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Movement Ecology of a Coastal Foundation Seagrass Species: Insights From Genetic Data and Oceanographic Modelling

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ABSTRACT

Aim: Seed dispersal plays a key role in shaping the distribution and genetic complexity of seagrass populations and affects their resilience capacity under disturbance. The endemic seagrass *Posidonia oceanica* is a key component of Mediterranean coastal ecosystems, but knowledge about movement ecology in this species is limited, especially regarding seed movement pathways and dispersal potential.

Location: Western coast of Sicily (central Mediterranean).

Methods: Beach-cast fruits of the Mediterranean seagrass *P. oceanica* were collected from nine localities along the Western coast of Sicily, along with adult shoots from eight putative donor meadows. We determined pair-wise genetic differentiation between established meadows and seed cohorts. Genetic assignment tests were used to infer the most likely meadow of origin of individual seeds and were complemented with forward and backward Lagrangian simulations of dispersal.

Results: A significant genetic differentiation was found between seed pools and the most-likely meadow of origin. The genetic assignment confirmed that seeds from the same cohort originated from multiple meadows and emphasised the presence of long-distance-dispersal (LDD) events (up to hundreds of km). Genetic connectivity appeared to be greater than that predicted by oceanographic simulations, which may reflect the longer temporal scales on which gene flow is shaped, in contrast to contemporary dispersal patterns. Lagrangian simulations highlighted that fruits were physically capable of dispersing beyond the study area and that the north Tunisian coast could be a key source of propagules for the populations studied.

Main Conclusions: Our study represents a significant step forward in the understanding of *P. oceanica* movement ecology and could guide meadows' conservation and restoration actions. Our findings are significant in a broader context outside of the research area and could be the basis of similar studies in other regions, especially considering the increasing number of fruiting events recorded across the Mediterranean likely associated with ocean warming.

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1 | Introduction

The movement ecology of individual organisms has a profound influence on population, community, and ecosystem dynamics over contemporary and evolutionary timescales. Also, it is associated with major current problems such as habitat fragmentation, climate change, and biological invasions (Nathan et al. 2008). For plants, unlike most animals, movement is limited to particular life-history stages, that is the dispersal of pollen or seeds, although clonal plants can spread through vegetative growth and fragmentation over small to medium distances (Levin et al. 2003). Seeds dispersal allows plants to colonise new habitats, reach sites where available resources favour regeneration, and escape pests and competition with siblings and mother (Wright et al. 2008). It also determines the spatial distribution and genetic structure of populations at local and landscape scales (Wright et al. 2008; Jahnke et al. 2016).

Despite their apparent uniformity, marine habitats are characterised by clear discontinuities, in terms of environmental conditions, water circulation patterns, geological history, and seascape features that profoundly affect species' connectivity. Indeed, these may act as dispersal barriers to gene flow, leading to genetic structuring and, eventually, isolation of populations (Evans et al. 2021). Movement patterns for most marine species are poorly characterised with respect to terrestrial systems, largely for practical reasons, such as the difficulty of tracking small propagules in large volumes of water (McMahon et al. 2014; Walther, Munguia, and Fuiman 2015). However, recent advances in ecological tools (e.g., telemetry techniques and oceanographic modelling) have allowed unprecedented insights into marine movement dynamics (Walther, Munguia, and Fuiman 2015).

Seagrasses are marine foundation species inhabiting coastal waters of most of the word's coasts, substantially contributing to key ecosystem services (Cullen-Unsworth et al. 2014; Nordlund et al. 2017). They are polyphyletic assemblages of basal monocots (order *Alismatales*) that reinvaded the marine environment in the early Cretaceous (Larkum, Orth, and Duarte 2006), and adapted to cope with structural and physiological challenges related to fully marine conditions (Olsen et al. 2016; Ma et al. 2024). Seagrasses exhibit two major reproductive modes, that is, vegetative and sexual reproduction. Thus, the formation of established meadows typically requires these two strategies to act in concert (Larkum, Orth, and Duarte 2006). Floating fruits represent the primary mode of seagrass dispersal into new locations, while, once seeds have settled, they typically expand by rhizomatous growth (Kendrick et al. 2012; McMahon et al. 2014). The production and dispersal of sexual propagules and the subsequent establishment of seedlings are thus critical life-history stages. Seeds' dispersal plays a key role in shaping the distribution and structure of seagrass populations (Kendrick et al. 2012; Furman et al. 2015; Ruiz-Montoya, Lowe, and Kendrick 2015; Sinclair et al. 2018). It also contributes to the genetic complexity of seagrass habitats, sustaining high overall genotypic diversity and weak genetic structuring at large spatial scales (Kendrick et al. 2017).

Due to increasing pressure from local human activities and changing climatic conditions, seagrasses are declining globally at a rapid rate (Strydom et al. 2020; Blanco-Murillo et al. 2022). Recovery of seagrasses from disturbance relies on the growth of surviving plants, as well as on the dispersal of seeds, seedlings' establishment and survival (McMahon et al. 2014). Thus, understanding the movement ecology of seagrasses would also provide a way to assess the resilience capacity of populations, including the (re)-colonisation of altered or fragmented habitats, and it could support effective management actions for conservation and restoration strategies (Kendrick et al. 2012; Evans et al. 2021; Pazzaglia et al. 2021; Provera et al. 2024). The protection of areas that are sources of sexual propagules or that receive high seed inputs, or both, should become a priority target for conservation programs (Balestri, Vallerini, and Lardicci 2017). Unfortunately, knowledge of the distribution of seagrass seeds and seedlings is scarce, and mostly based on casual observations, possibly because of the inherent difficulty in predicting where seeds will settle (Balestri, Vallerini, and Lardicci 2017).

Posidonia oceanica is one of the oldest and largest seagrass species, endemic to the Mediterranean Sea, where it forms dense meadows providing high-value ecosystem services including biodiversity support and climate change mitigation (Campagne et al. 2015; Pergent-Martini et al. 2021). *Posidonia oceanica* habitat has also been identified as a priority habitat under the European Commission Habitats Directive (92/43/EEC), and in several European countries, the species and/or the habitat are under specific legal protection. Flowering and recruitment (i.e., establishment of seedlings at a site) in *P. oceanica* have been generally considered episodic and unpredictable (Buia and Mazzella 1991; Diaz-Almela et al. 2006), and constrained by the nature of the substrate (Alagna et al. 2013, 2015; Badalamenti, Alagna, and Fici 2015). Flowers and fruits have been observed in the whole Mediterranean Sea, although with a large variability in frequency and intensity among different geographical areas as well as within the same meadows (Balestri 2004). Factors controlling flowering (and fruiting) occurrence in *P. oceanica* are not completely uncovered, but seem to be related to endogenous plant features, as shoot age (Balestri and Vallerini 2003; Rinaldi et al. 2023), ecological and genetic factors such as heterozygosity and relatedness (Jahnke et al. 2015). Currently, the reproductive effort of the species seems to be greater than in the past, possibly related to the strong increase in SST (Sea Surface Temperature) and in the frequency of heatwaves within the Mediterranean basin (Diaz-Almela, Marba, and Duarte 2007; Ruiz et al. 2018; Procaccini, Dattolo, and Ruocco 2023; Stipcich, La Manna, and Ceccherelli 2024). This has prompted the hypothesis that the species is reacting to climate change through an increased resource allocation to reproduction (Marín-Guirao et al. 2019).

Posidonia oceanica produces large positively buoyant fruits that may be transported hundreds of kilometres far from mother meadows under the influence of wind and surface currents before releasing seeds (Jahnke et al. 2017; Mari et al. 2020; Micheli et al. 2010; Serra et al. 2010). The seed is non-dormant, and germination occurs after its maturation inside the fruit; then, it can remain attached to the seedling for up to 2 years after germination, providing fundamental nutritional resources (Balestri et al. 2009). Investigations on the spatial patterns of seedlings' distribution at the local scale suggested a possible relationship among microhabitat type, seedling establishment, and survival

rates (Alagna et al. 2013). Despite the importance of seed dispersal in determining seagrass population structure, connectivity, and resilience, there are major gaps in our understanding of these processes in *P. oceanica*. Existing studies have mostly addressed realised connectivity among established meadows, based on genetic differentiation and assignment tests (Arnaud-Haond et al. 2007; Serra et al. 2010; Jahnke et al. 2017; Tutar et al. 2022), or used biophysical modelling approaches to simulate *P. oceanica* fruits dispersal patterns (i.e., potential connectivity) (Jahnke et al. 2017; Mari et al. 2020; Serra et al. 2010), and to identify connectivity hotspots (Mari et al. 2021). Works addressing primary source areas of sexual propagules and movement of dispersing seeds based on seed genetic assignment are almost absent. A first attempt to assess the probability of *P. oceanica* fruits dispersal, based on the comparison of the genetic makeup of beach-cast seeds and an adjacent meadow, was conducted in the Ligurian Sea (Italy) (Micheli et al. 2010). However, this study was limited by a small sample size and the use of low-resolution molecular markers (i.e., a few RAPD loci).

