



OPEN Long range gene flow beyond predictions from oceanographic transport in a tropical marine foundation species

Ana I. Tavares^{1✉}, Jorge Assis^{1,2}, Patrick D. Larkin³, Joel C. Creed⁴, Karine Magalhães⁵, Paulo Horta⁶, Aschwin Engelen^{1,7}, Noelo Cardoso⁸, Castro Barbosa⁹, Samuel Pontes⁹, Aissa Regalla⁹, Carmen Almada¹⁰, Rogério Ferreira^{1,11}, Ba Mamadou Abdoul¹², Sidina Ebaye¹², Mohammed Bourweiss¹³, Carmen Van-Dúnem dos Santos¹⁴, Ana R. Patrício^{15,16}, Alexandra Teodósio¹, Rui Santos¹, Gareth A. Pearson¹ & Ester A. Serrão^{1,17}

The transport of passively dispersed organisms across tropical margins remains poorly understood. Hypotheses of oceanographic transportation potential lack testing with large scale empirical data. To address this gap, we used the seagrass species, *Halodule wrightii*, which is unique in spanning the entire tropical Atlantic. We tested the hypothesis that genetic differentiation estimated across its large-scale biogeographic range can be predicted by simulated oceanographic transport. The alternative hypothesis posits that dispersal is independent of ocean currents, such as transport by grazers. We compared empirical genetic estimates and modelled predictions of dispersal along the distribution of *H. wrightii*. We genotyped eight microsatellite loci on 19 populations distributed across Atlantic Africa, Gulf of Mexico, Caribbean, Brazil and developed a biophysical model with high-resolution ocean currents. Genetic data revealed low gene flow and highest differentiation between (1) the Gulf of Mexico and two other regions: (2) Caribbean-Brazil and (3) Atlantic Africa. These two were more genetically similar despite separation by an ocean. The biophysical model indicated low or no probability of passive dispersal among populations and did not match the empirical genetic data. The results support the alternative hypothesis of a role for active dispersal vectors like grazers.

Long-range dispersal of marine organisms with passively transported propagules is often hypothesized to be mediated by ocean currents, a hypothesis that lacks much empirical testing despite its major ecological and evolutionary implications^{1,2}. Challenges related with empirically tracking the movement and outcome of passive

¹Center of Marine Sciences (CCMAR-CIMAR), Universidade do Algarve, Faro, Portugal. ²Faculty of Bioscience and Aquaculture, Nord Universitet, Postboks 1490, 8049 Bodø, Norway. ³Texas A&M University-Corpus Christi, Corpus Christi, TX, USA. ⁴Departamento de Ecologia, Universidade do Estado do Rio de Janeiro, Rio de Janeiro, RJ, Brazil. ⁵Área de Ecologia, Departamento de Biologia, Universidade Federal Rural de Pernambuco, R. Dom Manoel de Medeiros, s/n-Dois Irmãos, Recife, PE CEP 52171-900, Brazil. ⁶Laboratório de Ficologia, Departamento de Botânica, Universidade Federal de Santa Catarina, Florianópolis, SC 88040-970, Brazil. ⁷CARMABI Foundation, Piscaderabaai z/n, P.O. Box 2090, Willemstad, Curaçao, The Netherlands. ⁸CIPA, Centro de Investigação Pesqueira Aplicada, Bissau, Guinea-Bissau. ⁹IBAP-Instituto da Biodiversidade e Áreas Protegidas, Bissau, Guinea-Bissau. ¹⁰Faculdade de Ciências e Tecnologia, Universidade de Cabo Verde, Praia, Cabo Verde. ¹¹Dragões do Mar, Nova Estrela, Ilha do Príncipe, São Tomé and Príncipe. ¹²Parc Nationale du Banc d'Arguin (PNBA), Chami, Mauritania. ¹³Institut Mauritanien de Recherche Oceanographique et des Peches (IMROP), Nouadhibou, Mauritania. ¹⁴Universidade do Namibe, Namibe, Angola. ¹⁵MARE-Marine and Environmental Sciences Centre, ISPA-Instituto Universitário, Lisbon, Portugal. ¹⁶Centre for Ecology and Conservation, University of Exeter, Penryn, UK. ¹⁷CIBIO-InBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Vairão, Portugal. ✉email: ana.isa_@hotmail.com

dispersal units have narrowed our knowledge on population connectivity across most marine biodiversity³. Indeed, most marine species, particularly habitat-forming species (macroalgae, corals, or seagrasses), migrate via passively-dispersed propagules^{4,5}. Thus, these species, are expected to form metapopulations that are passively connected by the transportation of such dispersal stages⁶, but the processes mediating such transportation are poorly understood. Many such marine species, including seagrasses, have wide geographical distribution ranges, which contrasts with their predicted dispersal capacity or ability to maintain regular long-distance dispersal throughout their range^{7,8}. Biological features of the dispersal phase, its interaction with a range of abiotic, historical, and biotic factors, determine species range limits and gene flow among populations⁹, which significantly impact a species' distribution and persistence¹⁰.

Large-scale studies focused on seagrass population connectivity have been developed^{11–13} but none have addressed the long distance cross-ocean dispersal in the tropical Atlantic region¹⁴. Along this wide geographical region, seagrass populations might be isolated by biogeographic barriers such as vast oceanic distances (e.g., the thousands of kilometres that separate east and west Atlantic), lack of suitable habitat (e.g., freshwater discharge near the Amazon or Congo rivers), or main oceanographic currents (e.g. Caribbean Current and South Equatorial Current^{15,16}). Leading hypotheses predict that oceanographic currents determine most connectivity of passively dispersed stages, functioning as both barriers and promoters of gene flow. The tropical Atlantic region, rich in seagrass diversity¹⁴, has only local-scale assessments focused on seagrass genetic diversity, dispersal and connectivity^{16–18}. Four seagrass genera are known to dominate the tropical Atlantic—*Thalassia*, *Syringodium*, *Halophila*, and *Halodule*—which either occur as single species or intermixed¹⁹. However, only *Halodule wrightii* is distributed on both east and west tropical Atlantic coastal shores, serving as an optimal model for range-wide connectivity studies across pan-Atlantic spatial scales.

