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Climate change and the presence of invasive species will threaten the persistence of the Mediterranean seagrass community

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HIGHLIGHTS

- *Posidonia oceanica* is expected to be highly susceptible to projected climate change.
- The presence of native seagrass species will actually facilitate the predicted spread of the invasive *H. stipulacea*.
- Expected transition from large and slowgrowing to small and fast-growing seagrass species.
- Dead mattes of *P. oceanica* will be replaced by small and fast-growing seagrass species.
- Western and colder areas of the Mediterranean Sea might provide a refuge for *P. oceanica.*

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ABSTRACT

The Mediterranean Sea has been experiencing rapid increases in temperature and salinity triggering its tropicalization. Additionally, its connection with the Red Sea has been favouring the establishment of non-native species. In this study, we investigated the effects of predicted climate change and the introduction of invasive seagrass species (*Halophila stipulacea*) on the native Mediterranean seagrass community (*Posidonia oceanica* and *Cymodocea nodosa*) by applying a novel ecological and spatial model with different configurations and parameter settings based on a Cellular Automata (CA). The proposed models use a discrete (stepwise) representation of space and time by executing deterministic and probabilistic rules that develop complex dynamic processes. Model applications were run under two climate scenarios (RCP 2.6 and RCP 8.5) projected from 2020 to 2100 in four different regions within the Mediterranean. Results indicate that the slow-growing *P. oceanica* will be highly vulnerable to climate change, suffering vast declines in its abundance. However, the results also show that western and colder areas of the Mediterranean Sea might represent refuge areas for this species. *Cymodocea*

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nodosa has been reported to exhibit resilience to predicted climate scenarios; however, it has shown habitat regression in the warmest predicted regions in the easternmost part of the basin. Our models indicate that *H. stipulacea* will thrive under projected climate scenarios, facilitating its spread across the basin. Also, *H. stipulacea* grew at the expense of *C. nodosa*, limiting the distribution of the latter, and eventually displacing this native species. Additionally, simulations demonstrated that areas from which *P. oceanica* meadows disappear would be partially covered by *C. nodosa* and *H. stipulacea*. These outcomes project that the Mediterranean sea-grass community will experience a transition from long-lived, large and slow-growing species to small and fast-growing species as climate change progresses.

1. Introduction

Since the Industrial Revolution, the global climate has rapidly changed in response to anthropogenic activities (IPCC, 2023). The associated rising seawater temperatures and extreme climate events have severely altered the habitat conditions of most coastal ecosystems (McMichael et al., 2004; Harley et al., 2006). In addition, the arrival of exotic species into new habitats which is linked with anthropogenic activities and climate change effects represents another threat to the future functioning of many coastal ecosystems (Hobbs, 2000; Anton et al., 2019; Kroeker et al., 2020).

The semi-enclosed Mediterranean basin has been experiencing accelerated increases in temperature and salinity triggering its tropicalization (Bianchi and Morri, 2003; Borghini et al., 2014). In the Mediterranean basin, sea surface temperatures (SSTs) have significantly risen ~1.5 °C in the last decades (Pastor et al., 2020; Bulgin et al., 2020), warming more rapidly than most marine waters worldwide, and anomalously warm summers have increased in frequency, duration and intensity (Hulme, 2014; Oliver et al., 2018; Darmaraki et al., 2019). In its south-eastern basin, the Mediterranean Sea is connected with the Red Sea and Indian Ocean through the Suez Canal. Since its opening some 150 years ago, a continuous migration of exotic tropical species (i.e., fish, jellyfish), which established in the Mediterranean Sea ("alien" or non-indigenous species, NIS), has been observed. Recently, Zenetos and Galanidi (2020), reported on a total of 666 marine alien species established in the Mediterranean. Due to this vast amount of alien species, in a relatively isolated basin, the Mediterranean Sea is considered to be a hotspot of marine bioinvasions (Mannino et al., 2017). Some of these Lessespian migrants have been shown to interact with native species and have even become invasive (i.e., spreading in large numbers and eventually outcompeting the local species) untimely altering the local trophic web (Zenetos et al., 2005; Galil, 2008; Edelist et al., 2013; Garrabou et al., 2022).

Seagrasses are marine angiosperms inhabiting shallow and sheltered marine coastal environments. They are considered "ecosystem engineers" that structure habitats, providing ecological niches for a large number of associated species, and offering critical ecological goods and services worldwide (Terrados and Borum, 2004; Nordlund et al., 2018; Ricart et al., 2021). Mediterranean seagrass communities include five species, each one with different ecological attributes and environmental tolerances (Short et al., 2007). The two most abundant species are Posidonia oceanica (L.) Delile, and Cymodocea nodosa (Ucria) Ascherson. Posidonia oceanica (Posidoniaceae family) is endemic to the Mediterranean where it is the dominant species. It is a large-sized (up to 1-1.2 cm) and foundation species with a narrow ecological niche, low dispersal abilities and slow growth and recovery rates, causing this species to be highly vulnerable to global change and local stressors such as warming events or eutrophication (Marbà and Duarte, 2010; Marbà et al., 2014; Pazzaglia et al., 2020; Helber et al., 2021). In contrast, C. nodosa (family Cymodoceaceae) is a small to medium-sized (up to 40-50 cm) and fastgrowing species, with a broad biogeographical distribution, ranging from the Mediterranean to tropical and temperate Atlantic regions (Olivé et al., 2013; Chefaoui et al., 2016). This species is considered a colonizer species and can replace areas previously occupied by P. oceanica likely playing a similar ecological role (Cancemi et al., 2002;

Montefalcone et al., 2007).

Halophila stipulacea Ascherson (family Hydrocharitaceae), is a small and fast-growing tropical seagrass species native to the Red Sea, Persian Gulf and Indian Ocean. It was one of the first Lessepsian migrants to the Mediterranean, reported in the region for the first time only 25 years after the canal opened; since then it has spread in most of the eastern and central Mediterranean regions (Lipkin, 1975). Its current Mediterranean westernmost distribution was recently reported to be in the harbour of Cannes, France, (43.545° N, 7.022° E); notably, due to its recent documentation, this cannot yet be considered a stable population (Thibaut et al., 2022). In the Mediterranean, Halophila stipulacea has been found growing both in monospecific meadows and also in mixed meadows, cooccurring with P. oceanica and C. nodosa (Winters et al., 2020). Recent field studies and mesocosm experiments suggest that H. stipulacea is capable of growing faster, and developing denser meadows with larger belowground and aboveground structures when it interacts with native species compared to when it grows alone (Willette and Ambrose, 2012; Sghaier et al., 2014; Chiquillo et al., 2023).

