing vegetative growth, shoot survival, and post-dispersal settlement as density-dependent processes, and sexual reproduction as a density-independent process (**Figure 2**), may represent a well-balanced trade-off between accuracy (evaluated as the model's ability to explain binary observations of *P. oceanica* presence/absence throughout the Mediterranean basin) and complexity (evaluated as the number of calibration parameters). The selected model set-up has been used to evaluate simple metrics concerning realized connectivity and dispersal distance (**Figures 3, 4**), which formed the quantitative basis for the identification of *P. oceanica* functional hotspots (**Figure 5**). Marine sectors that can simultaneously play different ecological functions, such as retainer (high density, strong propagule retention), source (large outdegree connectivity, long outbound dispersal distance), or sink (large indegree connectivity, long inbound dispersal distance), have also been identified (**Figure 6**). From a modeling point of view, we believe that the approach presented in this work represents a clear improvement over previous applications



describing only either the demographic traits of single *P. oceanica* meadows (Duarte et al., 2006) or current-driven connectivity (Mari et al., 2020).

Like all modeling studies, ours is not devoid of limitations. Firstly, the spatial resolution of the metapopulation model is relatively coarse, as our computational units correspond to marine sectors with an areal extent of about 48 km². As customary in spatially explicit modeling applications, the choice of a reference spatial resolution represents a trade-off between accuracy, on the one hand, and robustness and applicability, on the other. Needless to say, this choice must also necessarily consider the spatial extent of the study area (in this case, the whole coastal region of the Mediterranean basin) and the temporal scale of the process of interest (in this case, multi-decadal metapopulation dynamics). A higher-resolution model would in fact allow us to more accurately represent local

demographic dynamics; however, it would prove harder to parameterize (hence, arguably, less robust) and simulate at the whole-Mediterranean and multi-decadal scale that the current study focuses on. While the latter issue is purely numerical and could be tackled by deploying enough computational power, the former remains difficult to address because of the fragmented availability of high-resolution data of consistent quality across the Mediterranean basin concerning both the ecology of *P. oceanica* and the circulation patterns of marine currents. Nevertheless, we acknowledge that a higher-resolution model may be more appropriate for fine-scale assessments of meadow-scale *P. oceanica* metapopulation dynamics. In that case, though, a different metapopulation approach should be used, one in which meadows are described as individual patches, whose size and shape can change over time because of clonal growth (Arnaud-Haond et al., 2012), and that are linked by