Seagrasses form one of the most productive and important ecological groups along with mangroves and corals. They are flowering marine angiosperms that can form dense meadows in shallow coastal waters around the world^{20,21}. Seagrasses play a strong role in structuring communities and have received much attention due to their large ecological and social significance²². However, they are under increasing pressure from anthropogenic activities and climate change^{23,24}. As a result, seagrass habitats are declining globally²³, becoming lost or fragmented, and further extinctions are forecasted under future climate change scenarios²⁵.

Seagrasses can reproduce sexually by seed production and asexually by vegetative clonal development²⁶ and each reproductive mode produces different types of propagules with diverse dispersal abilities^{4,9}. There are several circumstances that can drive seagrass propagule dispersal routes over time. Abiotic factors such as wind, waves, tides or currents can lead seagrass-detached fragments to be easily transported away from the source location²⁷. In contrast, seabirds, fish, sea turtles, and dugongs are examples of biotic vectors that may mediate seagrass migration and gene flow by transporting clonal propagules or dispersing seeds after passing through their digestive system^{28,29}, increasing the chances, or even boosting, their germination success³⁰. Moreover, propagule features such as seed buoyancy can mediate dispersal scenarios⁴. These biophysical interactions (between propagule features and transport mechanisms) are predicted to shape the extent of connectivity among seagrass meadows over large geographical scales and to determine population longevity^{4,8}.

To address this knowledge gap, this study aims to compare predictions and empirical data on large scale connectivity for the seagrass species *Halodule wrightii*, the tropical species with the most extensive geographic range across the Eastern and Western Tropical Atlantic Ocean³¹. As for all in most other seagrass species, *H. wrightii* reproduces asexually and sexually, and the extent of each reproduction mode influences dispersal, genetic diversity, and biogeography. Despite its widespread distribution, the species produces seeds that are neutrally to negatively buoyant, with an apparent lack of long distance dispersal means³². Seeds of *H. wrightii* are able to form persistent seed banks that can remain dormant up to 4 years³³. Therefore, seeds play an important role in the persistence of the species. *H. wrightii* can also colonize new areas through by asexual clonal growth of detached fragments that can survive in the water column for up to 1 month³⁴. Previous studies have explored the genetic structure and connectivity of *H. wrightii*^{8,18,35} but only focused on specific areas of its distribution. To date, there is not a comprehensive study that encompasses this tropical amphi-Atlantic seagrass, in contrast with other seagrass species located on a single side of this ocean, such as *Cymodocea nodosa*³⁶.

Here, we aim to test the hypothesis of ocean currents as the main vectors for dispersal of *H. wrightii* in the Atlantic Ocean by comparing oceanographic predictors with genetic information. This is the first study that considers the distributional range of *H. wrightii*. The main goal of the present study was to uncover the population genetic structure and connectivity of this habitat-forming seagrass species in the tropical Atlantic region. This species is an ideal model for range-wide connectivity studies due to its vast geographical distribution. Here, we ask if: (1) there is genetic structure among *H. wrightii* populations across distant biogeographic regions along the tropical Atlantic; (2) levels of genetic and genotypic diversity are similar among populations; (3) the main ocean currents explain the present genetic structure; or (4) if the latter could be explained by biotic transportation. These questions and hypotheses were approached by using microsatellite markers and biophysical modelling based on oceanographic transport to model connectivity along the vast *H. wrightii* distributional range.

Results

No evidence of null alleles nor linkage disequilibrium was found. For the *H. wrightii* ramet dataset, we obtained a total of 475 sampling units (ramets) successfully genotyped for eight microsatellite loci across 19 populations. For the genet-level dataset, after the removal of repeated copies of each genet, 176 individual genotypes remained for analysis. Measures of genetic diversity such as allelic richness (i.e., the mean number of alleles per locus within a population) and gene diversity, or expected heterozygosity (i.e., the probability that two randomly selected alleles at a particular locus will be different in a population) were generally low for ramet and genet level datasets within all populations (Fig. 1D; Tables S1 and S2), except for both populations in the Gulf of Mexico.