Here, we collected beach-cast *P. oceanica* fruits from nine localities along Western Sicily covering ~220 km of coast, along with adult shoots from eight adjacent putative donor meadows. In the study area, fruiting of *P. oceanica* populations has been recorded almost annually since 1997 in mid to late spring, primarily through observations of beach-cast fruits (*author personal observations*). Direct underwater observations are more limited due to the absence of long-term meadows' monitoring programs. All adult individuals and seeds were genotyped using 16 highly polymorphic microsatellite markers. We determined levels of genetic and genotypic richness of established meadows and seed cohorts, as well as their genetic differentiation. Our main scope was to identify key source locations of sexual propagules as well as areas that receive higher seed inputs, thus characterising the main patterns of connectivity in the study area. Genetic assignment tests to infer the meadow/s of origin of seeds and their movement pathways were complemented with forward and backward Lagrangian numerical simulations to assess all possible dynamical connections among seed sources based on surface sea currents. The coupling of genetic assignment of seeds and oceanographic connectivity modelling could provide information of critical importance for addressing the dispersal ability of this coastal foundation species, thus helping to define priority sites for conservation and/or for assisting management actions, including ecosystem restoration (Jahnke et al. 2020) to ensure persistence of healthy *P. oceanica* meadows.

2 | Methods

2.1 | Sample Collection

Posidonia oceanica fruits were collected from nine beaches (i.e., beach-cast fruits): San Nicola l'Arena (Trabia, PA)—NI_s, Isola delle Femmine (PA)—IF_s, Macari (San Vito Lo Capo, TP)—MAC_s, Cornino (Custonaci, TP)—CO_s, Valderice (TP)—VA_s, Marsala (TP)—MA_s, Torre Sibiliana (TP)—SI_s, Tre Fontane (Campobello di Mazara, TP)—FO_s and San Marco (Sciacca, AG)—SM_s along the Western coast of Sicily (Figure 1, Table 1) during late spring (May–June) 2021, coinciding with the peak of fruit release of this species in the study area (Alagna et al. 2013, 2015; Provera et al. 2024; Zenone, Alagna, et al. 2020; Zenone, Filippov, et al. 2020; Zenone et al. 2022). Mature, partially open fruits containing viable seeds were selected, then seeds were immediately extracted and transported to the facilities of IAS-CNR in Castellammare Del Golfo (Sicily). Seeds were left to germinate and grow for 6 months in aquaria (30 L) with continuous flow-through of natural seawater at a temperature of 20°C, salinity of 37 and under a 12:12 Light:Dark photoperiod (80 μmol q m^{-2} s^{-1}). At the end of this period, *ca*. 20 seedlings were randomly chosen for DNA extraction for each collection site (herein referred as 'seed cohorts'). The central and more mature leaves, *ca*. 10 cm long, were gently cleaned from epiphytes and dried with silica gel prior to DNA extraction. Along with *P. oceanica* fruits, we collected adult shoots from eight established shallow (~5 m depth) meadows (San Nicola l'Arena—NI, Isola delle Femmine—IF, Macari—MAC, Cornino—CO, Marsala—MA, Torre Sibiliana—SI, Tre Fontane—FO and San

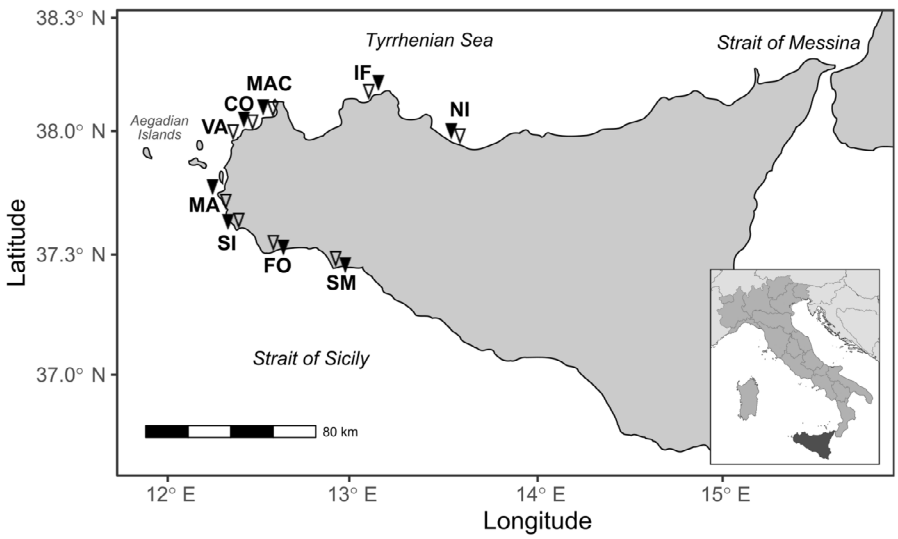

FIGURE 1 | Sampling sites for eight established meadows (black triangles) and nine seed cohorts (open triangles) of *Posidonia oceanica* along the Western coast of Sicily. CO, Cornino; FO, Tre Fontane; IF, Isola delle Femmine; MA, Marsala; MAC, Macari; NI, San Nicola l'Arena; SI, Torre Sibiliana; SM, San Marco; VA, Valderice.

TABLE 1 | Descriptive statistics for 8 *Posidonia oceanica* meadows and 9 seed cohorts collected in Western Sicily. For each sampling location, the following informations are shown: Acronym, geographical coordinates (latitude and longitude), depth, number of samples (N), number of multi-locus genotypes (MLGs), genotypic diversity (*R*), mean number of alleles per locus (N_A), number of private alleles (N_{PA}), allelic richness (A_R), observed (H_O) and unbiased expected (uH_E) heterozygosity, inbreeding coefficient (F_{IS}) and percentage of polymorphic loci (%*P*).

Sampling location		Latitude	Longitude	Depth	N	MLGs	*R*	N_A (SD)	N_{PA}	A_R (SD)	H_O (SD)	uH_E (SD)	F_{IS} (*p*)	%*P*
Established meadows														
San Nicola l'Arena (Trabia, PA)	NI	38°0′56.48″ N	13°37′ 8.17″ E	8 m	16	16	1.00	3.63 (2.2)	3	2.11 (0.6)	0.55 (0.2)	0.52 (0.2)	−0.068 (0.9)	100
Isola delle Femmine (PA)	IF	38°12′18.12″ N	13°14′24.79″ E	3 m	16	15	0.93	3.13 (1.7)	3	1.98 (0.5)	0.51 (0.3)	0.49 (0.2)	−0.063 (0.8)	94
Macari (San Vito lo Capo, TP)	MAC	38° 7′42.15″ N	12°43′35.28″ E	5-6 m	22	2	0.05	1.50 (0.5)	0	1.50 (0.5)	0.47 (0.5)	0.32 (0.3)	−0.857 (1.0)	50
Cornino (Custonaci, TP)	CO	38° 5′24.94″ N	12°39′16.20″ E	6 m	16	16	1.00	3.44 (2.0)	3	2.15 (0.6)	0.63 (0.3)	0.54 (0.2)	−0.169 (1.0)	94
Marsala (TP)	MA	37°48′48″ N	12°25′53″ E	4-5 m	19	15	0.78	3.13 (1.8)	1	1.89 (0.5)	0.50 (0.3)	0.43 (0.2)	−0.172 (1.0)	100
Torre Sibiliana (Marsala, TP)	SI	37°43′21.35″ N	12°28′6.20″ E	5 m	16	13	0.80	3.19 (1.7)	1	2.02 (0.6)	0.54 (0.3)	0.49 (0.2)	−0.150 (1.0)	100
Tre Fontane (Campobello di Mazara, TP)	FO	37°33′41.96″ N	12°42′24.80″ E	3 m	22	17	0.76	3.44 (2.1)	4	2.06 (0.6)	0.52 (0.3)	0.51 (0.2)	−0.067 (0.9)	100
San Marco (Sciacca, AG)	SM	37°29′54.88″ N	13° 0′53.45″ E	4 m	16	12	0.73	3.19 (1.6)	1	2.06 (0.5)	0.56 (0.3)	0.51 (0.2)	−0.117 (0.9)	94
Seed cohorts (beach-cast fruits)														
San Nicola l'Arena (Trabia, PA)	NI_s	38° 0′32.64″ N	13°37′40.08″ E	—	21	21	1.00	3.81 (2.1)	2	3.73 (2.1)	0.52 (0.2)	0.50 (0.2)	−0.048 (0.8)	100
Isola delle Femmine (PA)	IF_s	38°10′58.80″ N	13°13′59.54″ E	—	21	21	1.00	3.50 (2.3)	3	3.42 (2.2)	0.48 (0.3)	0.49 (0.2)	0.016 (0.4)	88
Macari (San Vito lo Capo, TP)	MAC_s	38° 7′32.14″ N	12°43′37.68″ E	—	18	18	1.00	3.75 (2.4)	3	3.74 (2.4)	0.59 (0.3)	0.52 (0.2)	−0.147 (1.0)	100
Cornino (Custonaci, TP)	CO_s	38° 5′31.63″ N	12°39′43.16″ E	—	21	21	1.00	3.31 (1.9)	0	3.26 (1.9)	0.49 (0.2)	0.51 (0.2)	0.004 (0.5)	94
Valderice (TP)	VA_s	38° 4′15.72″ N	12°37′48.71″ E	—	20	20	1.00	3.38 (2.0)	1	3.33 (1.9)	0.53 (0.2)	0.50 (0.2)	−0.069 (0.9)	100