Several studies have concluded that global climate change may eventually exceed the adaptive capacity of some of the native Mediterranean species, such as P. oceanica, causing the migration or disappearance of their ecological niche (Marbà and Duarte, 2010; Marín-Guirao et al., 2018; Chefaoui et al., 2018). This would result in local distribution losses and the emergence of new habitats potentially available to be colonized by warmer-adapted seagrass species (Chefaoui et al., 2018; Beca-Carretero et al., 2020a; Wesselmann et al., 2021a, 2021b). Cymodocea nodosa is generally well-adapted to the highest temperatures found in the Mediterranean Sea, and it is expected to cope with predicted increases in SST in most of the basin (Alberto et al., 2006; Chefaoui et al., 2016). Within the Mediterranean Sea, species substitution has been observed in degraded areas. For instance, extensive habitat regression of P. oceanica and, to a lesser degree, C. nodosa, has been attributed to anthropogenic disturbances such as trawling or anchoring with C. nodosa often occupying degraded areas previously inhabited by P. oceanica (Montefalcone et al., 2007; Pergent et al., 2014). More recently, the invasive species H. stipulacea has been observed settling in and replacing degraded habitats of native species, as well as interacting with and displacing native species (Sghaier et al., 2014). Particularly of concern is the growing evidence that this invasiveness plays an increasing role in shaping Mediterranean seagrass communities in the eastern and central areas of the basin (Winters et al., 2020).

Over the past decades, a variety of ecological modelling approaches, including dynamic, mechanistic, and biogeographical models, have been employed to simulate ecological processes in both terrestrial and marine ecosystems (Koenigstein et al., 2016). In the Mediterranean Sea, previous studies have employed ecological and spatial models to evaluate potential shifts in habitat suitability for the region's native seagrass species such as *P. oceanica* and *C. nodosa*, as well as the invasive species *H. stipulacea*, across different climate scenarios. These studies implemented a range of spatial models, including diverse SDMs like Maxent or envelope models (e.g., Chefaoui et al., 2018; Beca-Carretero et al., 2020a), often integrating species-specific physiological responses into these models to potentially generate more robust predictions of species distribution (Kearney and Porter, 2009; Gamliel et al., 2020; Wesselmann et al., 2021a, 2021b). Operating at a coarse resolution, these

models yielded a comprehensive regional perspective on how seagrass species might respond to climate conditions, these models, however, did not incorporate processes, such as species interactions, or environmental and anthropogenic disturbances occurring at the local scale. In certain scenarios, local processes can elucidate spatial species dynamics better than species-specific responses to climate settings. For example, the absence of a native species within its optimal environmental range might be related to the presence of an invasive species that competes with and displaces the native species from their natural habitat (Albano et al., 2021). To capture these local processes, models operating at finer spatial scales and capable of incorporating such mechanisms are essential. Mechanistic models include the cellular automata (CA) approach, which has been particularly capable of simulating complex spatial biological and ecological processes at fine scales (Breckling et al., 2011). Cellular automata models are discrete (stepwise) cell-oriented representations of space and time based on deterministic or probabilistic rules which can describe the species-environment relationship, physiological tolerances, and species interactions (Schonert and Milbradt, 2005). Since seagrasses are sessile species distributed in the seafloor, that can interact with each other and are sensitive to environmental changes, predictions about the dynamics and the future of these organisms are particularly suitable to be implemented in CA models. However, the application of CA models or similar models to the realm of seagrasses has so far been rather limited (Marsili-Libelli and Giusti, 2004; Kendrick et al., 2005; McArthur et al., 2013; Mayol et al., 2022; Llabrés et al., 2022, 2023).

By implementing a CA model, we aim here to address two main question: (i) How will climate changes including rises in SST and salinity alongside the effects of anomalous warm summer events, affect the future distribution of native Mediterranean seagrasses? (ii) How will the spread of invasive seagrass species affect the composition of native Mediterranean seagrass communities? Aiming to improve our predicting capacity by answering these questions, we developed climate scenario settings with three different configurations: (i) only native Mediterranean species, (ii) both native species and invasive *H. stipulacea*, and (iii) both configurations, with and without anthropogenic disturbances across four Mediterranean regions, spanning from eastern to western areas of the basin, likely encompassing the Mediterranean thermal range.

We hypothesized that the Mediterranean seagrass community will

experience a transition from a seagrass landscape that is dominated by long-lived and large species (*P. oceanica*) to a landscape dominated by small and fast-growing species as climate change progresses in this basin, and that the presence of *H. stipulacea* will become more common.

2. Material and methods

2.1. Study regions, environmental variables and climate scenarios

The CA model was applied in four different regions, from the east to the west, located at a similar latitude range $(34–38^{\circ} \text{ N})$: Region 1 (East [E]): $34.64042^{\circ} \text{ N}$, $33.04051^{\circ} \text{ E}$; region 2 (Central east [CE]): 37.00576° N, $25.28317^{\circ} \text{ E}$; region 3 (central west [CW]): $38.28694^{\circ} \text{ N}$, 15.59397° E; region 4 (West [W]): $38.970691^{\circ} \text{ N}$, $1.536368^{\circ} \text{ E}$ (Figs. 1; S1).

We used environmental variables of temperature and salinity available for present (2020) and future climate scenarios (2040–2050 and 2100) for two different greenhouse gas concentration projections including RCP 2.6 (representative concentration pathway; lowest carbon emission) and the RCP 8.5 (highest carbon emission) (IPCC, 2021) (Tyberghein et al., 2012; Assis et al., 2018, www.bio-oracle.org) (Table S2). We also included anomalous warm summer events in the model that were programmed as random events with an increased annual SST maximum of ~1.5–2 °C every 5–10 years (Baldi et al., 2006). However, we did not account for specific increases in their frequency, intensity, or duration over time, nor did we consider variations under different climate scenarios.

2.2. Seagrass species

We selected two native Mediterranean seagrass species, *P. oceanica* and *C. nodosa* alongside the invasive seagrass species *H. stipulacea*. Data of the occurrence of the studied seagrasses are reported in Fig. S3. In regions 1 (E), 2 (CE), and 3 (CW) (Fig. 1), the three seagrass species can co-exist (i.e., mixed meadows) and interact at shallow conditions (5–10 m) (e.g., Bianchi et al., 1999, 2019; Gambi et al., 2009; Nguyen et al., 2020a). In contrast, in region 4 (W), at least at present (the year 2023), only the native species is reported. Nevertheless, based on recent studies that predicted suitable habitat conditions based on SST and salinity for *H. stipulacea* by 2040–2050 (Gamliel et al., 2020; Beca-Carretero et al., 2020a; Wesselmann et al., 2021a, 2021b), the model was allowed to



Fig. 1. Map of the current distribution of *Posidonia oceanica, Cymodocea nodosa* and *Halophila stipulacea* in the Mediterranean basin, and the selected regions (black rectangle) to implement the models including the east (E), central east (CE), central west (CW) and west (W) region. Seagrass locations gathered from Telesca et al. (2015), Chefaoui et al. (2016, 2018), Winters et al. (2020), Beca-Carretero et al. (2020a), and the Global Biodiversity Information Facility (GBIF) at https://www.gbif.org/.

accommodate the expansion of the invasive. Distribution data was obtained from Telesca et al. (2015); Chefaoui et al. (2016), (2018); Winters et al. (2020); Beca-Carretero et al. (2020a); https://www.gbif.org/ (GBIF). Anomalous and duplicated seagrass locations were removed.