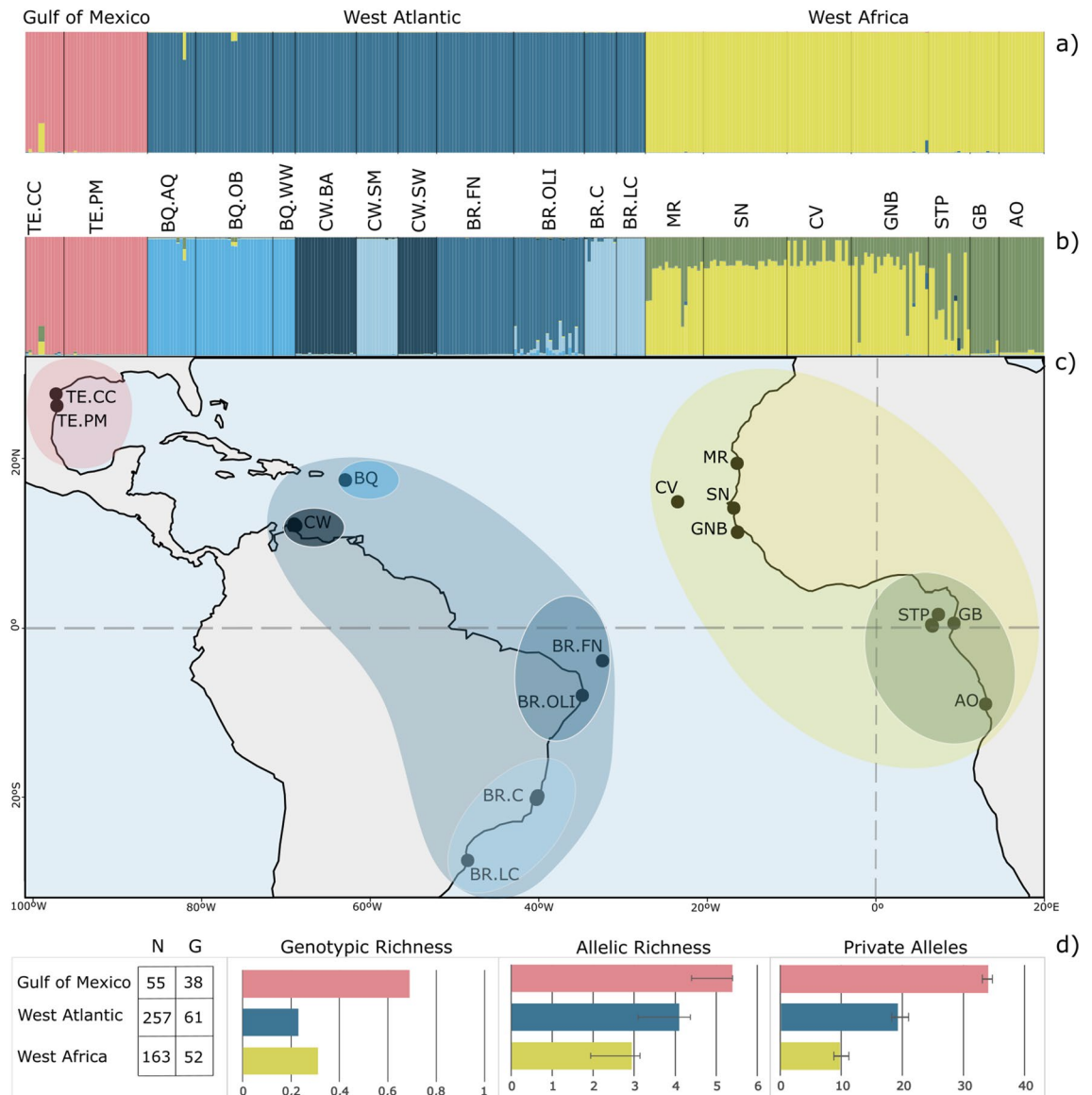


Figure 1. (a, b) Assignment of individuals to genetic groups that minimize Hardy–Weinberg and linkage disequilibria, estimated by STRUCTURE; colors depict the genetic subdivision based on $K = 3$ and $K = 7$ levels of subdivisions; Site names and coordinates are listed in Tables S1 and S4; (c) Sampling sites of *Halodule wrightii* with colors depicting the main highest genetic differentiation inferred with STRUCTURE ($K = 3$ groups); (d) Sample size (N); number of unique genotypes (G); genotypic richness, standardized allelic richness and standardized number of private alleles for the smallest common sample size. The figure was generated using R (version 4.2.2) and Inkscape 1.2.1 (<https://inkscape.org/>).

Likewise, private alleles ranged from high values in the same region to nearly no private diversity in several sites of the Caribbean region but also in West Africa (see Fig. 1D; Tables S1, S2). All the genetic diversity parameters when analyzed for the first hierarchical level of genetic structure ($k = 3$) revealed high estimates higher in Gulf of Mexico than the other clusters (Table S4).

Most of the inbreeding coefficients (F_{IS}) estimates were significantly negative for both datasets (Tables S1–S3), showing heterozygotes to be more prevalent than expected under Hardy–Weinberg equilibrium. The opposite scenario was observed for Gulf of Mexico, where heterozygote deficiency was prevalent (Tables S1 and S2). Also, F_{IS} values across the different locations in both datasets exhibit a wide range of negative values dispersion (Fig. S2). Genotypic richness (R) was highly variable among populations on both sides of the Atlantic, ranging across both extremes (Tables S1 and S2), from close to maximal contribution of sexual propagation (in the east Atlantic 88% of sampled shoots were distinct genets in Santana and Gabon, and in the west 93% were distinct in the Gulf of Mexico) to predominance of a single clone (only 8% were distinct genets in Angola in the east and in Curaçao in the west).

Pairwise differentiation (F_{ST}) between groups showed higher differentiation between West Africa against the other groups but differentiation was lower among West Africa populations (Fig. S3).

The factorial correspondence analysis (FCA) revealed a first major genetic differentiation between the Gulf of Mexico and the remaining sites, and these latter also split into east and west, resulting in three genetic clusters: Gulf of Mexico, east Atlantic (West Africa), remaining west Atlantic (Brazil and Caribbean) (Fig. 2). The STRUCTURE analysis, along with DAPC and PCA indicated the same three genetic clusters and at a more fine-scale differentiation these were subdivided into seven clusters (Fig. 1A and Fig. S4). These revealed a differentiation between southern and northern populations in Africa, admixed in Sao Tome and Principe, and a differentiation into four clusters in the Caribbean-Brazil region, admixed in Curaçao (Fig. 1B, C). Also, STRUCTURE plot for $K=7$, revealed more similarities between one of the Curacao populations (CW.SM) and the ones on south Brazil (Fig. 1).

The data compiled from literature (Table S5, supplemental material) and biodiversity databases, yielded 1815 known locations for the species. This resulted in 183 distinct source/sink sites aggregated at 1 km, which were included in the biophysical modeling. The particle simulations delivered 668,499 particles over a 10-year period. These revealed a sharp decline in potential connectivity with distance (Fig. S1), with high probabilities for propagule retention near the source locations (Fig. S1). Most connectivity events were predicted to take place only at regional scales (average distance of connectivity events: 330.42 ± 450.11 km; maximum: 3766.80 km), with low probabilities of connectivity (average probability of connectivity: 0.10 ± 0.19) due to few pair-wise site connectivity events (average number of events: 36.67 ± 70.65) (see Supplementary Information). The models predicted large scale oceanic transportation from Fernando Noronha (offshore Brazil) to Barbados in the Caribbean Sea (Fig. 3). Geographic distant regions had no probability of connectivity mediated by ocean currents (i.e., no connectivity events occurred at all from/to these sites in the 10 years of simulations), indicating zero probability that currents could be predominantly responsible for the dispersal and genetic differentiation of *H. wrightii* across such spatial and temporal scales.

Discussion

The genetic structure of the seagrass *H. wrightii* over its distributional range revealed three main genetic groups separated geographically at different spatial scales (from a broad to a regional scale), that did not completely match predictions from oceanographic transport of propagules (seeds or shoots) by currents. These results showed that although ocean circulation is an important factor in marine population structure¹, long-distance dispersal is likely a very rare event. The results support the hypothesis that rare events of occasional biotic transportation might have been responsible for connectivity between *H. wrightii* populations that belong to distinct genetic clusters.