(Continues)

TABLE 1 | (Continued)

Sampling location		Latitude	Longitude	Depth	N	MLGs	R	N_A (SD)	N_{PA}	A_R (SD)	H_O (SD)	uH_E (SD)	F_{IS} (p)	%P
Marsala (TP)	MA_s	37°44′34.41″ N	12°28′18.57″ E	—	19	19	1.00	3.31 (2.1)	2	3.28 (2.0)	0.51 (0.3)	0.48 (0.2)	−0.073 (0.9)	100
Torre Sibiliana (Marsala, TP)	SI_s	37°43′25.34″ N	12°28′19.22″ E	—	21	21	1.00	4.13 (2.4)	4	3.39 (2.4)	0.48 (0.2)	0.52 (0.2)	0.067 (0.1)	100
Tre Fontane (Campobello di Mazara, TP)	FO_s	37°34′18.84″ N	12°43′58.91″ E	—	20	20	1.00	3.69 (2.3)	2	3.65 (2.2)	0.56 (0.2)	0.54 (0.2)	−0.018 (0.6)	94
San Marco (Sciacca, AG)	SM_s	37°30′26.24″ N	13° 0′53.00″ E	—	20	20	1.00	3.81 (2.2)	2	3.77 (2.1)	0.55 (0.3)	0.56 (0.2)	0.025 (0.3)	100

Marco—SM) located in nearby areas (Figure 1, Table 1). These meadows were considered potential sources of the collected seeds. At each site, *ca*. 30 individual plants were collected via snorkelling at least five meters apart to minimise the risk of sampling the same genotype. Immediately after collection, leaf samples (*ca*. 10 cm long) were gently cleaned from epiphytes and dried with silica gel. As for seedlings, *ca*. 20 individuals were used for DNA extraction, for a total of 324 analysed samples (including adults and seeds).

2.2 | DNA Extraction and Microsatellite Analysis

About 60 mg of leaf tissue from seedlings and adult individuals was powdered in TissueLyser (Qiagen), and genomic DNA was isolated with the Macherey-Nagel NucleoSpin 96 Plant II kit. After isolation, DNA quality was checked by 1% agarose gel electrophoresis. All samples were genotyped at 16 microsatellite loci (Procaccini and Waycott 1998; Alberto et al. 2003; Arranz et al. 2013), assembled in two separate multiplexes and amplified by PCR using a QIAGEN Multiplex PCR Kit. Selected microsatellite regions and multiplex assembly are reported in Table S1. Genotyping was performed using an ABI Prism 3730 automated DNA sequencer (Applied Biosystems) with the PCR conditions detailed in Tutar et al. (2022). Peak identification and scoring were performed using the Peak Scanner Software 2 (Applied Biosystems).

2.3 | Genotypic and Genetic Diversity, Outlier Detection

The presence of identical multilocus genotypes (MLGs) was assessed by the software Gimlet (Valière 2002), and all the following analyses were performed only on different MLGs. For each population or seed cohort, genotypic diversity was assessed as the R ratio: $R = (G-1)/(N-1)$, where G is the number of genotypes and N is the number of individuals (Dorken and Eckert 2001). We assessed the presence of null alleles using MicroDrop (Wang and Rosenberg 2012). Linkage disequilibrium (LD) and deviations from Hardy–Weinberg expectations (HWE) at each locus and across loci were tested with Genepop 4.7.5 (Rousset 2008), using 10,000 dememorisations, 1000 batches, and 10,000 iterations per batch. The statistical significances of LD pairwise comparisons were determined by applying the Bonferroni correction for multiple comparisons [α (0.05) divided by the number of tests]. Finally, we calculated the probability of identity (PI) in GenAlEx 6.5 (Peakall and Smouse 2012) to get an indication of the minimum number of loci needed for genetic tagging for each population or seed cohort. The mean number of alleles per locus (N_A), private alleles (N_{PA}), observed heterozygosity (H_O), unbiased expected heterozygosity (uH_E), and percentage of polymorphic loci (%P) were estimated with GenAlEx. Population-specific F_{IS} (with 1023 permutations) was calculated with Arlequin 3.5.2 (Excoffier and Lischer 2010). Mean allelic richness (A_R) was calculated using the R package DiveRsity 1.9.90 (Keenan et al. 2013) using the rarefaction method to correct for variation in sample size. To identify putative outlier loci within the microsatellite set, a neutrality test was performed using two F_{ST}-based approaches, implemented in Lositan (Antao et al. 2008) and BayeScan (Foll and Gaggiotti 2008). Lositan was run with

the following settings: 50,000 simulations under neutral mean F_{ST}, and forced mean F_{ST} options, a confidence interval of 0.95 and an infinite allele model. BayeScan was used with default settings, resulting in the same probability threshold as used for Lositan. We considered as real outliers only those shared between the two methods.

2.4 | Genetic Differentiation and Population Structure

Different methods were used to determine the extent of gene flow and movement among seed cohorts in relation to the genetic structure of the established meadows. Specifically, we calculated Weir and Cockerham's F_{ST} in Arlequin, and G'_{ST} (Hedrick 2005) and D_{est} (Jost's D, Jost 2008) in GenAlEx, for pairwise comparisons, including between meadows and seed cohorts. The significance of D_{est}/G'_{ST} and F_{ST} comparisons was based on 9999 and 1000 permutations, respectively. An Analysis of Molecular Variance (AMOVA) was performed in GenAlEx with 9999 permutations to assess the portioning of variation within and between groups (established meadows and seed cohorts). A bayesian clustering analysis was then performed with Structure 2.3.4 (Pritchard, Stephens, and Donnelly 2000) for $K2$–$K10$ to identify genetic structure among established meadows and seed groups, separately, with the options admixture model, run length 100,000, 100,000 MCMC iterations, and correlated allele frequencies. Each K consisted of 10 independent runs. Structure output was estimated with Evanno ΔK (Evanno, Regnaut, and Goudet 2005) in Structure Harvester (Earl and Vonholdt 2012) and visualised with Clumpak (Kopelman et al. 2015). We also used the R package Adegenet 2.1.4 (Jombart 2008) to perform a discriminant analysis of principal components (DAPC) (Jombart and Collins 2015) for the adults and seeds' datasets, separately.

2.5 | Genetic Connectivity Between Established Meadows and Assignment of Seeds

GeneClass2 (Piry et al. 2004) was used to estimate (i) first-generation (F_0) migrants (FGMs), (ii) perform self-assignment of adult individuals from established meadows, and (iii) compute genetic assignment of beach-cast seeds of unknown origin. For migrant detection in established meadows (i), the statistical criterion for likelihood estimation was L_home/L_max (i.e., the ratio of the likelihood computed from the population where the individual was sampled [L_home] over the highest likelihood value among all populations sampled, including the one where the individual was collected [L_max]) (Piry et al. 2004). The partially Bayesian criterion of Rannala and Mountain (1997) was selected for likelihood computations. Associated probabilities were computed using a Monte-Carlo resampling algorithm (Paetkau et al. 2004) with 1000 permutations and a type I error of 0.05. For the self-assignment task (ii), which estimates the likelihood that an individual belongs to the population where it was sampled, the Paetkau et al. (2004) resampling algorithm was used with 100,000 simulation steps and a type I error of 0.01.