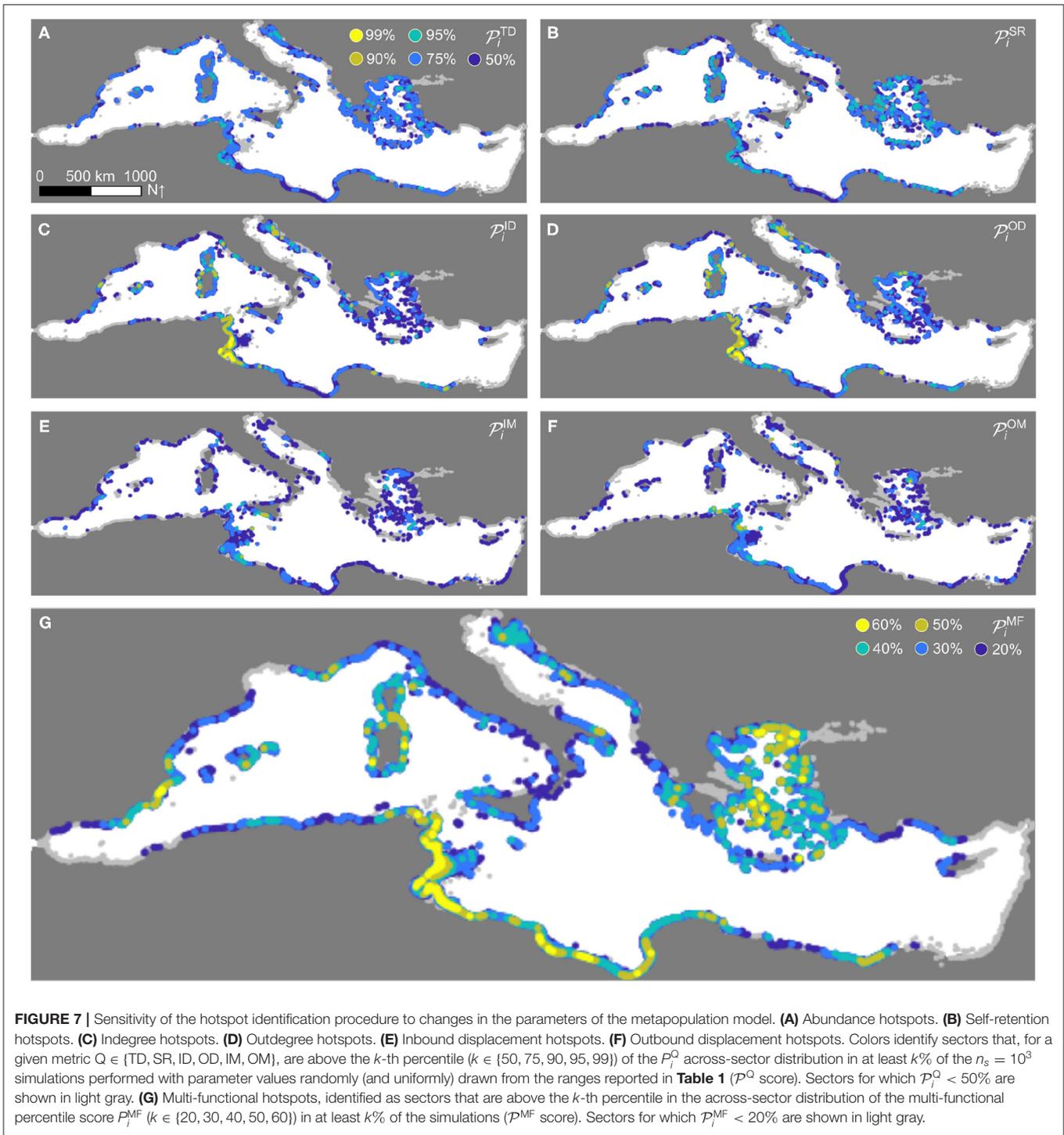


FIGURE 7 | Sensitivity of the hotspot identification procedure to changes in the parameters of the metapopulation model. **(A)** Abundance hotspots. **(B)** Self-retention hotspots. **(C)** Indegree hotspots. **(D)** Outdegree hotspots. **(E)** Inbound displacement hotspots. **(F)** Outbound displacement hotspots. Colors identify sectors that, for a given metric $Q \in \{TD, SR, ID, OD, IM, OM\}$, are above the k -th percentile ($k \in \{50, 75, 90, 95, 99\}$) of the P_i^Q across-sector distribution in at least $k\%$ of the $n_s = 10^3$ simulations performed with parameter values randomly (and uniformly) drawn from the ranges reported in **Table 1** (P^Q score). Sectors for which $P_i^Q < 50\%$ are shown in light gray. **(G)** Multi-functional hotspots, identified as sectors that are above the k -th percentile in the across-sector distribution of the multi-functional percentile score P_i^{MF} ($k \in \{20, 30, 40, 50, 60\}$) in at least $k\%$ of the simulations (P^{MF} score). Sectors for which $P_i^{MF} < 20\%$ are shown in light gray.

hydrodynamic connectivity through fruit dispersal and, possibly, other mechanisms that might be relevant at this scale, such as seed resuspension (McMahon et al., 2014) and the exchange of vegetative fragments (Di Carlo et al., 2005). At an even higher spatial resolution, seagrass clonal dynamics may also be described with spatially explicit, individual-based models in which each shoot (or each branch) represents an interacting agent (Kendrick

et al., 2005; Sintes et al., 2005), or with integro-differential models (Ruiz-Reynés et al., 2017).

Another limitation of the present work is that of having disregarded temporal trends in both habitat suitability and current-driven connectivity. Indeed, evidence exists that *P. oceanica* populations have been regressing in the Mediterranean over the past decades (Telesca et al., 2015),

and projections suggest that the localized effects of global climate change might exacerbate this trajectory of change in decades to come, with worst-case scenarios projecting a 75% loss by 2050 and functional extinction by the end of the century (Chefaoui et al., 2018). The warming of the marine environment is currently considered one of the most severe threats for seagrasses, including *P. oceanica* (Duarte et al., 2018). Thermal stress may have multiple negative effects on *P. oceanica*, including increased shoot mortality, limited growth, faster leaf senescence, and reduced seedling germination (Marbà and Duarte, 2010; Guerrero-Meseguer et al., 2017). However, the observation that rising temperatures may affect the phenology of *P. oceanica*, with non-trivial consequences for both individual plants and meadows (Peirano et al., 2011), and the high plasticity of the species (González-Correa et al., 2007b), possibly leading to higher rates of sexual reproduction (Balestri et al., 2017), increase the uncertainty of climate-related projections. Among the other factors related to global climate change, enhanced stratification (Coma et al., 2009), sea-level rise (Pergent et al., 2015), meteorological extremes (Guerrero-Meseguer et al., 2017), and water acidification (Ravaglioli et al., 2017) are all expected to play a role in determining the future suitability of the Mediterranean coasts for *P. oceanica*, albeit with localized and likely contrasting directions of change. Climate change is also projected to have an impact on water circulation in the Mediterranean Sea (Adloff et al., 2015), with possible implications for ecological connectivity and, ultimately, conservation (Coleman et al., 2017). In this context, the ever-expanding availability of Earth Observation data may be used in conjunction with species distribution modeling to project the future distribution patterns of *P. oceanica*, thus also informing large-scale conservation programs (Pasetto et al., 2018).