2.3. Cellular automata model

2.3.1. Cellular automata applied to seagrass ecosystems

We implemented a mechanistic model applying a cellular automaton (CA) background using a discrete (stepwise) representation of space and time (Breckling et al., 2011) to simulate distribution patterns of Mediterranean seagrass species in response to climate change scenarios and interactions with *H. stipulacea* (Fig. 2). The model is based on grid cells, which are the unit of operation and can have different states (i.e., presence of specific seagrass species, and/or empty areas). These cell states update from generation to generation (time scale of one year) through the application of rules. The model was programmed in Java using the Mason framework (Luke et al., 2005). In this study, a two-dimensional CA model was parameterized to simulate shallow conditions (~ 5–10 m).

2.3.2. Cellular automata components

The grid: The model was based on a 48.35 m \times 48.35 m array of hexagonal cells with a diameter of 20 cm (90,000 cells), each hexagon cell with an area of $\sim 260 \text{ cm}^2$. The size of the cells was chosen according to the annual growth rates of the three modelled species, thus allowing to capture the colonization processes on an annual basis (*see details below*). For each simulation, regardless of the specific Mediterranean region (east, central east, central west and west; regions 1–4), the 2338m² array was consistently employed.

Cell states: Each cell (hexagon) (Fig. S4) was defined with five potential states, though only one state can define the cell's condition during any given time period. Firstly, the presence of any of the three species represents a distinct state, with one cell state for *P. oceanica*, one for *C. nodosa* and another for *H. stipulacea*. The fourth state represents dead mattes of *P. oceanica*. *Posidonia oceanica* typically develops large and aged belowground structures (rhizomes and roots) that create mattes which remain in the seafloor for up to hundreds of years forming resistant structures that lift the seafloor for meters, even if the shoots of *P. oceanica* are dead (Romero et al., 1994; Mateo et al., 1997). Lastly, an empty cell (sand) represents the fifth state, defined as an area potentially colonisable by any seagrass species. Dead cells of *C. nodosa* and *H. stipulacea* were also considered as empty cells (sand) because short



Fig. 2. Workflow of the cellular automata (CA) model parametrization, calibration, independent validation, and simulation.

and fast-growing species usually do not produce large belowground compartments that allow them to persist after a destructive event such as sand deposits or storms (Marbà and Duarte, 1995; Vidondo et al., 1997).

2.4. Model rules

The seagrass development on a specific cell and the colonization of an adjacent cell depends on four factors: (i) environmental conditions and climatic thresholds, (ii) species-specific colonization probabilities, (iii) the state of the surrounding neighbouring cells, and (iv) the number of surrounded cells (Fig. S4).

2.4.1. Environmental tolerances

For each seagrass species, three climatic thresholds were defined based on minimum and maximum temperature and salinity parameters (Tyberghein et al., 2012; Assis et al., 2018). Climatic thresholds were categorised into: (i) optimal conditions for growth, where seagrasses (cell) live and can colonize an adjacent cell; (ii) suboptimal conditions for growth, where seagrasses (cell) can live but cannot grow and thus cannot colonize an adjacent cell, and finally, (iii) unsuitable conditions for living where seagrasses die and turn into an empty cell, "or dead matte" in case of P. oceanica (Fig. 3). These species-specific climatic thresholds were derived from an extensive literature survey, including field observations and laboratory experiments (Tables S5 and S6), as well as spatial analyses (Fig. S7). For the literature review, we exclusively utilized data from Mediterranean populations for P. oceanica and C. nodosa. In the case of H. stipulacea, we expanded our dataset to include populations from the Red Sea due to the scarcity of Mediterranean data. However, we omitted populations from the Caribbean Sea due to their geographical remoteness. Spatial analyses involved calculating density curves using the seagrass spatial distribution data (Fig. S3) and spatial data of both minimum and maximum SST and salinity. These density curves were referred to as 'environmental response curves'. Following this, we established the three climatic thresholds based on quartiles (further explanations in Fig. S7 and Table S8). The final climatic threshold values were determined by averaging results from both approaches: the literature review and the environmental response curves. These averaged values were then integrated into the model parameterization (Table S9).

The species-specific environmental thresholds are applied according to the following scenarios: If both environmental descriptors, temperature and salinity, were under optimal conditions for growth, the state of



Fig. 3. Temperature (Panel A) and salinity (Panel B) tolerances of the seagrass species *Posidonia oceanica, Cymodocea nodosa* and *Halophila stipulacea*. Green colour represents optimal conditions for growth, orange represents suboptimal conditions for growth, and red colour unsuitable conditions for living.

the seagrass was optimal. However, if one of the environmental tolerances (i.e., temperature), indicated optimal conditions for growth and the other one (i.e., salinity) was only suboptimal, the state of the seagrass became suboptimal. If both environmental tolerances were suboptimal, the state of the seagrass remained suboptimal. Finally, if one environmental tolerance was optimal or suboptimal and the other one was unsuitable, the final condition turned unsuitable. It is noteworthy that, once the survival threshold for both temperature and salinity has been exceeded, the species distribution was progressively reduced at a rate of 10 % per increase of 0.1 $^{\circ}$ C or increase of 0.065PSU in salinity.

2.4.2. Colonization based on the state of the surrounding cells

In the model, in addition to environmental tolerances, we incorporated a probability of occupying a surrounding neighbouring cell based on three factors: (i) the annual growth rate of each species in relation to the defined cell size, (ii) the species' affinity with the different cell states, and (iii) the number of surrounding cells of each species (Fig. S4). As a result, three potential colonization types were considered: (1) a species vs. an empty cell (sand), (2) a species vs. a dead matte of *P. oceanica*, and (3) one species vs. another species.

2.4.2.1. Species-specific growth rates. Species-specific growth performance was calculated based on rhizome elongation rates compiled from a literature survey (Table S10), and then related to the cell diameter (0.2 m). Seagrass vegetative expansion and habitat colonization occur via rhizome growth (Marbà and Duarte, 1998; Marbà et al., 2004). Particularly, *C. nodosa* and *H. stipulacea* possess similar annual horizontal growth rates of ~0.3 m yr⁻¹ based on field and experimental measurements, while the annual growth rates of *P. oceanica* were ~ 0.01 m yr⁻¹.

2.4.2.2. Colonization of adjacent empty cells. When species interact with an empty cell (sand), we considered two options based on the described annual growth rates. The first case involved species with annual growth rates equal to or exceeding the cell size (0.2 m), particularly *C. nodosa* and *H. stipulacea*. These species have a 100 % probability of colonizing neighbouring empty cells (sand) annually. In this case, we applied an 'affinity factor' for the sediment (sand), derived from Chiquillo et al. (2023) (Figs. S11 and S12). According to this study, *C. nodosa* had a 24 % probability of colonizing neighbouring sandy cells, while *H. stipulacea* had a 12 % probability. These probabilities were determined based on changes in density and percentage of cover observed during the meso-cosm interaction experiment (Chiquillo et al., 2023). In the second case, which applies only to *P. oceanica*, the colonization probability was determined by dividing the annual growth rate (0.01 m) by the cell length (0.2 m), resulting in a 5 % probability (Fig. S11).