Genetic structure and connectivity. *Large scale connectivity.* The significant genetic differentiation between West Atlantic, Gulf of Mexico, and West Africa, indicates restrictions to gene flow between these three main genetic lineages of *H. wrightii*. This was also supported by the biophysical modelling that revealed a null or very low probability of connectivity mediated by ocean currents between distant geographic regions (e.g., between east and west Atlantic coastlines) and suggested that most of the gene flow mediated by currents occurs at a regional scale (up to ~1230 km, Fig. S1). Such skewed relationship between oceanographic connectivity and

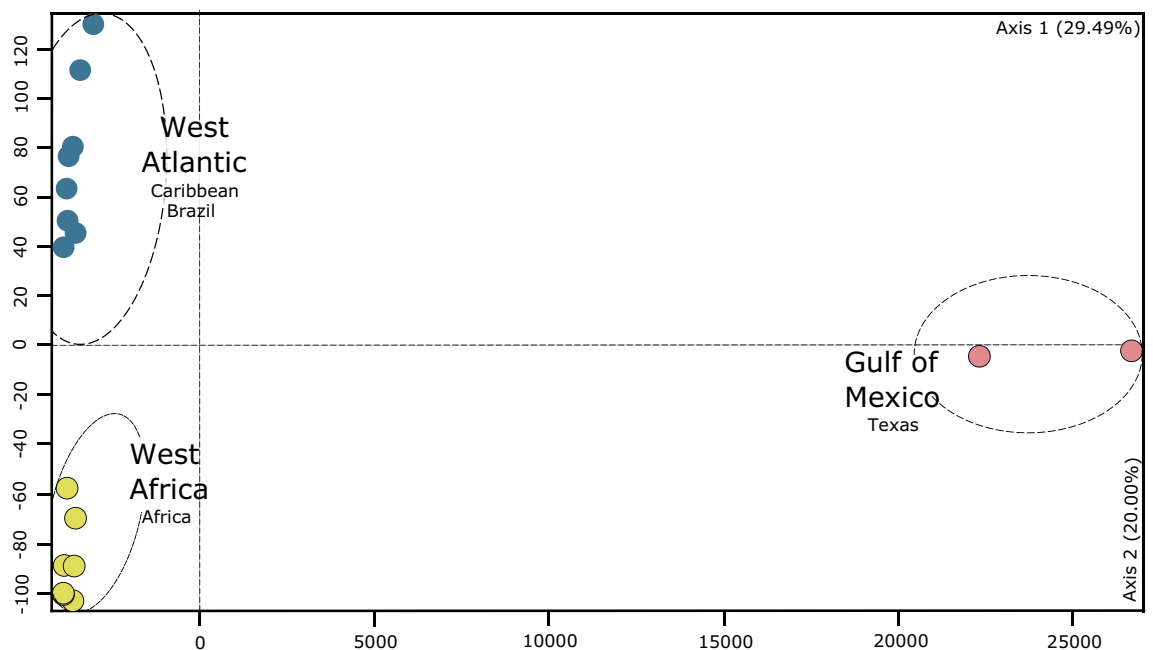


Figure 2. Genetic differentiation of populations of *Halodule wrightii* illustrated by factorial correspondence analysis (FCA). Distances in the plot are proportional to genetic divergence, illustrating that the divergence between the Gulf of Mexico and the other populations is much higher than that among any other populations.

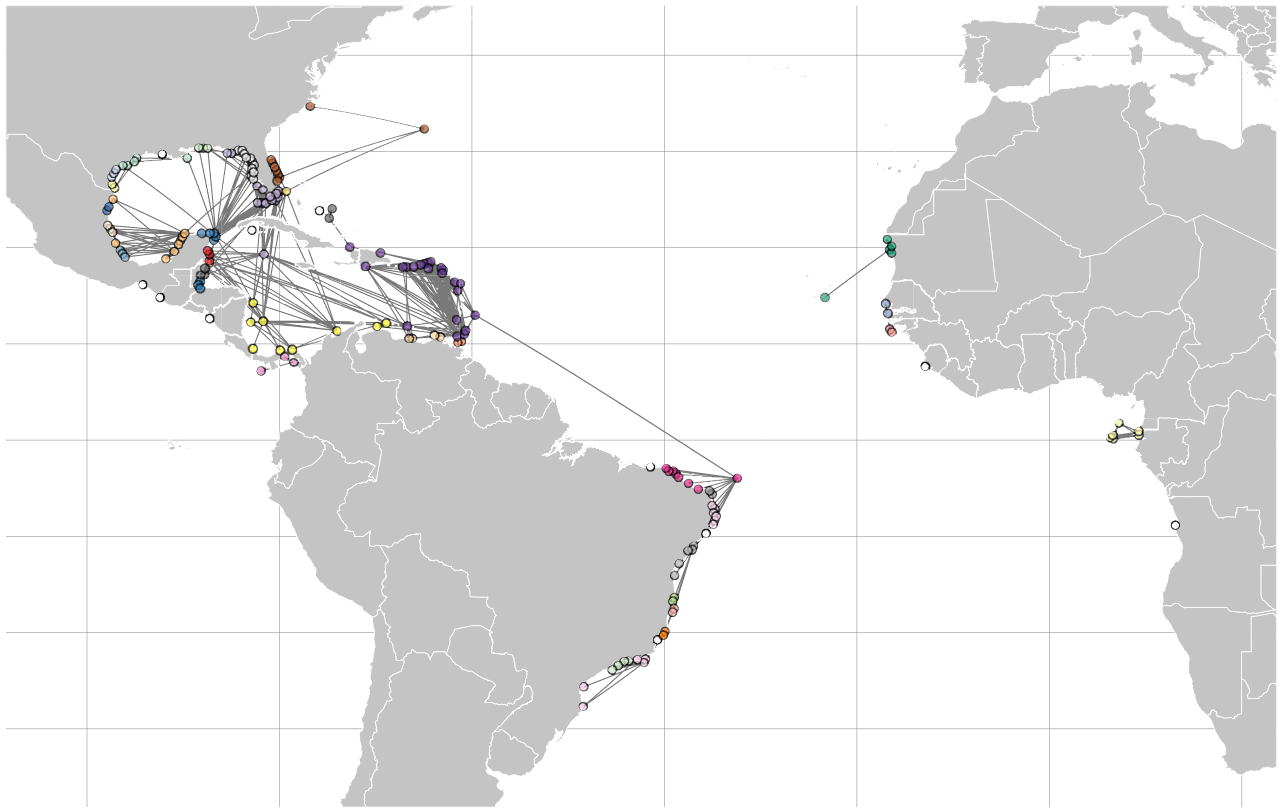


Figure 3. Potential connectivity among *Halodule wrightii* populations that have been reported in literature and databases (see Table S5), estimated from simulations of transport by ocean currents data. The figure was generated using R (version 4.2.2).