From a conservation perspective, our modeling results suggest that *P. oceanica* ecological hotspots are quite unevenly distributed along the Mediterranean coastline. We found that the region centered in the Gulf of Gabès plays an especially important role in the large-scale metapopulation dynamics of the species. Interestingly, the genetic diversity of *P. oceanica* is significantly higher in this region than anywhere else (Arnaud-Haond et al., 2007), suggesting the existence of a contact zone between the otherwise genetically disconnected populations of *P. oceanica* inhabiting the Western and Eastern basins of the Mediterranean Sea (Serra et al., 2010). As a matter of fact, high population density, strong connectivity and long-distance dispersal are all ingredients that are expected to favor population connectivity and, as a consequence, effective gene flow. Genetic diversity is one of the factors contributing to the capacity of a species to cope with climate change (Dawson et al., 2011). Therefore, preserving genetic diversity should be a priority target in the conservation of *P. oceanica*, given the bleak road ahead projected for Mediterranean seagrasses subject to regional climate change (Jordà et al., 2012; Chefaoui et al., 2018).

Marine protected areas seem to be an effective tool for the conservation of *P. oceanica*. Some field studies have in fact found no evidence of meadow decline in several protected marine sites, in stark contrast with the average trajectory of change

(González-Correa et al., 2007b). In this regard, our analysis has shown that a considerable spatial gap in protection may exist for Mediterranean seagrass populations. In fact, while many of the lesser *P. oceanica* hotspots laying along the European coasts occur within or close to marine protected areas, virtually all of the crucial North-African ones are located hundreds of kilometers away from the closest sites of marine protection. This disparity could indeed represent an issue for the conservation of the species, which would require protection plans to be devised at a pan-Mediterranean spatial scale. Clearly, legal protection is not enough to safeguard *P. oceanica* populations, as field observations also suggest that deep meadows in marine protected areas may be not healthier than those in unprotected areas (Montefalcone et al., 2009). As an example, ineffective management of protected areas, especially concerning boat anchoring, can have detrimental consequences for *P. oceanica* meadows (e.g., La Manna et al., 2015).

The identification of a clear spatial protection gap should raise the question of how to strategically coordinate conservation efforts, possibly in a trans-boundary way (Katsanevakis et al., 2015), to ensure that resources are allocated where they are most likely to be effective (McCarthy et al., 2010). Designing protection at the scale of the whole Mediterranean Sea is clearly a major challenge, not only from an ecological point of view, but also from social, political, and economic perspectives. Twenty-one countries in three continents face the Mediterranean, with diverse human populations including many ethnic and cultural groups and, often, complicated political trajectories (Pergent et al., 2017). Proposed international plans for the expansion of Mediterranean protection are quite diverse in the underlying technical approaches, conservation goals, spatial extents, and geographic locations; however, consensus exists among different plans about some key Mediterranean regions accounting for about 10% of the areal extent of the basin (Micheli et al., 2013). Specifically, large-scale plans most often focus geographically on the Alboran Sea, the Balearic Archipelago, the Ligurian Sea, the region extending from the Gulf of Gabès to the Sicily Channel through the Tunisian Plateau, and some stretches of the Adriatic, Ionian, Aegean, and Levantine Seas, with small overlaps (mostly limited to the Ligurian Sea) with existing protected areas. Notably, most of the marine regions that we have identified as possible *P. oceanica* hotspots are indeed comprised within this list, suggesting that further synergies in large-scale protection planning may be possible.

In conclusion, in this work we have shown how a relatively simple metapopulation model, fed with georeferenced information from habitat distribution modeling and Earth Observations, can be used to integrate demographic and dispersal processes to analyze the spatiotemporal dynamics of an important foundation species, the endemic seagrass *P. oceanica*, at the scale of the whole Mediterranean Sea. Results from metapopulation modeling can then be used to identify key targets for international protection based on reproducible and quantitative procedures, thus contributing to a much-needed prioritization of conservation actions in the Mediterranean large marine ecosystem. Looking ahead, trying to anticipate

how changing environmental conditions and increasing human pressure will ultimately affect *P. oceanica* ecological hotspots in the Mediterranean Sea is made difficult at present by the presence of multiple uncertainty sources. Our study suggests that any such predictions ought to be based on a reliable framework for the description of basin-scale and long-term metapopulation dynamics.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The relevant web links are given in the text. The data and the code to perform numerical simulations of the metapopulation model are available at: <https://github.com/lorenzo-mari/posidonia-metapop>.

AUTHOR CONTRIBUTIONS

LM performed the simulations and data analysis. All authors contributed to designing the experiments, interpreting the

results, and drafting the manuscript, and read and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2021.628976/full#supplementary-material>

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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