2.4.2.3. Colonization of adjacent seagrass cells. We assumed that the growth of *P. oceanica* remained unaffected by the presence of other seagrass species (e.g., Vidondo et al., 1997; Guidetti et al., 2002; Montefalcone et al., 2007). Therefore, *C. nodosa* and *H. stipulacea* cannot colonize cells already occupied by *P. oceanica* Similarly, *P. oceanica* cannot expand into areas where *C. nodosa* and *H. stipulacea* are present, primarily due to its low annual growth rates (Table S10). Thus, the colonization probabilities of *C. nodosa* and *H. stipulacea* in areas already occupied by *P. oceanica*, and vice versa, are all 0 %.

The probabilities for interactions between *C. nodosa* and *H. stipulacea* were obtained from recent studies in the Mediterranean Sea. The probability of *C. nodosa* colonizing areas occupied by *Halophila stipulacea* is 0 %. This conclusion is based on findings reported in Chiquillo et al. (2023) and Sghaier et al. (2014), where both studies documented significant habitat regression of *C. nodosa* in the presence of *H. stipulacea*. The final scenario arises when *H. stipulacea* interacts with *C. nodosa*. In this case, colonization probabilities reach 78 %. These values are derived from annual coverage changes documented by

Sghaier et al. (2014), as well as changes in plant density and seagrass coverage of *H. stipulacea* interacting with *C. nodosa*, as reported in Chiquillo et al. (2023) (*Explanation in* Fig. S11).

2.4.2.4. Colonization of adjacent dead mattes of *P. oceanica cells.* The colonization of dead mattes of *P. oceanica* was programmed for *P. oceanica, C. nodosa* and *H. stipulacea.* The probability of the modelled seagrass species to colonize a dead matte of *P. oceanica* was set to be two times higher than the probability to colonize empty cells. Consequently, the final colonization probabilities for the dead matte of *P. oceanica* were as follows: *P. oceanica* 10 %, *C. nodosa* 48 %, and *H. stipulacea* 24 %. These assumptions were based on field studies reporting on the affinity of seagrass species to colonize this substrate (Montefalcone et al., 2007; Gambi et al., 2009; Bianchi et al., 2019; Almela et al., 2008; Wesselman et al., 2021b) (Table 1), and on our field observations and expertise. In this support, Fig. S12 displays *H. stipulacea* and *C. nodosa* inhabiting the *P. oceanica* dead matte, rather than adjacent sandy zones.

Deterministic and probabilistic rules were generated for cell transitions between different states as follows: (i) When a seagrass species occupies a cell, all surrounding empty cells are assigned an equal probability of colonization. (ii) In cases where an empty cell is surrounded by multiple cells of the same seagrass species, the colonization probability of the empty cell is multiplied by the number of adjacent seagrass cells of that species. (iii) When an empty cell is surrounded by more than one seagrass species, a weighted probabilistic procedure is applied, taking into account the number of cells of each species and their respective colonization probabilities. The final outcomes of cell transitions between states were generated using random simulations. These simulations considered the defined probabilities for each species and the number of cells of each species involved. To achieve this, we utilized a Java-based algorithm designed to generate random outcomes with varying probabilities.

2.5. Model simulation

Simulations ran for 80 years depicting the SST and salinity levels from 2020 to 2100, with one year considered as one generation. Usually, Mediterranean seagrass species, including *H. stipulacea*, drastically reduce growth rates during unfavourable conditions in colder months in wintertime (Pérez and Romero, 1994; Guidetti et al., 2002; Nguyen et al., 2020a; Beca-Carretero et al., 2020b). Thus, each year included two seasons, a cold season (6 months), during which all species did not grow, and a warm season (6 months), during which growth conditions were programmed to be optimal, hence the model was updated in 6 monthly time steps. All scenario simulations were repeated 6 times with different random seed configurations.

2.5.1. Map configuration and initial setup

The configuration of the initial seagrass maps with the presence, distribution and extent of each species at the beginning of model simulation was based on datasets provided by the authors of this study, and on previous studies of the Mediterranean Sea (e.g., Bianchi et al., 1999, 2019; Gambi et al., 2009; Winters et al., 2020). Specifically, two main seagrass configurations were created, both with the same spatial dimension (48.35 \times 48.35 m). In the first configuration, only native

species, *P. oceanica* (34 %) and *C. nodosa* (41 %), were included in the model. This configuration was applied for the four regions (E, CE, CW and W) of the Mediterranean Sea.

In the second configuration, *H. stipulacea* was included in the model but applied only for regions E, CE and CW, in which the seagrass landscape configuration was composed by an initial distribution of *P. oceanica* (34%), *C. nodosa* (25%) and *H. stipulacea* (16%). In region 4, the initial condition was characterized by 34% distribution of *P. oceanica* and 41% of *C. nodosa*. The arrival of *H. stipulacea* during 2040–2060 was programmed under two potential scenarios. The first one included the arrival of a low density of fragments of *H. stipulacea* (3–5 fragments [1 fragment = 1 cell] in total) from 2040 to 2060, while the second simulation included a high density of *H. stipulacea* (10–15 fragments) from 2040 to 2060.

2.5.2. Destructive events

We included three destructive events in the model. These events represented random mortality processes of seagrass cells, which allowed improving the realism of the simulations (Fonseca et al., 2000; Giusti and Marsili-Libelli, 2006). The first and second 'natural' events occurred annually during the cold season and represented storms and sand waves, respectively. Storms and sand waves are common Mediterranean environmental perturbations that result in burial of local seagrass plants, which, depending on conditions can cause seagrass death (Marbà and Duarte, 1995; Boudouresque et al., 2009; Oprandi et al., 2020). These winter destructive events only affected C. nodosa and H. stipulacea (Ceccherelli et al., 2018). As a result of its action, affected seagrass cells turn into empty cells. We programmed 12-18 random destructive events annually, which was equivalent to $10 - 15m^2 \text{ yr}^{-1}$ of seagrass loss. Previous studies have shown that P. oceanica is typically not damaged by such destructive events, primarily due to the large size of the plants (>1 m tall), the presence of large rhizome mattes and the protective barrier formed by the dense canopy, making it difficult for sediment to enter and accumulate over time (Romero et al., 1994; Mateo et al., 1997).

The third destructive event was programmed each year in the summer season and it simulated the anchoring activity of boats. Mechanical damage of seagrass beds in the Mediterranean due to anchoring-boat operations is the most common anthropogenic cause of physical destruction of seagrass habitats (Francour et al., 1999; Milazzo et al., 2004). We included 15–17 random events per year; each event destroyed the equivalent of $0.5 - 1m^2$ which was applied to all the three seagrass species in the four regions.

2.5.3. Assumptions of the model

The model was built with the following assumptions: (i) in each single cell, death of shoots was in equilibrium with the appearance of new shoots within each seagrass species, (ii) populations from areas 1 to 4 (E, CE, CW and W) had the same tolerances to environmental conditions; (iii) seagrass species-specific colonization rates were kept constant across its optimal range of SST and salinity. In regions 1, 2 and 3 (E, CE and CW), the seagrass spatial organization and initial percentage of cover for each species (*P. oceanica, C. nodosa* and *H. stipulacea*) were the same. However, in region four (W), *H. stipulacea* was absent until 2040–2060. (iv) In all regions, the destructive events had the same intensity and periodicity.