distance has been previously reported from biophysical model predictions, regardless of the dispersal potential of the species of interest. Additional studies using biophysical modelling to address the role of oceanographic connectivity to the distribution of, e.g., mangrove forests (high dispersal) and macroalgae (reduced dispersal) also showed null or very low predicted probability of connectivity across large water masses^{37–39}. Besides the null probability of transport by currents, distance and habitat discontinuity are likely to cause isolation between east and west Atlantic shores, as well as other physical processes, such as waves and direct forcing by winds, that are not accounted for in the HYCOM model. Predictions of long distance connectivity patterns through ocean currents benefit from knowledge of key life history traits such as seed or shoot viability times and establishment success⁴. Some of these details are unknown for *H. wrightii*, although there is information on such life traits for other seagrass species^{40,41}, few of which facilitate oceanic rafting such as positively buoyant seeds or fruits^{27,42}. However, *H. wrightii* has low seed dispersal potential because its seeds develop near the sediment at the base of the shoots and are negatively buoyant. Detached fragments may therefore be more likely to raft with ocean currents and they can survive floating in the water column up to 4 weeks³⁴, although the subsequent establishment success has not been determined. Yet the ability of seeds to remain in a dormancy stage for at least up to 46 months³³ supports the possibility that they might remain viable during occasional long-range dispersal, by either abiotic or biotic vectors.

Abiotic transport by ocean currents may not require the capacity to float if seeds become entangled on other floating rafts, such as those formed by *Sargassum*, that can cross the Atlantic Ocean in less than 2 weeks⁴³, a timeframe shorter than the viability of *H. wrightii* seeds and detached shoots. Rafting *Sargassum* have been recorded to move up the North Brazil current to the Caribbean and eastward towards western Africa^{44,45} and seagrass fragments have been found among *Sargassum* rafts^{46,47}. Moreover, migratory species like sea turtles⁴⁶ and seabirds⁴⁸ use *Sargassum* mats and may facilitate dispersal. Alternative or complementary to ocean currents, seagrass propagules may also be transported to suitable habitat by grazers that use these mats as foraging sites.

Despite its low abiotic dispersal potential, *H. wrightii* has a wide distribution with variable genetic differentiation, and among all tropical seagrasses of the western Atlantic it is the only species that has colonized the eastern side of this ocean, which suggests long-distance dispersal capabilities. This apparent paradox supports the hypothesis of an important role for biotic transportation of its seeds by grazers, as proposed in other studies⁸. Megaherbivores, including dugongs, green turtles, some birds and fish, use seagrass as one of their food sources, and promote dispersal of seagrass seeds⁴⁹. Successful seagrass endozoochory (i.e., seed dispersal by animals after passage through their guts) has been reported for fish, sea turtles and birds^{7,28,50,51}. The dispersal distances of such animals known to feed among seagrass meadows would allow long-ranging dispersal (e.g., 277 to 652 km in green turtles or 173 to 234 km by dugong²⁹). The reported digestion times for such herbivores, 6–7 days for

dugongs^{29,52} and 1–2 weeks for green turtles⁵³, are compatible with a moderate scale of long-range transport. Satellite tracking of green turtles in Atlantic Africa shows travel of 40 to > 1000 km between *H. wrightii* sites⁵⁴ and genetic data indicate cross Atlantic green turtle migration⁵⁵. Still, direct cross-Atlantic biotic dispersal seems unlikely or at least uncommon within average digestion time scales of grazers. Migratory routes of green turtles that feed on *H. wrightii*⁵⁶ include several mid-Atlantic islands that are nesting grounds⁵⁵, and could serve as occasional stepping-stones, although seagrass presence is mainly unknown in such islands⁵⁷. It is relevant that a green turtle found dead in Senegal had been nesting in Trindade Island 5 months before⁵⁸. All this information and our data indicate that transoceanic dispersal must be a very rare event, because the distances may be too vast to allow continuous gene flow even by biotic vectors, and there is a remote hypothesis that stepping stone islands could facilitate occasional dispersal of viable seeds. However, even if propagule dispersal is successful, post-settlement survival may be low, dependent on ending dispersal in a favorable environment³⁴.

Fine scale connectivity. On the western Atlantic coastline, the biophysical model revealed high probability of oceanographic connectivity between populations, but the genetic differentiation into distinct clusters showed that gene flow is restricted among them. Genetic data revealed isolation between Gulf of Mexico, Caribbean, and Brazil despite the high probability of transport by oceanographic currents, particularly between the Caribbean and Gulf of Mexico. However, no apparent gene flow barrier exists between the Caribbean and the Gulf of Mexico, in contrast with the genetic structure shown in our findings and in previous seagrass studies using microsatellites^{16,42}. This is suggesting that this genetic differentiation might be due to recolonization events that occurred in the Caribbean and Gulf of Mexico after the last glacial maximum⁵⁹.

The low probability of connectivity between the Caribbean and Brazil coincides with a biogeographical barrier created by the discharge from the deltas of the Amazon and Orinoco rivers, among others⁶⁰. This barrier, which runs for around 2300 km, separates the Brazilian coast from the Caribbean region and affects the genetic structure and dispersal of different marine animal organisms as fish or coral species^{61,62}. Yet, this barrier is not matched in our genetic data, that suggests gene flow among these regions. Thus, it is plausible to hypothesize that biotic dispersal might also play a role in increasing *H. wrightii* dispersal potential between these regions. Sea turtles and manatees are known to feed on *H. wrightii* meadows in these regions⁶³, and for some species, these areas are part of their migratory pathways⁶⁴. Moreover, our data also suggests a closer level of similarity between population of these two regions ($k = 7$ structure plot; Fig. 1). However, this result must be interpreted with caution as it might be attributed to homoplasy (i.e., individuals with different ancestries that mutate at a locus to the same allele). Homoplasy due to mutation is expected to occur for microsatellite markers due to their allele size and high mutation rates. Therefore, it is important to consider the potential for homoplasy when using microsatellites to infer relationships among individuals or populations.

Despite the restricted ocean-driven dispersal potential of *H. wrightii*, population genetic differentiation was non-significant across most populations in West Africa, indicating significant inter-population connectivity. The genetic structure of *H. wrightii* in Africa and in general, the genetic evidence indicating long-distance migration where it is not predicted, and high differentiation in some places at short distances, support the hypothesis of animal-mediated transportation⁸.