For the genetic assignment of beach-cast seeds of unknown origin (iii), the Rannala and Mountain (1997) method was selected as a criterion for computation. The probability of a meadow being a seed source was computed via a Monte-Carlo resampling algorithm (Paetkau et al. 2004) with 1,000,000 simulation steps and a type I error of 0.01. The analysis was conducted using the matrix of adult individuals from established meadows as the reference dataset after the removal of individuals identified as first-generation migrants (Jahnke et al. 2017; Underwood et al. 2007). The genetic assignment procedure is highly sensitive to genetic homogeneity. In our analysis, the level of genetic differentiation between populations ($F_{ST} = 0.076$, see Section 3.2) should be sufficient to provide a reliable assignment (Christie et al. 2017).

2.6 | Lagrangian Modelling of Seed Dispersal

In order to characterise the potential (oceanographic) connectivity across sites in the study area, Lagrangian trajectories were simulated by means of ocean surface current fields provided by a general circulation model for the Mediterranean Sea (as in Jahnke et al. 2017; Tutar et al. 2022). The main idea was to evaluate particles' arrival probability, within a given time window, from a *P. oceanica* source to a target site. Only meadow locations could be considered for the analysis, as the model does not allow considering sites on the coastline (e.g., beaches). The numerical trajectories were let free to evolve throughout the central Mediterranean basin; thus, they could also reveal 'colonisation' patterns outside the geographical boundaries of the research area domain. The Lagrangian simulations, here presented, relied upon the Mediterranean Forecasting System (MFS; https://medforecast.bo.ingv.it/) analysis fields for the year 2021, in the period April–June, which largely overlap the time of *P. oceanica* fruits collection in the study area. MFS provides daily velocity fields on a grid of 1/16° horizontal spatial resolution and 72 vertical levels (Dobricic and Pinardi 2008; Tonani et al. 2008; Oddo et al. 2009). The MFS core consists of a hydrodynamic, eddy-permitting model, with a variational data assimilation scheme, widely described elsewhere (e.g., Tonani et al. 2009; Dobricic and Pinardi 2008). To simulate the action of the missing velocity components, filtered out by the spatio-temporal resolution, a 'sub-grid' Lagrangian turbulence kinematic model was added to the numerical trajectory equations (Lacorata, Palatella, and Santoleri 2014; Lacorata and Vulpiani 2017; Lacorata et al. 2019). A key parameter for the calibration of the kinematic Lagrangian model (KLM) is the value of the mesoscale turbulent mean dissipation rate, $\varepsilon \sim O(10^{-9})\ m^2/s^3$, directly measured from Mediterranean drifter trajectories (http://www.myocean.eu) by means of dynamical system techniques, that is, the Finite-Scale Lyapunov Exponents (FSLE) (see, e.g., Corrado et al. 2017 and references therein for applications of this methodology to evaluate scale-dependent dispersion properties from surface drifter data). The KLM's role is to adjust the relative dispersion rates of the numerical trajectories as close as possible to the corresponding observational values (Lacorata, Palatella, and Santoleri 2014). This type of modelling apparatus was recently employed in various studies related to oceanographic connectivity in the Mediterranean Sea (Palatella et al. 2014; Maffucci et al. 2016; Torri et al. 2018; Falcini et al. 2020).

Both forward and backward-in-time Lagrangian numerical simulations were carried out to investigate all possible dynamic connections between sites in the study area. Backward-in-time

dispersion models can efficiently reconstruct drifters (such as seeds) trajectories by linking known arrival positions to potential sources. For the forward (direct) motion, 8000 numerical particles were released on the sea surface, in correspondence with each meadow site, and followed for a total time of 3 weeks (21 days). Valderice (VA) was excluded from the analysis since it is a collection site with no adjacent meadow. The trajectory evolution was followed over a 3-week period (21 days). This timeframe is generally considered the average lifetime of *P. oceanica* floating fruits (Serra et al. 2010; Jahnke et al. 2017), although experimental data are scarce. Preliminary observations revealed that when beach-cast fruits were returned to the sea and left floating within a ring of small floating buoys, seed release occurred after a maximum of 7 days (*unpublished data*). However, the date of detachment of the fruits from the mother plant was not known, hence the dehiscence time could be underestimated by days to weeks.

The probability that a particle, coming from a source site 'A', is recovered in a target site 'B' is assumed to be proportional to the fraction of time spent in proximity of 'B', that is, within a distance from the coast of the order of the grid step of the model, of order ~ O(1) km, in correspondence of the target site. Backward (reverse) trajectories were initialised in proximity of each target site, and the probabilities of coming from a given source site (inside or outside the system) were evaluated according to the aforementioned procedure. The choice of a large-scale ocean circulation model for the trajectory simulations does not allow a very accurate description of the coastal dynamics (Ruiz-Montoya, Lowe, and Kendrick 2015) but, on the other hand, it offers the opportunity to explore a wide domain around the study area, including open sea circulation features of the central Mediterranean basin. Further details about Lagrangian modelling methods are available in the Appendix of Supporting Information.

3 | Results

3.1 | Genetic and Clonal Diversity, Outlier Detection

Genotypic diversity (R) was generally high across the established meadows ($R = 0.73$–1), with the only exception of MAC, where only two distinct MLGs were found over 22 sampled individuals. All seed cohorts were composed of unique MLGs ($R = 1$) (Table 1).

Significant deviations from HWE ($p < 0.05$) were observed for 9 loci across adult populations [22 of 128 tests (17%)], and for 7 loci across seed cohorts [17 of 144 tests (12%)]. In the adults' dataset, we found significant linkage disequilibrium (LD) in 9 of 120 tests across all populations (8%) after applying Bonferroni correction, while the loci did not show evidence for LD in the seeds' dataset. The PI was low, ranging from 4.81E−04 in MAC to 3.82E−10 in CO, and from 4.84E−09 in VA_s to 9.49E−11 in SM_s.

Among meadows, NI, CO, and FO showed the largest number of alleles per locus (N_A) and a high % of polymorphic loci ($\%p = 94$–100). SI_s, NI_s and SM_s were the seed cohorts with the largest number of N_A and $\%p = 100\%$ (Table 1). N_A and mean allelic richness (A_R) were significantly higher ($N_A = p < 0.01$; $A_R = p < 0.001$, unpaired t-test) in seed cohorts ($N_A = 3.63$; $A_R = 3.51$) relative to meadows ($N_A = 3.08$; $A_R = 1.97$). Observed heterozygosity (H_O) and mean expected heterozygosity (uH_E) were similar among adult individuals ($H_O = 0.54$; $uH_E = 0.48$) and seeds ($H_O = 0.52$; $uH_E = 0.51$) (Table 1). As well, a similar number of private alleles (N_{PA}) was present across meadows ($N_{PA} = 2.0$) and seed cohorts ($N_{PA} = 2.1$). *P. oceanica* meadow of FO had the largest number of private alleles ($N_{PA} = 4$), while among seed groups, the highest number of N_{PA} was observed in SI_s ($N_{PA} = 4$) (Table 1). F_{IS} was always negative among established meadows (from −0.857 in MAC to −0.063 in IF), whereas among seed cohorts it ranged from −0.147 in MAC_s to 0.067 in SI_s (Table 1).

The outlier analysis of adult individuals from established meadows with Lositan identified Po-4-3 as a locus under positive selection, while Pooc-044B02 and Pooc-333 were under balancing selection (Table S2). On the contrary, Lositan detected no outlier loci for the seed cohorts' dataset. BayeScan confirmed Po-4-3 as an outlier locus for the adults' dataset, while no outlier loci were identified for the seeds' dataset (Table S3). As Po-4-3 was confirmed as an outlier by two statistical approaches, we considered it a 'real' outlier and removed it from all further analyses of the adults' dataset and adult-seeds' dataset.

3.2 | Genetic Differentiation and Population Structure of Meadows and Seed Cohorts

The overall genetic distance among the established meadows [$F_{ST} = 0.076$; G'_{ST} (Nei) $= 0.095$; $D_{est} = 0.098$] was more than the double of that detected among seed cohorts [$F_{ST} = 0.034$; G'_{ST} (Nei) $= 0.036$; $D_{est} = 0.043$]. This general pattern of differentiation was also supported by DAPC results (Figure 2a,b).

Considering all genetic distance indices, a low but significant pairwise differentiation was detected among all *P. oceanica* meadows, with few exceptions (Tables S4, S6, S8). Especially northern populations of NI, and IF formed unique clusters, while SI, MA, and SM mostly grouped together in the DAPC (Figure 2a). Among seed cohorts, there were no significant differences (neither with F_{ST}, G'_{ST} or D_{est}) between CO_s and VA_s, as well as SI_s vs. MAC_s, CO_s, and VA_s (Tables S5, S7, S9). The DAPC of seeds was largely consistent with this pattern (Figure 2b).