Table 1

Probabilities of colonization of each species (in %) in relation to the different states of the neighbouring cell. Colonization probabilities are defined based on the probability of one single cell to colonize one neighbouring cell.

| Colonization probabilities (%) | P. oceanica | C. nodosa | H. stipulacea | Dead matte | Empty |
|--------------------------------|-------------|-----------|---------------|------------|-------|
| Posidonia oceanica | Х | 0 | 0 | 10 | 5 |
| Cymodocea nodosa | 0 | Х | 0 | 48 | 24 |
| Halophila stipulacea | 0 | 78 | Х | 24 | 12 |

2.6. Model calibration in baseline scenarios

In order to establish baseline scenarios, the model was calibrated for the present climate scenario (constant SST and salinity) under two different seagrass species compositions: (i) native Mediterranean seagrass species only (*P. oceanica* and *C. nodosa*), and (ii) Mediterranean native and invasive seagrass species (*H. stipulacea*). The calibration processes included a number of simulations encompassing a variation of parameters and processes (i.e., environmental thresholds, growth rates or species interaction) for which the literature search provided heterogeneous values.

2.7. Independent model validation

The independent model validation followed the hierarchical approach described in Kubicek et al. (2015) by assessing each of the model levels separately. This included (i) the reaction of the species to environmental influences, (ii) the interaction between species and (iii) the development of the seagrass community on the overall model level. The model processes and results on each of these levels were checked individually against literature and expert knowledge. On the level of the whole simulation, results were validated with respect to specific seagrass community dynamics, including a situation that included only native seagrass species (Bonacorsi et al., 2013; Burgos et al., 2017) and a situation that included both native and invasive seagrass species (Sghaier et al., 2014).

3. Results

3.1. Model calibration

3.1.1. Base line conditions with native seagrass species

The first scenario simulated the interaction between native seagrass species, *P. oceanica* and *C. nodosa*, without anthropogenic disturbances under current climate conditions over 80 years. Under this scenario, a steady expansion of the habitat distribution (percent of cover) of *P. oceanica*, from 34 to 36 % was observed while the percent cover of *C. nodosa* remained stable (41–42 %) (Fig. S13A).

3.1.2. Base line conditions with native and invasive seagrass species

This baseline scenario was run to test the interactions between native and the invasive seagrass species *H. stipulacea*. In this simulation, the distribution of *P. oceanica* remained almost constant over time, with the same slight increase from 34 to 36 % in 80 generations. In the meantime, *C. nodosa* drastically decreased its coverage from 25 to 2.5 %, whereas, *H. stipulacea* was able to significantly increase its area distribution from 16 to 31 %, mostly explained by its capacity to displace *C. nodosa* and to a lesser extent due to its ability to colonize empty areas (Fig. S13D).

3.2. Independent model validation

3.2.1. Independent validation with native seagrass species

The independent validation simulating changes of the spatial distribution of *P. oceanica* was confirmed by simulating the real case reported in the Gulf of St Florent, in Corsica, France (42.724° N, 9.316° W) (Bonacorsi et al., 2013). They reported an increase in the seagrass coverage from 7.2km² to 11.7km² between 1974 and 2006 (Fig. S14 A). Our model adequately reproduced the reported seagrass pattern during 32 years with an increase in the extent of *P. oceanica* from 8.3 to 12.8 % (Fig. S14D).

The independent validation simulating the interaction between the native Mediterranean species *P. oceanica* and *C. nodosa* was validated by simulating a real case of Liguria, in Italy, in the northwest of the Mediterranean Sea, a region with high human pressures including mechanical disturbances (Fig. S15) (Burgos et al., 2017). In this study, a gradual substitution of *P. oceanica* by *C. nodosa* in shallow waters (3–16 m depth)

has been documented since 1960. This study reported an annual loss of 1.9 % for *P. oceanica*, in parallel to an annual increment of 2.3 % for *C. nodosa*. Our model adequately reproduced the observed patterns in seagrass replacement over time, with an annual habitat expansion of 4.3 % of *C. nodosa* and a habitat loss of 2.9 % for *P. oceanica* (Fig. S15D).

3.2.2. Independent validation with native and invasive seagrass species

In this validation, we simulated a real case of interactions between *C. nodosa* and *H. stipulacea* that occurred in the Mediterranean Sea, in the harbour of Marina Cap, Monastir, in Tunisia (35.778° N, 10.834° W) from 2011 to 2014 (Sghaier et al., 2014). In that study, a rapid replacement of Mediterranean native species by the invasive *H. stipulacea* was observed. In 2011, *C. nodosa* covered an area of ~80 %, and *H. stipulacea* ~ 20 % (Fig. S16A). However, by 2014, *H. stipulacea* already occupied 90 % of the harbour and nearly completely displaced *C. nodosa*, which by the end of the measurement period, was reduced to 10 % cover. Our model successfully reproduced the same pattern in 6–7 years (Fig. S16D).

3.3. Model simulations

Under the scenario of lower carbon emissions (RCP 2.6), the simulation outcomes reveal different species-specific seagrass responses according to the location of the modelled Mediterranean regions. In the warmest region in the east (Region E), our model that included only native seagrass species projected an overall loss of 33 \pm 2 % in the total habitat seagrass coverage by 2100 in comparison with present conditions (Fig. 4A). On the one hand, a drastic decline in P. oceanica habitat coverage occurred by 2050-2060, and its extent continued to drop until it was reduced by >70 % by the end of the century (Fig. 5A). On the other hand, C. nodosa slightly increased its habitat by 2 %, and was able to colonize some areas previously occupied by P. oceanica. When the simulations included H. stipulacea, a fast replacement of C. nodosa by the invasive H. stipulacea was observed, with C. nodosa experiencing a reduction of 84 \pm 3 % in its coverage in comparison with its initial coverage, while in parallel H. stipulacea increased its coverage by 71.5 \pm 4 % by the end of the century (Fig. 6A). Under the scenario of higher carbon emission (RCP 8.5), the collapse and potential extinction of P. oceanica was predicted to occur between 2050 and 2060, when temperatures reached values higher than 35 $^\circ C$ during anomalous warm summers. In this same scenario, the collapse of C. nodosa was expected to take place by the end of the century. Thus, almost all the native seagrass habitats (<1 %) (Fig. 5B) disappeared. However, when H. stipulacea was included in this simulation, total seagrass coverage was 48 \pm 3 %, out of which *C. nodosa* occupied <1 %, and the remaining habitat was occupied by the invasive H. stipulacea (Fig. 6B).