Genetic diversity. Genetic diversity contains the footprints of population stability, mating, and dispersal ecology, and is therefore used here as a proxy of the historical ecology of the populations. The higher genetic diversity of *H. wrightii* in the Gulf of Mexico supports previous reports^{18,35} suggesting the Gulf of Mexico should be a genetic hotspot for seagrass conservation. This suggests long-term stability without major bottlenecks.

Additionally, genetic diversity decreased in range-edge populations in both the east and west Atlantic (Angola and south Brazil, respectively), as reported for other seagrass, mangrove, and coral species. Low diversity at range edges is common^{11,65} and might be influenced by less suitable habitat increasing the reliance on clonal propagation, population bottlenecks or a relatively recent founder event during colonization of these regions from a larger more central population, resulting in genetic variation loss.

In comparison to other tropical seagrass species, the general microsatellite genetic diversity of *H. wrightii* was lower than *Enhalus acoroides*⁶⁶, *Thalassia testudinum*¹⁶ and *Zostera japonica*⁶⁷, but equivalent to *Halophila beccarii*⁶⁸, *Cymodocea serrulata*¹¹, *Syringodium filiforme*¹⁷ and *Zostera marina*⁶⁹. Across the *H. wrightii* populations, negative inbreeding coefficients (F_{IS}) were obtained, which is common in seagrass species^{16,18,70} and supports the hypothesis of selection favoring heterozygous individuals.

Genotypic richness. Although, *H. wrightii* has been able to achieve such a vast distribution, its dispersal success alone cannot ensure establishment, because that is also influenced by survival, viability, and growth capacity of plants originated from seeds and fragments. The balance between sexual reproduction and clonal growth can be represented by the genotypic richness. Despite the small sample sizes in some populations, our findings revealed that genotypic richness of *H. wrightii* is very variable among locations. Higher genotypic richness values were found in populations located at the center of the distribution. Higher genotypic diversity (i.e., a population with a larger number of distinct genotypes or clones) may enhance productivity and community recovery^{71,72}. Seagrass genotypic diversity can range from near monoclonal³⁶ to very high⁷³.

Reduced genotypic richness can be a common scenario for coastal populations found at the species' range edge^{36,74}. Indeed, clonal propagation was the dominant reproductive mode prevalent in southern marginal populations across east and west Atlantic, showing edge-of-range reduced sexual reproduction relative to populations at center of the species' range (geographic parthenogenesis)^{75,76}. Such a pattern could be attributed to limited population sizes, geographical isolation, climate oscillations, and poor seed dispersal from other source populations. However, the northern marginal population in West Africa (Banc d'Arguin, Mauritania), revealed a much

higher genotypic richness compared to other marginal populations. This may be due to the Banc d'Arguin's habitat suitability for seagrass species, as opposed to what would be predicted for a marginal range. The Banc d'Arguin is huge, protected, shallow, and nutrient-rich, with inputs of desert dust from the east and coastal upwelling from the northwest⁷⁷. Furthermore, this tropical seagrass species is projected to expand there with climate change⁷⁸.

Our findings showed that *H. wrightii* relies primarily on clonal propagation throughout the Caribbean region. Seagrasses reproduce both sexually and asexually, and their relative proportions may depend on several factors, including the level of disturbance⁷⁹. Specifically, events that destroy seagrass meadows create opportunities for rapid colonization and growth by new shoots or clonal fragments, faster than through seed production^{80,81}. There are reports of fast establishment of *H. wrightii* after a hurricane (e.g. hurricane Wilma in 2005⁸²). Thus, we hypothesize that the low genotypic richness found among Caribbean populations of *H. wrightii* could be due to past disturbances followed by fast colonization⁸³ through asexual reproduction of previously established or selected genotypes.

Overall, *H. wrightii* showed a low mean of genotypic richness ($R=0.38$), lower when compared to the mean genotypic richness found for other Atlantic seagrass species such as *Zostera noltii* ($R=0.85$)⁸⁴, *Zostera marina* ($R=0.61$)⁸⁵ or *Thalassia testudinum* ($R=0.55$)⁷³, but comparable to *Syringodium filiforme* ($R=0.37$)¹⁷. However, seagrass populations can show a wide range of genotypic richness, from high rates of sexual reproduction⁸⁶, to high levels of clonality⁷³ such as in *Z. noltei*⁸⁷ and also *H. wrightii*^{18,35}.

Concluding remarks

We found discordance between genetic differentiation and predicted ocean connectivity patterns, suggesting a role for other means of dispersal, such as the hypothesis of grazers mediating transport. This study underlines the importance of taking multi-pronged approaches to understand meta-population dynamics and connectivity. Using genetic data and modelling predictions enabled us to study the dispersal and connectivity patterns at different spatial scales while testing hypotheses of ocean currents mediating connectivity.

Genetic differentiation requires time for evolutionary processes to accumulate population differences. Therefore, although differentiation requires the lack of homogenizing gene flow, the absence of differentiation can be caused by either gene flow or insufficient time for differentiation among recently isolated populations, also designated as shared ancestral polymorphism. We used genetic methods as an empirical indicator of gene flow patterns, and biophysical modeling through propagule dispersion simulations to complement our findings. All these methods, like any other ways of assessing connectivity, have inherent drawbacks that should be highlighted. Genetic differentiation is affected by historical factors, such as founder events, bottlenecks, and variable population sizes. While this offers a significant advantage in discussing such processes, it also poses a limitation in addressing dispersal as the single cause of the patterns, given the simultaneous influence of these other processes. Additionally, the possibility of remaining ancestral polymorphism could create the false impression of contemporary gene flow even where populations are presently isolated. These complex demographic processes like population bottlenecks, founder events, or changes in population size over time can affect the genetic structure of populations in addition to gene flow. In our data interpretation, we therefore considered that there are other ecological factors besides ocean currents, such as habitat continuity and biological dispersal features, that may have an impact on gene flow, raising the hypotheses of influences of large flow of major rivers in breaking habitat continuity, and grazer-mediated transport.

Our results also shed light on the population genetic variability of an important tropical seagrass across its entire range. This new information for *H. wrightii* can be used to highlight areas where local protection is necessary or where populations could be managed in a metapopulation strategy. It could also be used as a baseline for future comparisons of the genetic diversity and differentiation of this species, motivating further research. The study also comprises a valuable and unique species distribution baseline confirmed by genetic tools, which may be particularly useful in future studies for example of cases where the validity of putative sister taxa to *H. wrightii* may be unclear.