All seed cohorts were significantly genetically differentiated from their putative meadow of origin based on F_{ST}, G'_{ST}, and D_{est} coefficients (Tables 2, S10, S11). This provides evidence that they contain seeds from multiple sources. The structure analysis identified $K = 6$ as the most likely number of clusters across established meadows. However, at lower Ks ($K = 2$–3) a sub-division of northernmost (NI, IF, MAC, and CO) and southernmost populations (MA, SI, FO, and SM) was evident (Figure S1). For seed cohorts, $K = 2$ as the most likely number of clusters (Figure S2); however, the differences in estimated probability among Ks were relatively small, and there was a strong degree of admixture between clusters. Further

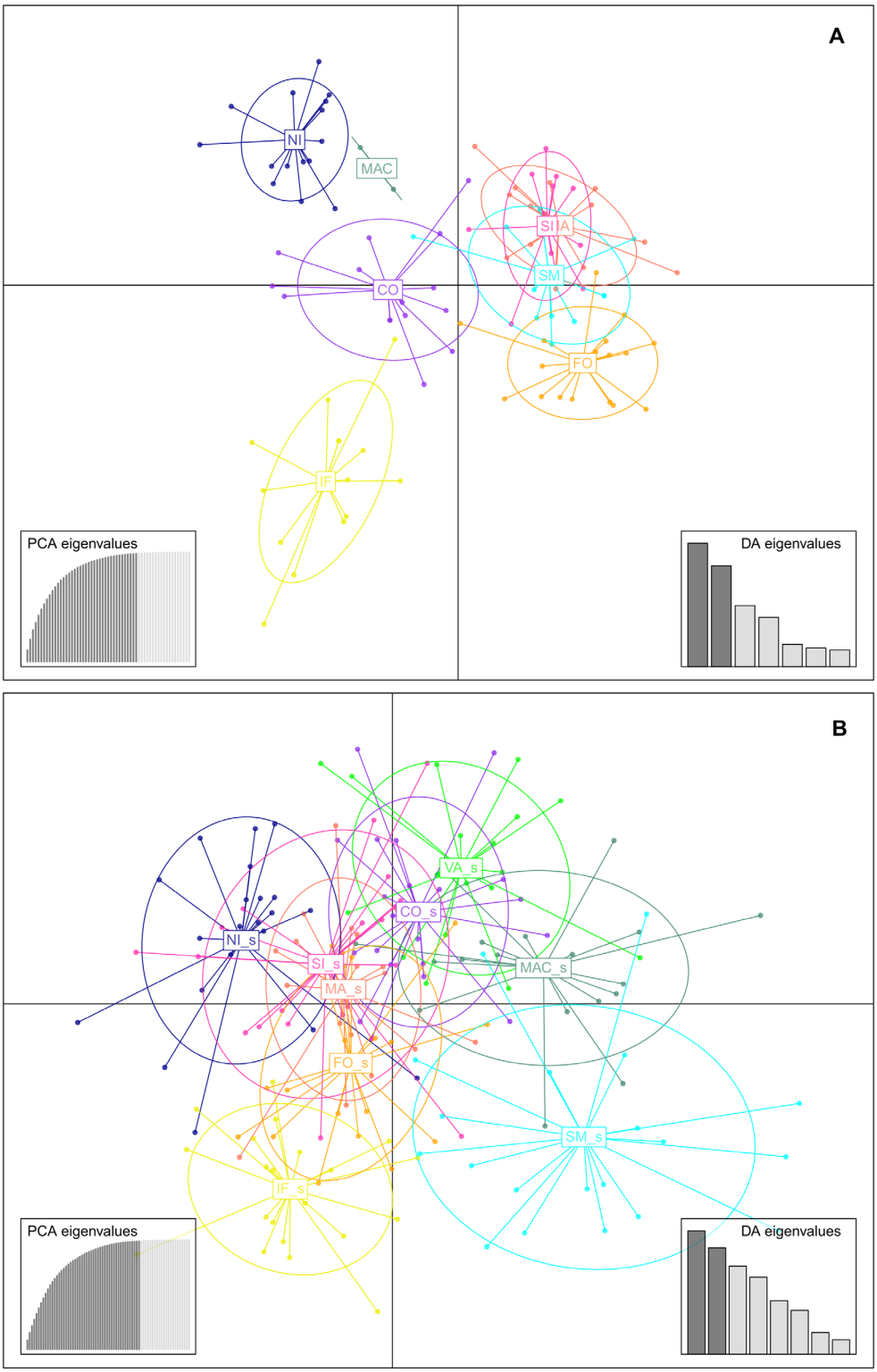

FIGURE 2 | Discriminant analysis of principal components (DAPC) for the adults' (A) and seed cohorts' datasets (B) of *Posidonia oceanica* in Western Sicily. Each dot represents an individual contained in a population/cohort by a circle. CO, Cornino; FO, Tre Fontane; IF, Isola delle Femmine; MA, Marsala; MAC, Macari; NI, San Nicola l'Arena; SI, Torre Sibiliana; SM, San Marco; VA, Valderice.

sub-structuring becomes evident when assuming higher *K*s ($K = 3$–6), as the close relationship between CO_s and VA_s (Figure S2).

The AMOVA showed that the majority of variance was present within individuals (95%) (Table S12).

3.3 | Genetic Connectivity Among Meadows and Individual Assignment of Seeds

Only 63 out of 106 (59.4%) adult individuals were correctly assigned to the meadow of origin, indicating quite strong connectivity of *P. oceanica* in the study area. CO and FO had the

TABLE 2 | Pairwise F_{ST} matrix (below the diagonal) and significance level (above the diagonal) based on 1023 permutations between 8 established meadows and 9 seed cohorts ('s') of *Posidonia oceanica* in Western Sicily considering only neutral loci.

	NI	IF	MAC	CO	MA	SI	FO	SM	NI_s	IF_s	MAC_s	CO_s	VA_s	MA_s	SI_s	FO_s	SM_s
NI		***	*	**	***	***	***	***	**	***	***	***	***	***	**	***	***
IF	0.091		*	**	***	**	***	***	***	***	***	**	**	*	***	***	***
MAC	0.124	0.145		**	**	**	**	ns	*	**	**	**	**	**	*	**	**
CO	0.023	0.045	0.053		***	**	***	*	***	***	**	***	**	**	*	**	***
MA	0.107	0.096	0.088	0.061		***	***	*	***	***	***	***	***	***	**	***	***
SI	0.067	0.067	0.173	0.049	0.045		**	***	***	***	ns	*	***	**	**	***	***
FO	0.053	0.081	0.182	0.053	0.119	0.046		***	***	***	***	*	**	***	**	**	ns
SM	0.067	0.068	0.091	0.026	0.020	0.042	0.056		***	ns	*	**	**	*	ns	*	**
NI_s	0.027	0.078	0.069	0.030	0.053	0.064	0.103	0.052		***	***	***	***	***	***	***	***
IF_s	0.072	0.096	0.126	0.051	0.059	0.076	0.074	0.013	0.083		***	***	***	***	**	***	***
MAC_s	0.059	0.051	0.150	0.027	0.040	0.007	0.040	0.017	0.063	0.033		*	***	***	ns	**	***
CO_s	0.040	0.039	0.131	0.035	0.058	0.017	0.017	0.024	0.047	0.050	0.012		ns	**	ns	**	***
VA_s	0.033	0.049	0.123	0.030	0.059	0.032	0.043	0.029	0.030	0.066	0.026	−0.003		***	ns	***	***
MA_s	0.070	0.031	0.092	0.023	0.028	0.025	0.062	0.023	0.040	0.059	0.023	0.023	0.038		**	***	***
SI_s	0.021	0.053	0.092	0.017	0.028	0.028	0.035	0.009	0.029	0.023	0.010	0.000	0.001	0.026		*	***
FO_s	0.072	0.052	0.102	0.036	0.052	0.030	0.029	0.018	0.068	0.041	0.018	0.018	0.030	0.022	0.014		**
SM_s	0.055	0.077	0.117	0.039	0.073	0.041	0.010	0.027	0.073	0.049	0.025	0.027	0.036	0.038	0.033	0.023	

Abbreviations: CO, Cornino; FO, Tre Fontane; IF, Isola delle Femmine; MA, Marsala; MAC, Macari; NI, San Nicola l'Arena; SI, Torre Sibiliana; SM, San Marco; VA, Valderice.
*$p < 0.05$.
**$p < 0.01$.
***$p < 0.001$.

largest percentage of right (self) assignment (69% and 65%, respectively), while SM had the lowest one (25%) (Table 3). GeneClass2 identified 14 significant first-generation migrants (FGMs) across meadows (13%, $p < 0.05$) (Table 3). These are inferred to represent individual long-distance dispersal events (LDD), with genotypes travelling a distance between a minimum of ~30 km (FO-SM) up to a maximum of ~200 km (SM-NI).