A different seagrass response was observed under the RCP scenario 2.6 in the central west and east regions (Regions CW and CE) (Figs. 4, S17). In both regions, the extent of P. oceanica and C. nodosa meadows remained relatively constant during the simulations because environmental conditions did not exceed the species' temperature and salinity tolerances. When invasive species were included in the simulations, H. stipulacea expanded its area at the expense of C. nodosa (Fig. 6C and D). In contrast, under the scenario of higher carbon emissions, RCP 8.5, our models reported two contrasting patterns of native seagrass. Specifically, in region Central East (CE), which was colder than region Central West (CW), a collapse of P. oceanica was predicted to take place by 2080-2090, whereas C. nodosa was predicted to experience an increase of 11 % in its coverage, partially explained by its capacity to colonize dead mattes of P. oceanica (Figs. 5D and 7). By comparison, in Region 3 (CW), the collapse of P. oceanica was predicted to take place by 2060-2070. In this region, C. nodosa was predicted to lose 87 % of its total coverage sometime between 2080 and 2100, when temperatures are expected to reach >35 °C. Again, when H. stipulacea was included in the simulations, the invasive species was able to significantly displace C. nodosa, dramatically increasing its area, and becoming the most



Fig. 4. Changes (\pm SD) in total seagrass cover (%) at the end of the 80-year simulation (year 2100) in each Mediterranean region (1, 2, 3 and 4) under each climate scenarios RCP 2.6 and RCP 8.5. Left panels (A, C, E and G) represent scenarios with only native seagrass species, *Posidonia oceanica* and *Cymodocea nodosa*, and right panels (B, D, F, H and I) represent scenarios with native and the invasive species *Halophila stipulacea*. LD: low density of shoots of *H. stipulacea*, HD: high density. AD: Anthropogenic disturbances.



Fig. 5. Temporal changes $(\pm$ SD) in the native Mediterranean seagrass cover (%) from 2020 to 2100 in each region (1, 2, 3 and 4) under each climate scenarios, the RCP 2.6 (Left panels A, C, E and G) and RCP 8.5 (Right panels B, D, F and H).

abundant seagrass species in both regions by the end of the century (Figs. 6 and 7).

In the westernmost modelled area of the Mediterranean basin (Region West [W]), the model was programmed to mimic the arrival of H. stipulacea by 2040-2060 under low and high species density levels. Under the RCP 2.6 climate scenario, the native seagrass species P. oceanica and C. nodosa did not experience any habitat regression even by 2100, whereas under the RCP 8.5 scenario, the decline of P. oceanica was predicted to occur by 2090-2100. However, when the invasive seagrass was included in the simulations, C. nodosa experienced a coverage loss due to its interaction with H. stipulacea. For instance, under the RCP 8.5 climate scenario and with the lowest arrival density of H. stipulacea fragments, C. nodosa decreases its coverage by 6 % in comparison with its initial coverage, whereas with the arrival of higher number of fragments of the invasive H. stipulacea, C. nodosa reduced its extension by 63 %. Interestingly, in the western region under the RCP 2.6 scenario, the simulation included the arrival of the low density of fragments of the invasive species, which reached the maximum habitat seagrass coverage by the end of 2100, with an increase of >7 % coverage in comparison with initial conditions in 2020 (Figs. 4 and 7; S17).

Overall, and common to all simulations, the implementation of anthropogenic disturbances in the models increased the patchiness of the seagrass meadows and significantly reduced its coverage area. *Posidonia oceanica*, the seagrass species that is characterized by the lowest growth rates among these three seagrass species, was the most affected seagrass. Part of the coverage area lost by *P. oceanica* was occupied by *C. nodosa* and *H. stipulacea* (Figs. 4 and 7). For instance, the most negative effect of anthropogenic disturbances was observed under the RCP 8.5 scenario with native species in region East (E), where the seagrass habitat shrunk by 21 %, in comparison with non-disturbed simulations (Fig. 4).

4. Discussion

4.1. Application of cellular automata models in seagrass ecosystems

With global change affecting marine ecosystems and ecological dynamics, it is fundamental to develop robust models to project species' spatial patterns, biological interactions and changes in ecosystem functioning along with provided services (Occhipinti-Ambrogi, 2007; Fletcher and Fortin, 2018). In this study, we present a novel rule-based simulation model that describes seagrass physiological thresholds, seagrass inter- and intra-species interactions and disturbance dynamics under different climate settings in the Mediterranean Sea. The CA model demonstrated a high capacity to reproduce seagrass dynamics that have already been observed in the Mediterranean Sea. Specifically, the validation of our models with real cases successfully replicated both (i) longterm and short-time processes of seagrass interactions between native with and without invasive seagrass species in the Mediterranean basin (Bonacorsi et al., 2013; Sghaier et al., 2014; Burgos-Juan et al., 2016; Burgos et al., 2017). In our model, we generated a system in equilibrium between annual seagrass habitat gains and losses through mortality events as was widely described in studies in the Mediterranean Sea (Marbà and Duarte, 1995; Oprandi et al., 2020), and is recommended for spatial ecosystem simulations (e.g., DeAngelis and Waterhouse, 1987; Uchmański and Grimm, 1996). The implementation of mortality/ destructive events in ecological and dynamic models, including CA approaches, improves the realism of the simulations (Fonseca et al., 2000; Giusti and Marsili-Libelli, 2006). Overall, the parameterisation of ecological and dynamic models is, in some cases, very complex due to the fact that specific and accurate data do not exist, or because available data were not generated for the purpose of developing such models (e.g., Fletcher and Fortin, 2018).



Fig. 6. Temporal changes (±SD) in total Mediterranean seagrass cover (%) from 2020 to 2100 in each region (1, 2, 3 and 4) under each climate scenarios, the RCP 2.6 and the RCP 8.5. LD: low density of shoots of *H. stipulacea*, HD: high density.

4.2. Responses to climate scenarios

Model projections showed that effects of climate change including increases in SST and salinity alongside anomalous warm summers, will affect Mediterranean seagrass species landscape, generating a shift in the seagrass composition and distribution under future climate scenarios (Daru and Rock, 2023).

Our simulations pointed out that forecasted rises in SST of ${\sim}3\text{--}4~^\circ\text{C}$

and salinity levels of \sim 0.7–1.1PSU by the end of this century (IPCC, 2021) will exceed the adaptive and acclimation capacity of the large and slow-growing endemic *P. oceanica*, causing its habitat loss in most of the Mediterranean basin. This will result in the emergence of novel habitats in most of the Mediterranean basin potentially available for colonization by more resilient species, such as *C. nodosa* and *H. stipulacea* (Jordà et al., 2012; Chefaoui et al., 2018; Beca-Carretero et al., 2020a; Llabrés et al., 2023). More negative effects will be observed in warmer regions

| | Posidonia oceanica Cymodocea nodosa Halophila stipulacea Dead matte of <i>P. oceanica</i> Empty area Empty area | | | | |
|------------|--|-------------------------|-------------------------|---------------------|-----|
| RCP 2.6 () | Region 1 (East) | Region 2 (Central East) | Region 3 (Central West) | Region 4 (West) | |
| RCP 2.6-AD | | | | | |
| RCP 8.5 | | | | | |
| RCP 8.5-AD | | | | | |
| RCP 2.6 (I | Region 1 (East) | Region 2 (Central East) | Region 3 (Central West) | Region 4 (West)/ LD | Reç |
| RCP 2.6-AD | | | | | |
| RCP 8.5 | | | | | |
| RCP 8.5-AD | | | | | Ę |

Fig. 7. Final maps the seagrass cover at the end of the 80-year simulations (2100) in each region (1, 2, 3 and 4) under the RCP scenario 2.6 and 8.5 without anthropogenic disturbances (AD), and with AD. Panel A incudes the native species *Posidona oceanica* and *Cymodocea nodosa*; and panel B the native species and *Halophila stipulacea*. LD: low density of shoots of *H. stipulacea*, HD: high density.