Methods

Study area and sampling. The present study encompasses the distributional range of *H. wrightii* along the east and west Atlantic coastlines (Fig. 1C), which ranges from Mauritania (19.5° N, 16.5° W; Africa) to Angola (9.0° S, 13.0° E; Africa) and from Gulf of Mexico (27.7° N, 97.3° W; USA), including the Caribbean Sea, to Brazil (27.6° S, 48.4° W; Brazil). A variable number of shoots was collected with local permissions at 32 localities (Table S1) according with each country guidelines. Samples collected before 2018 were taken mostly from herbarium collections, resulting in distinct sample sizes. Following 2018, approximately 20 shoots were sampled in shallow and subtidal areas (up to 5 m depth depending on water turbidity) by keeping a minimum distance of approximately 1 m between each sampling unit. At some locations, only small patches were found, resulting in a lower sample size (Table S1). After field collection, all individual plants were dehydrated on silica gel drying crystals. Specimens were identified first by the local teams and later by EAS, voucher samples of the dried plants or their DNA were deposited at the herbarium of the University of Algarve (see Data availability statement).

DNA extraction and genotyping. Genomic DNA was extracted using the NucleoSpin Plant II Kit (Macherey–Nagel, Duren, Germany) following the protocol from the supplier. Individuals were genotyped for eight microsatellite markers (Table S6) developed for *H. wrightii*^{18,88}. Polymerase chain reactions (PCRs) were performed in a total volume of 15 µL, containing 1× Colorless GoTaq® Flexi Buffer (Promega, Madison, WI, USA), 2 mM MgCl₂ (2.5 mM), 10 mM forward and reverse primers, 0.2 mM of dNTP's, 1 U GoTaq G2 Flexi DNA Polymerase (Promega, USA) and 5 mL of diluted template DNA (several dilutions for different populations). PCR conditions included an initial denaturation step at 95°C for 5 min, followed by 30 cycles of 95°C for 30 s,

T_a for 30 s, extension at 72 °C for 30 s and a final extension at 72 °C for 10 min. Amplified fragments were separated on an ABI3130 XL automated DNA sequencer (Applied Biosystems, Waltham, MA, USA, at the CCMAR sequencing facility), with 0.25 mL GeneScan™ 500" LIZ Size Standard (Applied Biosystems, UK) plus 9.75 mL of Hi-Di formamide, after denaturation at 95 °C for 5 min. Alleles were manually scored using STRAND (Veterinary Genetics Laboratory, University of California, Davis; <http://www.vgl.ucdavis.edu/STRand>), and binned using the R package 'MsatAllele'⁸⁹. To minimize all ambiguities, a manual review of microsatellite amplification and scoring was conducted, and the final genotyping alleles for each sample were obtained after a double-check reading process to reduce scoring errors.

DNA statistical analyses. The software Micro-Checker 2.2.3⁹⁰ was used to check for null alleles to avoid bias in estimating genetic parameters. The package 'RClone'⁹¹ of R software v.3.6.2⁹² was used to assess clonality for all individuals, because seagrass can proliferate vegetatively and the number of shoots can represent duplicate genotypes from the same clone. To verify if individuals with the same number of multi-locus genotype (MLG) were true clones, P_{sex} was calculated, i.e., the probability of finding identical MLGs resulting from distinct sexual reproductive events⁹³. When P_{sex} threshold was below 0.01, the identical MLGs were considered the same clone (i.e., genet). Following previous theoretical assumptions⁹⁴ we estimated population genetic metrics with our dataset spited into (1) a ramet level dataset, that includes genetic information for all genotyped individuals, and (2) a genet level dataset, where only the genets were kept (after P_{sex} estimates). For the second set of data (genet-level), only unique genets per population were considered for genetic diversity analysis. The proportion of genets (G) found among the individuals sampled (N) was used to estimate genotypic diversity in each population, using the clonal richness (R) index, $R = (G - 1) / (N - 1)$, ranging from 0 (one single clone) to 1 (when all sampling units analyzed were from different genets).

Microsatellite genetic diversity was quantified for each population by estimating allele frequencies, mean standardized allelic richness ($\bar{A}$) adjusted for the minimum genet sample size, standardized number of private alleles ($P\bar{A}$), Nei's gene diversity (H_E), observed heterozygosity (H_O) and inbreeding coefficients (F_{IS}), using GENETIX 4.05⁹⁵. We have interpreted our results in the context of previous theoretical studies, with a particular focus on the distribution of F_{IS} values among loci and populations for both datasets. By comparing both, we aim to assess whether the clonal rates in populations result in differences in F_{IS} values^{96,97}. Also, by examining the distribution of F_{IS} values per locus per site, it may be possible to understand the extent to which asexual and sexual reproduction may be involved at a particular location. A factorial correspondence analysis (FCA) was performed to determine the genetic relationship between populations using GENETIX 4.05. To estimate the distribution of genets among genetic groups that minimize Hardy–Weinberg and linkage disequilibrium, a Bayesian assignment of genotypes to K groups was made using the program STRUCTURE⁹⁸. The value K was estimated from the mean log-likelihood for each K value and the ΔK statistic⁹⁹ to identify the optimal number of populations groups. This was analyzed for K ranging from 2 to 23 with ten replicates per value and a 50,000 burn-in followed by 500,000 MCMC replicates per iteration. All runs were performed in parallel on multiple cores using the R package 'ParallelStructure'¹⁰⁰. A discriminant analysis of principal components (DAPC) and a Principal component analysis (PCA) implemented in the R package adegenet 2.1.10¹⁰¹ were used to complement structure analysis. Genetic differentiation was estimated between sites (FST).

Biophysical modelling. Biophysical modeling based on simulations of propagule dispersion coupled with network analysis was used to estimate the connectivity potential of *H. wrightii*. The simulations used daily data of ocean currents assembled from the Hybrid Coordinate Ocean Model (HYCOM), a hindcast of high-resolution three-dimensional ocean velocity fields (regular 1/12-degree horizontal grid with 40 depth layers). This model can resolve key oceanographic processes such as oceanic fronts, eddies, meandering currents, and filaments because it integrates the effect of precipitation, wind stress, wind speed and heat. When hindcast data on ocean current direction and intensity is combined with biological features of pelagic viable time in biophysical modelling, the component of connectivity that is exclusively mediated by ocean currents can be predicted. This modelling approach was previously validated using demographic and genetic data for macroalgae, seagrasses, limpets, mussels, fish, echinoderms, and crustaceans^{102–104}.