Across seed cohorts, only FO_s had the largest percentage of individual seeds (over the total n° of seeds collected at each location) assigned to the local meadow (FO, 60%) (Table 3, Figure 3). Seeds collected at all the other sites were assigned to multiple locations, including local (in bold in Table 3) and mostly non-local meadows (Table 3, Figure 3), suggesting mixing of dispersing seeds across the study area. FO, CO, MA, and SI were the meadows providing sexual propagules to the largest number of seed cohorts (i.e., key sources), including those collected hundreds of kilometres far (Table 3, Figure 4). The meadow at Tre Fontane (FO) was identified as a seed source for all locations in the study area, with varying percentages of contributed seeds (Table 3, Figure 4). The dispersal distance associated with seeds assignment between collection sites and established meadows ranged from 0.3 to 184 km, with a mean of 64 km (Table 3).

Globally, the largest percentage of seeds at each site were assigned to southernmost (S) *P. oceanica* populations (mostly FO and MA), with the only exception of NI, that shows a prevalence of seeds from northernmost (N) meadows (48% N, 43% S) and IF where the same percentage of seeds was assigned to northernmost and southernmost localities (38% N, 38% S) (Figure 3).

3.4 | Oceanographic Connectivity

The results of forward and backward-in-time simulations after 21 days of passive dispersal are presented in Figures S3, S4. Model-based oceanographic connectivity matrices for forward and backward-in-time simulations appear in Figure 5. The dark boxes appearing in the oceanographic connectivity matrices, corresponding to very unlikely row-column connections, are the signature of dynamical constraints imposed by the local marine surface circulation to the mean Lagrangian advection, that is, the preferential direction followed by the trajectories, depending on the initial conditions.

Overall, patterns of particle dispersal identified the main coastal flow going southward from NI to SM, hence the NI → SM and SM → NI Lagrangian pathways were not equiprobable. Particles released from NI and IF drifted to both the west and the east, but failed to reach the southernmost localities (i.e., FO and SM) (Figure S3). Also, parts of the particles were probably lost in the open sea areas and do not meet the coast in a suitable time for settlement (Figure S3). Particles originating from MAC, CO, and partially MA were drifted both northward and southward, potentially connecting all populations in the study area (Figure 5A, Figure S3). SI, FO, and SM-sourced particles mostly drifted south-east and possibly reached the Malta coast (Figure S3).

Backward simulations revealed, in five cases (MAC, CO, MA, SI, and FO), significant (non-zero probability) Lagrangian connections with sources outside the study area, specifically the northern Tunisian coast, near Tunis (Figure 5B, Figure S4). This scenario is compatible with the presence of the Algerian Current which, at the entrance of the strait of Sicily, splits into three branches: one flowing eastward into the southernmost region of the Tyrrhenian Sea (responsible, in this specific case, of the long-range dynamical connection between Sicilian and Tunisian coasts) and the other two flowing through the strait, namely, the Atlantic Tunisian Current and the Atlantic Ionian Stream (Bèranger et al. 2004). As Tunisia (TUN) was recognised as an additional potential seed source, we also present forward-in-time simulations for this location in Figure S5, and TUN was included in the connectivity matrices of Figure 5. NI appeared to be among the most isolated meadows, as it could not receive seed inputs from other localities. On the contrary, FO exhibited the largest connectivity, as it could receive drifting propagules from all but NI analysed locations (Figure 5B, Figure S4).

4 | Discussion

This is the first large-scale study in which patterns of connectivity and dispersal in *P. oceanica* are investigated by means of a comparative genetic assessment of sexual propagules (seeds), along with adult shoots from established meadows. Genetic data were complemented with forward and backward Lagrangian particle tracking simulations to assess all possible dynamical connections between sources of dispersal vectors (i.e., floating fruits) based on sea surface currents. A similar study has been conducted on the congeneric species *P. australis* across the coastal waters of south-western Australia (Sinclair et al. 2018).

Posidonia oceanica is characterised by sporadic and unpredictable flowering and fruiting (Balestri 2004), with large variations occurring across regions and individual meadows (Diaz-Almela et al. 2006; André et al. 2023). Along the NW Sicilian coast, fruiting has been observed almost annually in mid to late spring and seeds collection along the Sicilian coast during late spring has been reported by several studies (Alagna et al. 2013, 2015; Zenone, Alagna, et al. 2020; Zenone, Filippov, et al. 2020; Zenone et al. 2022; Provera et al. 2024). However, no information is currently available on seed provenance and major sources of sexual propagules. These massive fruiting events occurring in this research area offer a precious opportunity to determine the main dispersal pathways and levels of genetic connectivity among meadows. This information is extremely relevant as it could guide proper conservation efforts and/or seeds-based restoration actions (e.g., Provera et al. 2024).

4.1 | Large Genetic and Genotypic Diversity of *P. oceanica* in the Study Area

The present analysis of individuals from eight Sicilian *P. oceanica* meadows, covering ~220 km coast from Palermo to Sciacca, revealed a high level of genetic and genotypic (clonal) diversity across the study area, as indicated by a large mean R value (0.76 ± 0.30), and high levels of mean observed heterozygosity

TABLE 3 | Results of the assignment tests of established meadows (adults) and seed cohorts ('s'), and data for the 14 detected first-generation migrants (adults) of *Posidonia oceanica* along the Western coast of Sicily obtained with GeneClass2.

Established meadows

Home location	Correctly assigned individuals (*self-assignment*)	N° of recent migrants	Assigned location (exclusion probability)	Distance travelled (~km)
NI	56%	3	SM (0.036)	212
			SI (0.027)	154
			FO (0.015)	184
IF	53%	1	SM (0.002)	169
MAC	50%	0	—	
CO	69%	2	MA (0.041)	51
			SM (0.026)	114
MA	60%	1	SM (0.021)	76
SI	54%	2	CO (0.022)	53
			SM (0.032)	58
FO	65%	2	CO (0.031)	87
			SI (0.029)	30
SM	25%	3	FO (0.035)	28
			FO (0.004)	28
			MA (0.045)	76
	Total	14 (13%)		

Beach-cast seeds of unknown origin

'Home' location (beach)	Individual assignment to meadows (%) $p > 0.1$	N° total assigned individuals (%)	Distance travelled (~km)	N° not assigned individuals
NI_s	MA (33); **NI (29);** CO (19); FO (10)	19 (90%)	MA (142); NI (1); CO (101); FO (184)	2
IF_s	CO (24); MA (19); NI (14); FO (14); SI (5)	16 (76%)	CO (59); MA (98); NI (44); FO (146); SI (110)	5
MAC_s	CO (28); FO (28); SI (22); MA (6)	15 (83%)	CO (9); FO (92); SI (62); MA (48)	3
CO_s	FO (52); **CO (24);** SI (10)	18 (86%)	FO (87); CO (0.7); SI (53)	3
VA_s	FO (40); CO (30); MA (10); NI (5); SM (5)	18 (90%)	FO (83); CO (3); MA (39); NI (100); SM (108)	2
MA_s	CO (26); FO (26); SI (16); **MA (11);** NI (11); SM (5)	18 (95%)	CO (51); FO (42); SI (11); MA (9); NI (142); SM (76)	1
SI_s	FO (33); NI (19); MA (14); CO (10); **SI (5)**	17 (81%)	FO (30); NI (154); MA (11); CO (53); SI (0.3)	4
FO_s	**FO (60)**; MA (10); SI (5); IF (5)	16 (80%)	FO (3); MA (42); SI (30); IF (146)	4

(Continues)

TABLE 3 | (Continued)

Beach-cast seeds of unknown origin				
'Home' location (beach)	**Individual assignment to meadows (%) $p > 0.1$**	**N° total assigned individuals (%)**	**Distance travelled (~km)**	**N° not assigned individuals**
SM_s	FO (60); CO (5); **SM (5)**	14 (70%)	FO (28); CO (113); SM (1.2)	6
	Total	151 (83%)		

Note: The analysis is based on only neutral loci. Travelled distance (~km) refers to the minimum possible geographic distance travelled via water between the collection site and the assigned location of origin. In bold, % seeds assigned to the local meadow.
Abbreviations: CO, Cornino; FO, Tre Fontane; IF, Isola delle Femmine; MA, Marsala; MAC, Macari; NI, San Nicola l'Arena; SI, Torre Sibiliana; SM, San Marco; VA, Valderice.