(E, CE and CW), where temperatures will rise the most, in comparison with the western and coldest modelled region, particularly accentuated under the scenario of higher carbon emissions (RCP 8.5). Our model did not forecast a habitat loss of P. oceanica in the western region of the Mediterranean Sea, suggesting that this area can represent a refuge for P. oceanica during this century, as was recently reported applying spatial distribution models (Chefaoui et al., 2018). Furthermore, deeper and colder areas can also serve as a refuge for this species as a strategy to cope with predicted warming (Jordà et al., 2020). Our simulations showed that collapses of P. oceanica would be accelerated by the effects of anomalous warm summers, highlighting the fact that in the majority of cases, the populations cannot recover from these events. Indeed, P. oceanica meadow collapses have been observed in natural habitats suggesting that some populations are beginning to be exposed to lethal temperatures (Marbà and Duarte, 2010; Thomson et al., 2015; Strydom et al., 2020). Notably, studies performed under controlled conditions have highlighted the increased fragility of meadows growing in highly eutrophic areas when exposed to elevated water temperatures. These findings emphasize the importance of environmental quality in ensuring greater resilience against climate change (Pazzaglia et al., 2020, 2022).

In contrast, the native and fast-growing species C. nodosa will be less affected by climate change than the endemic species *P. oceanica* during this century. Our simulations predicted that this species will be able to survive the future climate conditions in almost all regions of the basin, except in the warmest areas on the eastern coast where SST over 34 $^\circ\text{C}$ will be reached, particularly under the RCP 8.5 scenario. Our results partially differ from those observed by Chefaoui et al. (2018) who predicted a collapse of this species in central Mediterranean areas. The potential ability of this species to acclimatise to the climatic conditions predicted for the future might be related to the tropical origin of the genus, and the tropical affinity of the species, currently distributed in lower latitudes and inhabiting warmer regions such as the Canary Islands (Chefaoui et al., 2016). In this line, recent experimental evidence suggests that C. nodosa can acclimate to predicted warming conditions in the Mediterranean Sea by the end of this century (\sim 34 °C) (Beca-Carretero et al., 2018; Marín-Guirao et al., 2018; Ontoria et al., 2019).

Our CA model forecasted that H. stipulacea would profit from increases in temperature and salinity experienced during this century in the Mediterranean; our model predicted that these changes will favor its expansion in the basin, as was observed in previous modelling studies (Gamliel et al., 2020; Beca-Carretero et al., 2020a; Wesselman et al., 2021a). Indeed, our projections did not report any habitat loss of this species during this century, not even at maximum expected SST of >35°C in the eastern coast under the scenario of highest carbon emissions. These observations are supported by the fact that native H. stipulacea populations from the Persian Gulf and the Indian Ocean, are regularly exposed to temperatures of 30-31 °C, often reaching a maximum of 34 °C in summer (Tyberghein et al., 2012; Naser, 2014; Campbell et al., 2015). Recent studies (Nguyen et al., 2020b; Beca-Carretero et al., 2022) with native plants from the Gulf of Aqaba and invasive plants from the Mediterranean Sea reported negative photo-physiological and morphological responses of native plants to experimental temperatures of 32 °C. Invasive plants, instead, were un-affected/or even favoured by warming. A higher activation and plasticity of genes involved in thermal stress responses explained at least some of these differences (Nguyen et al., 2020b). In addition, recent studies reported that forecasted increases in salinity will not negatively affect the healthy state of H. stipulacea (Oscar et al., 2018; Beca-Carretero et al., 2020a), as was expected, being H. stipulacea an euryhaline species (Den Hartog, 1970). However, recent investigations suggest that P. oceanica will be more vulnerable to expected salinity levels above ~39PSU (Ruíz et al., 2009). Overall, taken together, the reported modelling, experimental and in situ evidence, demonstrated the potential future habitat expansion of H. stipulacea under climate change scenarios in the Mediterranean basin.

4.3. Seagrass interactions

Simulations of biological interactions between *P. oceanica, C. nodosa* and *H. stipulacea* revealed that neither of the two latter species were able to displace the climax species *P. oceanica*, suggesting that under current conditions for growth, *P. oceanica* could maintain, and even moderately increase its coverage over time.

In most of the modelled regions (E, CE, and CW), simulations demonstrated a drastic replacement of the native species *C. nodosa* by the non-native species *H. stipulacea* under optimal conditions for the growth of both species. This result was further accentuated under unsuitable conditions for growth for the Mediterranean native species. This fast replacement was previously documented in the Marina Cap Monastir (Tunisia) where the invasive *H. stipulacea* increased its cover by a factor > 10 from 2011 to 2014 displacing the native *C. nodosa* population (Sghaier et al., 2014). In this line, a recent study by Chiquillo et al. (2023) showed that *H. stipulacea* grows faster in the presence of *C. nodosa*, which, on the contrary, reduced its density significantly; a similar trend was observed when *H. stipulacea* was grown in interaction with Caribbean seagrass species under current climate conditions (Chiquillo et al., 2023). In this study, *H. stipulacea* significantly reduced its colonization rates when expanding alone in sandy sediments.

On the other hand, in the western region where the model was parameterized with the arrival of a reduced number of fragments of *H. stipulacea*, our simulations showed reduced negative impacts on the meadows of *C. nodosa*, highlighting the potential stable state with the coexistence of both species through the creation of mixed meadows (Winters et al., 2020). These outcomes suggest that the spread of *H. stipulacea* and its interaction with *C. nodosa* was dependent, to a greater or lesser degree, on the abundance of the invasive species, in line with patterns reported by Chiquillo et al. (2023).

When mechanical disturbances through anchoring were included in the model, P. oceanica tended to loose coverage that was not recovered over time because of its slow growth rates. In these simulations, dead mattes of P. oceanica were partially colonized by both C. nodosa and H. stipulacea, favouring the creation of two seagrass seascape configurations depending on the intensity and timescale of the phenomena. In this support, under lower anthropogenic pressure, the formation of mixed seagrass meadows where P. oceanica, C. nodosa and H. stipulacea coexist was observed in different regions of the Mediterranean Sea (Gambi et al., 2009; Winters et al., 2020). Whereas, under simulated more intense negative anthropogenic effects, P. oceanica is generally replaced by C. nodosa and/or H. stipulacea as was documented in disturbed regions of the Mediterranean Sea (Cancemi et al., 2002; Montefalcone et al., 2007; Thibaut et al., 2022). Interestingly, C. nodosa in most regions of the Mediterranean Sea shows a colonizer or pioneer behaviour, although, in regions where P. oceanica has been replaced by this species, C. nodosa can shift its ecological strategy, behaving as climax species, as it does in the Canary Islands (Reyes et al., 1995; Alberto et al., 2006). Since C. nodosa and H. stipulacea are dramatically different in size compared to the iconic P. oceanica, they create meadows that differ significantly in structural, functional and dynamic characteristics. Therefore, seagrass species substitution, from large to small-size and fast growth species, can lead to a significant loss in meadow complexity, functional traits, trophic interactions, and the number and value of ecosystem services they provide (Jordà et al., 2012; Winters et al., 2020), as was recently reported in the Caribbean Sea, and in the Banc d'Arguin in western Africa (Viana et al., 2019; Chefaoui et al., 2021). Dead mattes of P. oceanica colonized by H. stipulacea may increase sediment stabilization and may even favor the carbon absorption capacity of these renewed seagrass ecosystems (Wesselmann et al., 2021a, 2021b). The spread and colonization of *H. stipulacea* can be enhanced by the degradation of marine seagrass ecosystems because of its proven resilience and capacity to survive in polluted or degraded habitats but also because of its great recovery capability after stress situations (Van Tussenbroek et al., 2017; Winters et al., 2020; Beca-Carretero et al.,

2022).