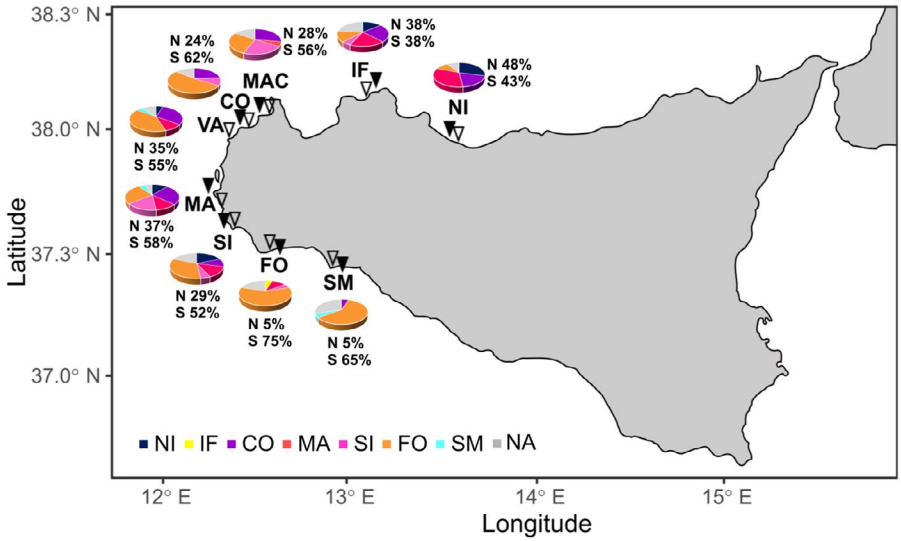

FIGURE 3 | Results of individual seed assignment tests of *Posidonia oceanica* along the Western coast of Sicily. For each collection site, the pie-chart shows % seeds, for each cohort, belonging to a putative meadow of origin based on GeneClass2 outputs. Cumulative % seeds assigned to northernmost (N = NI, IF, MAC, and CO) or southernmost (S = MA, SI, FO, and SM) meadows are also indicated. CO, Cornino; FO, Tre Fontane; IF, Isola delle Femmine; MA, Marsala; MAC, Macari; NI, San Nicola l'Arena; SI, Torre Sibiliana; SM, San Marco; VA, Valderice. Established meadows: Black triangles, seed cohorts: Open triangles. NA = not assigned.

and allelic richness ($H_O = 0.54 \pm 0.05$; $A_R = 1.97 \pm 0.21$), with the only exception of the population from Macari (MAC), which appears to be composed by few clonal individuals, a possible misleading finding resulting from sampling a fairly large but isolated patch of *P. oceanica* surrounded by sand. The population of Cornino (CO) possess the largest values of clonal and genetic diversities ($R = 1.0$; $H_O = 0.63$; $A_R = 2.1$). Overall, the observed levels of clonal and genetic diversity are similar to those found for *P. oceanica* meadows in the central Mediterranean Sea, including other Sicilian populations ($R = 0.7$ and $H_O = 0.5$; Arnaud-Haond et al. 2007; Serra et al. 2010; Procaccini, Dattolo, and Ruocco 2023). Across the whole Mediterranean, *P. oceanica* populations in the Strait of Sicily show the highest average number of alleles and clonal diversity, in line with the previously raised hypothesis that this area could act as a transition or 'hybridization' zone between Eastern and Western Mediterranean groups (Arnaud-Haond et al. 2007; Serra et al. 2010). However, recent findings indicate comparable high levels of genetic and genotypic diversity along sectors of the Greek coasts and at the Easternmost distribution limit of the species (Litsi-Mizan et al. 2024; Tutar et al. 2022).

4.2 | Evidence of High Genetic Connectivity and Long-Range Dispersal of *P. oceanica*

In this study, we combined multiple dispersal measures to provide insights into real-time physical seed dispersal pathways (between the collection site and the inferred source meadow) and quantify both potential (through beach-cast seed assignment) and realised (through the detection of FGMs) genetic connectivity of *P. oceanica* in the study area. The analysis also spans across different temporal scales, as seed dispersal pathways based on genetic assignments reflect contemporary gene flow, while genetic distances between established meadows result from past recruitment events (Sinclair et al. 2018).

We found that beach-cast seed pools ('seed cohorts') exhibited much less genetic differentiation and structure than the established *P. oceanica* meadows. In addition, our study highlighted a significant genetic differentiation between all seed cohorts and the most likely meadow of origin (i.e., the local meadow). In support of these findings, genetic assignment tests provided evidence that such cohorts typically contain seeds from multiple

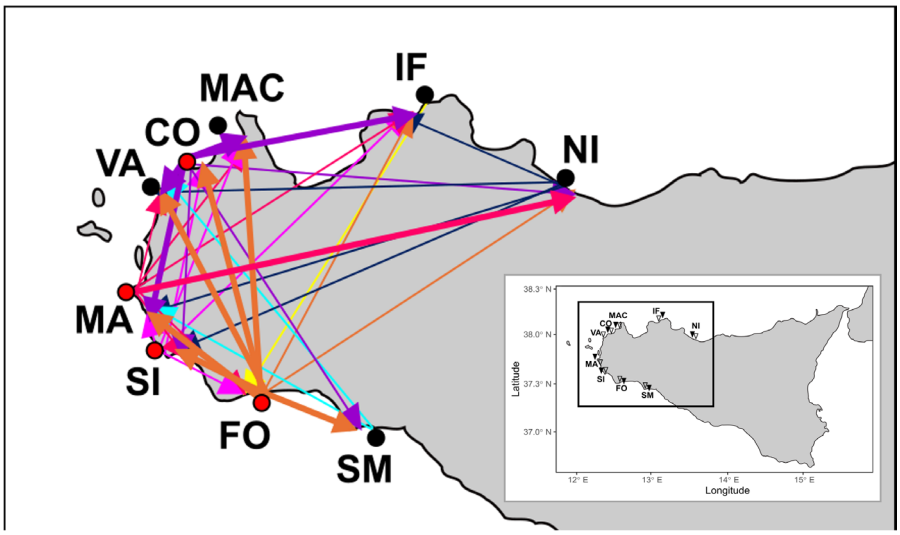

FIGURE 4 | Geographic visualisation of seed dispersal routes in *Posidonia oceanica* along the Western coast of Sicily, based on GeneClass2 assignment tests. Only seed dispersal events beyond the local meadow are displayed. Meadows that are identified as the best sources are indicated by red dots. Dispersal routes are coloured according to the source meadow (pop colours as in Figures 2 and 3), and the thickness reflects major (≥ 5 assigned seeds) or minor (< 5 assigned seeds) contribution to the seed cohort. For legibility, only the position of the established meadows is displayed on the enlarged map, except for Valderice (VA) for which the position of the collection site is shown. CO, Cornino; FO, Tre Fontane; IF, Isola delle Femmine; MA, Marsala; MAC, Macari; NI, San Nicola l'Arena; SI, Torre Sibiliana; SM, San Marco; VA, Valderice.

non-local sources, while local meadows only provide a minor contribution to the local seed pools. Similarly, a preliminary study in the Ligurian Sea found that *P. oceanica* beach-cast fruits likely originated from distant meadows, transported by currents, rather than from nearby meadows (Micheli et al. 2010). In our study, the only exception was at Tre Fontane (FO_s), where the largest proportion of seeds (60%, over the total seeds collected at that location) was assigned to the nearest meadow (FO), indicating that this meadow acts as a strong retainer (i.e., a place where released propagules can successfully remain in situ).

The genetic assignment of individual seeds, as well as the detection of first-generation migrants (FGMs) within established meadows, revealed the presence of several LDD events (*sensu* Sinclair et al. 2018), with genotypes travelling distances up to hundreds of km. However, we cannot exclude the presence of other issues, for instance, the FGMs detected in our study could also be the results of step-by-step 'migration' of genotypes, not representing real long-distance dispersal events.

The greatest seed dispersal events occurred between central and southernmost populations (CO ↔ FO), in both directions. The meadows of FO, CO, MA, and SI were identified as those providing sexual propagules to the largest number of seed cohorts (i.e., key source sites).

The northernmost populations of San Nicola (NI) and Isola delle Femmine (IF) were apparently slightly isolated from the main patterns of connectivity. However, genetic assignment tests of both adults and seeds revealed these meadows could be the target of long-distance dispersal events from other meadows in the study area. In support of this, both meadows showed among the highest levels of genetic and genotypic richness, indicative of high levels of sexual reproduction and/or recruitment of foreign genotypes.