4.4. Limitations and uncertainties

Despite the successful replication of seagrass dynamics and interactions in the Mediterranean Sea, our CA model has certain limitations and uncertainties that should be acknowledged. To parametrise the CA model, we developed, among others, two main assumptions. First, temperature and salinity thresholds were kept constant in the four modelled regions for each species considering that no correlation between thermal and salinity responses to latitudinal or in situ environmental conditions were observed for the Mediterranean (Bennett et al., 2022). However, other experimental evidences suggest latitudinalspecific adaptions and varying thermal responses among populations, including the native species P. oceanica and C. nodosa and the invasive species H. stipulacea (e.g., Marín-Guirao et al., 2018; Nguyen et al., 2020b). Therefore, when interpreting seagrass dynamics under the implemented climate scenarios, it should be kept in mind that their responses are highly dependent on the defined environmental thresholds. Nevertheless, to smooth this dependence from the threshold, we endowed the species with a progressive loss of distribution at a rate of 10 % per increase of 0.1 °C in temperature or 0.065PSU in salinity once their survival threshold was exceeded. Second, we assumed fixed growth rates for each species during optimal conditions for growth, because, data extracted from the literature review showed no correlation between growth performance and latitudinal or local environmental conditions. Nevertheless, growth rates of seagrass are known to change according to climate settings, latitudes and local environmental conditions (Lee et al., 2007; Beca-Carretero et al., 2019; Deguette et al., 2022). Lastly, a gap of knowledge was identified in the parametrization of the CA models related to the colonization capacity of C. nodosa and H. stipulacea on dead mattes of P. oceanica because no quantitative data could be obtained from the literature. For these reasons, we believe future studies of seagrass reactions to environmental factors might help to improve the parameterization, accuracy, and flexibility of the simulations, enhancing future model performances.

Moreover, it is uncertain how future climatic conditions will influence the ability of species to acclimate to the predicted scenarios. Recent studies have shown that experimental heatwaves can have positive effects on primed P. oceanica seedlings and plants, increasing their resilience and potentially preparing them to cope with future scenarios of warming (Nguyen et al., 2020c; Pazzaglia et al., 2022; Stipcich et al., 2022). Also, P. oceanica's flowering events were favoured by rising temperatures (Ruiz et al., 2018; Marín-Guirao et al., 2019). Collectively, these studies may suggest that P. oceanica is less vulnerable to future environmental conditions than we projected. Furthermore, caution is necessary when extrapolating our results based on species interactions, as there is currently limited evidence explaining the underlying mechanisms of interaction and the colonization success of the target species, particularly H. stipulacea in relation to other seagrass species. Lastly, these models were conducted to simulate shallow systems, therefore the results obtained here should not be extrapolated to deeper ranges where other model parameterisations could be necessary and would have to be tested separately.

4.5. Implications for management

The results presented here have critical implications for the management of Mediterranean seagrass ecosystems in the face of climate change and invasive species. The projected impacts of rising sea temperatures and salinity levels in the Mediterranean Sea, pose a significant threat to the endemic and slow-growing *P. oceanica*, and the native *C. nodosa*, potentially leading to their extinction within the Mediterranean. However, there is also some hope in the potential of discovering populations or genotypes, that exhibit greater resistance to high temperatures and salinities. Such "super genotypes" could be used in basin-

wide restoration or translocation efforts. In addition to the potential loss of the Mediterranean's native species, all predictions for the region, point to the spreading of the invasive H. stipulacaea in the Mediterranean Sea, emphasizing the need for adaptive management strategies. Proactive measures, including the creation of a containment plan and an early warning system for the presence of invasive species, are essential. Additionally, our study highlights the vulnerability of P. oceanica to mechanical disturbances such as anchoring, that has potential long-term consequences for meadow coverage. Indeed, our simulations clearly demonstrate that mechanical disturbances will lead to the faster spreading of H. stipulacea. Taken together, these results emphasize that management efforts should focus on minimizing anthropogenic pressures to ensure the persistence of this foundational species, giving it more time to adapt to climate change and reducing the potential spread of invasive species. Addressing these threats and integrating spatial planning and risk assessment into the development of decision support systems will significantly enhance management strategies for conserving Mediterranean seagrass ecosystems in a changing climate scenario.

5. Conclusions

This study represents one of the first applications of a CA to investigate the effects of climate change and introduction of a non-native seagrass species on seagrass community dynamics, offering a stepwise approach of model parameterization which can be transferred to other areas.

Our simulation model successfully reproduces observed seagrass dynamics in the Mediterranean Sea and provides valuable insights into the potential impacts of global change on seagrass ecosystems. The model projections indicate that rising SST and salinity levels, alongside anomalous warm summers, will have varying effects on different seagrass species in the Mediterranean basin. The results indicate that both native species, particularly the slow-growing P. oceanica, will be highly vulnerable to climate change, experiencing significant declines in their abundance. However, the findings also reveal that the western and colder areas of the Mediterranean Sea could potentially serve as refuge areas for this species. The models demonstrated that H. stipulacea thrived at the expense of C. nodosa, resulting in limitations to the distribution of the latter and ultimately displacing the native species. Additionally, simulations showed that areas where P. oceanica meadows vanished will be partially occupied by C. nodosa and H. stipulacea. These outcomes suggest that the Mediterranean seagrass community will experience a transition from long-lived and large species to small and fast-growing species as climate change progresses. This study will contribute to current global efforts of seagrass monitoring, management, and conservation, generating essential information that will help to predict potential areas of vulnerability of native seagrass species and help to monitor the spread of H. stipulacea. However, the model also has limitations and uncertainties, including complex parameterization, assumptions on temperature and salinity thresholds, fixed growth rates, and insufficient data on colonization capacity. Addressing these limitations in future studies can enhance accuracy, flexibility, and understanding of seagrass ecosystem responses to climate change in the Mediterranean Sea.

CRediT authorship contribution statement

P. BC, F·S and H.R. designed the model and the computational framework and analysed the data. F·S carried out the implementation. P BC, R.Z and K·C performed the review analyses and collected data. P. BC wrote the manuscript with input from all authors. P. BC, G.W, G.P., M.T and H.R conceived the study and were in charge of overall direction and planning.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi. org/10.1016/j.scitotenv.2023.168675.

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