The long-distance dispersal events detected in our study (up to 200 km) were also hypothesized for other seagrass species with floating reproductive structures. These studies predicted dispersal events occurring over scales from 10 s to 100 s km (Källström et al. 2008; Tanaka et al. 2011; Nakajima et al. 2014; Ruiz-Montoya, Lowe, and Kendrick 2015; Grech et al. 2016; Sinclair et al. 2018; Triest et al. 2018). In some extreme cases, as for the two tropical seagrasses *Enhalus acoroides* and *Thalassia hemprichii*, strong currents from frequent typhoons could increase the maximum dispersal range of fruits to as much as 400 km (Lacap et al. 2002). In *Zostera noltii*, it has been hypothesized that dispersal and germination of seeds contained in spathes of floating shoots may occasionally occur and impact gene flow among populations at up to 600 km (Jahnke et al. 2016).

4.3 | Comparison of Genetic and Oceanographic Modelling of Dispersal

Lagrangian simulations of dispersal illustrated the most likely pathways particles travelled from/to established meadows based on hydrodynamic forces and provided potential for contemporary oceanographic connectivity within and beyond the study area. Our analysis highlighted that the mean coastal flow was directed southward, from NI to SM, while the opposite Lagrangian pathway (from SM to NI) was not equiprobable. This is somehow in contrast with seed dispersal routes based on genetic assignment, as southern populations appeared to provide sexual propagules to northernmost sites (although the opposite pattern was also detected). This apparent discrepancy between genetic movement pathways and the evidence of a preferential north-to-south coastal transport direction remains, at present, an open question. Although model simulations indicate that seeds originating from the southernmost meadows have a very low probability to travel upstream, a remote possibility that

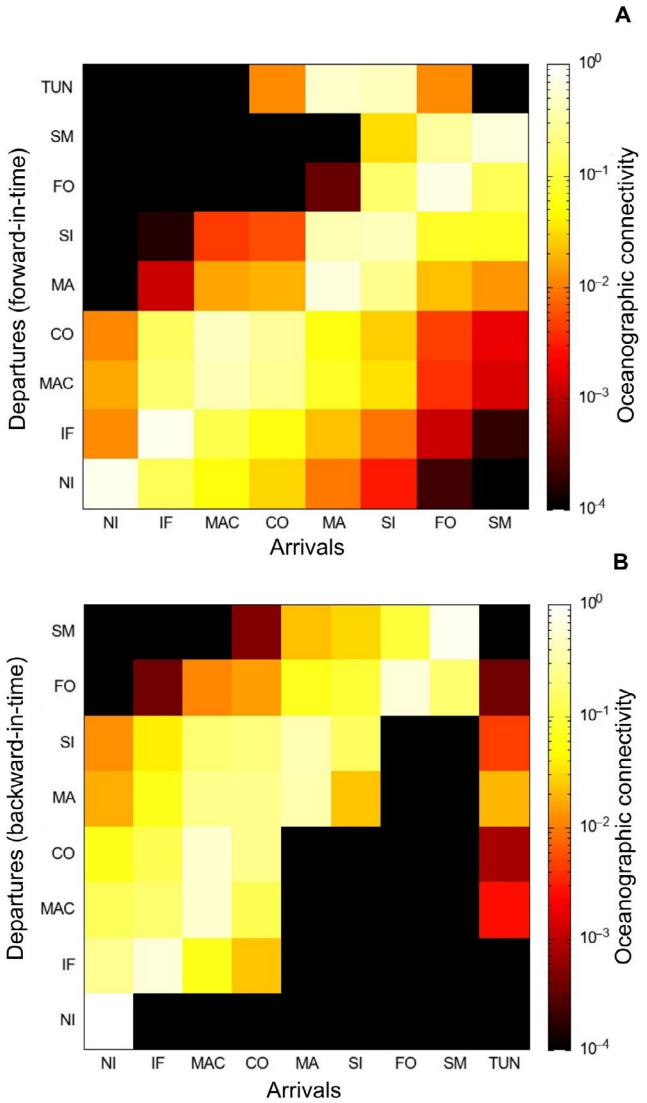

FIGURE 5 | Oceanographic connectivity matrices for forward-in-time (A) and backward-in-time (B) Lagrangian simulations. Colour bars represent the probability of site-to-site connections, within a 21-day time interval, normalised to the sum over all columns for each row. San Nicola l'Arena—NI, Isola delle Femmine—IF, Macari—MAC, Cornino—CO, Marsala—MA, Torre Sibiliana—SI, Tre Fontane—FO, and San Marco—SM, Tunisia—TUN.

this might actually occur, due to minor coastal circulation features not accurately captured by the model, cannot be ruled out. However, both physical modelling and population genetics substantially agreed in identifying main patterns of dispersal across central-southernmost Sicilian populations, with the greatest level of potential and realised connectivity in this research area domain.

Back trajectories indicated significant Lagrangian connections with source locations beyond the study area, as the northern Tunisian coast, where *P. oceanica* meadows have been described (Serra et al. 2010; Telesca et al. 2015). These sites could play an important role as a source of propagules for many locations across the study area. This is coherent with findings by Mari et al. (2020), which described the region centred on the Strait of Sicily as characterised by remarkable intercontinental connectivity. In particular, the Tunisian coast was identified among the top-100 *P. oceanica* connectivity hotspots in the Mediterranean (Mari et al. 2020).

In general, genetic connectivity (potential, through beach-cast seed assignment, and realised, via FGMs, which represent successful recruitment) appeared to be higher than potential oceanographic connectivity, as previously observed in *P. oceanica* along the northern Turkish coastline (Tutar et al. 2022). Discrepancies between genetic and oceanographic data may be explained by several factors, including the longer temporal scales on which gene flow is shaped, in contrast to contemporary sea-current dispersal dynamics. Genetic history of populations and past evolutionary events are especially important as they influence current patterns of differentiation and connectivity among populations (Serra et al. 2010; Chefaoui, Duarte, and Serrão 2017). Furthermore, it should be considered that oceanographic simulations were only produced for the year of seed collection (2021), while inter-annual fluctuations of the transport properties along the major marine currents may cause exceptional dispersal patterns due to the occurrence of extreme weather events (see, e.g., Palatella et al. 2014). Other studies comparing genetic and physical connectivity across a range of species not necessarily find a good agreement between both approaches (see, e.g., Serra et al. 2010; Johansson et al. 2015; Quigley et al. 2022; Tavares et al. 2023). For example, localised ecological conditions can influence the genetic structure of populations in a way that cannot be captured by the biophysical models (Johansson et al. 2015; Quigley et al. 2022). Generally, the two methods corroborated the findings of each other in the same aspects, while also providing unique insights, and thus a multidisciplinary biophysical-genetic approach is always recommended to best describe connectivity patterns (Quigley et al. 2022).

5 | Conclusions

Understanding which populations act as sources or sinks, and the direction of gene flow, can help to focus conservation and restoration efforts more effectively and predict how populations might respond to future environmental pressures. In this study, we identified key sources of sexual propagules in *P. oceanica* along the Western coast of Sicily, based on the genetic assignment of beach-cast fruits. The importance of these meadows for the overall connectivity of *P. oceanica* in the study area should be monitored throughout the years to confirm main seed dispersal routes and eventually propose these as special targets for conservation measures. It is worth mentioning that two Marine Protected Areas (MPAs) are present within the research area domain, the Egadi Islands MPA, which covers 54,000 ha and includes the islands of Favignana, Levanzo, Marettimo, and the MPA of Capo Gallo and Isola delle Femmine near Palermo. Understanding potential and realised connectivity could be especially important for the design of new MPAs, the managing of existing ones or the establishment of networks of MPAs, to implement large-scale conservation strategies (Andrello et al. 2015; Lagabrielle et al. 2014).

As a foundation species, *P. oceanica* is of critical importance to ecosystem functions and habitat provisioning in coastal areas. Our study represents a step forward for the understanding of *P. oceanica* movement ecology in terms of species' dispersal ability and seed movement pathways. Furthermore, it complements existing studies on *P. oceanica* genetic and oceanographic connectivity across the species distribution range in the Mediterranean Sea.

Author Contributions

M.R. and G.P. conceived the ideas and designed the study. I.P., A.Z., M.M., and V.M.G. conducted the sampling activities and the seedling maintenance. M.R. conducted all the molecular laboratory work with a significant help from E.D., J.P., and I.P. M.R. conducted the genetic data analyses. G.L. and L.P. conducted the Lagrangian modelling analysis. M.R., G.P., and F.B. led the interpretation of data. M.R. led the writing of the manuscript. All authors contributed to drafting the manuscript, data interpretation and approved the final version.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All the data underlying this article are available in the article and in its Supporting Information.

Peer Review

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Supporting Information

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