Individual virtual particles were released on a daily basis (matching HYCOM temporal resolution) from source / sink sites, where the species is known to occur, spaced 1 km apart (spatial resolution of the simulation) over the course of a year. These particles simulate *H. wrightii* rafts strictly transported on the ocean surface, and as in other studies at large spatial scales^{102–104} no shape or density of rafting fragments is considered. Occurrence records describing the species distribution were compiled from the literature and biodiversity information facilities (OBIS and GBIF). The simulation encompassed locations distributed along the east and west Atlantic coastal shores. On the east Atlantic, the simulation included the west coast of Africa from Angola to Mauritania (~6250 km of coastlines from -10.0° to 21.5° latitude) and on the west Atlantic, from Florida to south Brazil (~13,000 km of coastlines from -30° to 28° latitude). A high-resolution polygon was used to define landmasses¹⁰⁵. Every hour of simulation, the model determined the position of all drifting rafts while fitting a bilinear interpolation estimate over the velocity fields to smooth ongoing trajectories. Rafts were permitted to float for up to 60 days (extreme propagule duration estimate). Rafts that arrived at a coastline or got lost in the open ocean (outside of the model domain) were excluded from the simulation. Trajectories were aggregated to build asymmetric matrices of pairwise probability of connectivity between source/sink sites, by dividing the number of virtual rafts released from site *i* that reached site *j*, by the total number of rafts released from site *i*. For the ten-year period 2008–2017, interannual variability was analysed by running individual simulations per year. The overall approach of the biophysical modelling is documented in¹⁰⁶ and the source code is openly available at: <http://github.com/jorgeassis/biophysicalModelling>.

Graph theory was used to generate networks that allow the visualization of connectivity patterns. The graph nodes (individual source / sink locations) and the strength of edges (probability of connectivity) were structured using a connectivity matrix based on a 10-year average of individual simulations. Stepping-stone probability estimates were determined using the graph, by using a product function over the probabilities of connectivity along the shortest paths between all pairs of sites, as found with Floyd–Warshall's algorithm, which minimises the sum of log-transformed probabilities. This approach aimed to capture all multigenerational potential connectivity across the study region, beyond the time frame considered in the biophysical simulations^{102–104,107}. Graph analyses were performed in R⁹², using the package igraph.

Data availability

The datasets presented in this are openly available in Figshare at: <https://figshare.com/s/3ed8c460b0f71559184a>.

Received: 30 August 2022; Accepted: 2 June 2023

Published online: 05 June 2023

References

1. Cowen, R. K., Gawarkiewicz, G., Pineda, J., Thorrold, S. R. & Werner, F. E. Population connectivity in marine systems an overview. *Oceanography* **20**, 14–21 (2007).
2. Cowen, R. K. & Sponaugle, S. Larval dispersal and marine population connectivity. *Ann. Rev. Mar. Sci.* **1**, 443–466 (2009).
3. Pineda, J., Hare, J. A. & Sponaugle, S. U. Larval transport and dispersal in the coastal ocean and consequences for population connectivity. *Oceanography* **20**, 22–39 (2007).
4. McMahon, K. *et al.* The movement ecology of seagrasses. *Proc. R. Soc. B Biol. Sci.* **281**, 1795 (2014).
5. Kinlan, B. P. & Gaines, S. D. Propagule dispersal in marine and terrestrial environments: A community perspective. *Ecology* **84**, 2007–2020 (2003).
6. Harris, P. T. 4—Biogeography, benthic ecology, and habitat classification schemes. in *Seafloor Geomorphology as Benthic Habitat* (eds. Harris, P. T. & Baker, E. K.). 61–91. <https://doi.org/10.1016/B978-0-12-385140-6.00004-9> (Elsevier, 2012).
7. Wu, K., Chen, C.-N.N. & Soong, K. Long distance dispersal potential of two seagrasses *Thalassia hemprichii* and *Halophila ovalis*. *PLoS ONE* **11**, e0156585 (2016).
8. Tavares, A. I. *et al.* Seagrass connectivity on the west coast of Africa supports the hypothesis of grazer-mediated seed dispersal. *Front. Mar. Sci.* **852**, 1 (2022).
9. Kendrick, G. A. *et al.* Demographic and genetic connectivity: The role and consequences of reproduction, dispersal and recruitment in seagrasses. *Biol. Rev.* **92**, 921–938 (2017).
10. Palumbi, S. Population genetics, demographic connectivity, and the design of marine reserves. *Ecol. Appl.* **13**, 146–158 (2003).
11. Arriegado, D. M. *et al.* Genetic diversity and structure of the tropical seagrass *Cymodocea serrulata* spanning its central diversity hotspot and range edge. *Aquat. Ecol.* **49**, 357–372 (2015).
12. Sinclair, E. A. *et al.* Seeds in motion: Genetic assignment and hydrodynamic models demonstrate concordant patterns of seagrass dispersal. *Mol. Ecol.* **27**, 5019–5034 (2018).
13. Triest, L., Sierens, T., Menemenlis, D. & Van der Stocken, T. Inferring connectivity range in submerged aquatic populations (*Ruppia* L.) along european coastal lagoons from genetic imprint and simulated dispersal trajectories. *Front. Plant Sci.* **9**, 806 (2018).
14. Short, F., Carruthers, T., Dennison, W. & Waycott, M. Global seagrass distribution and diversity: A bioregional model. *J. Exp. Mar. Bio. Ecol.* **350**, 3–20 (2007).
15. Jahnke, M. *et al.* Population genetic structure and connectivity of the seagrass *Thalassia hemprichii* in the Western Indian Ocean is influenced by predominant ocean currents. *Ecol. Evol.* **9**, 8953–8964 (2019).
16. van Dijk, K., Bricker, E., van Tussenbroek, B. I. & Waycott, M. Range-wide population genetic structure of the Caribbean marine angiosperm *Thalassia testudinum*. *Ecol. Evol.* **8**, 9478–9490 (2018).
17. Bijak, A. L., van Dijk, K. & Waycott, M. Population structure and gene flow of the tropical seagrass, *Syringodium filiforme*, in the Florida keys and subtropical Atlantic region. *PLoS ONE* **13**, e0203644 (2018).
18. Larkin, P. D., Maloney, T. J., Rubiano-Rincon, S. & Barrett, M. M. A map-based approach to assessing genetic diversity, structure, and connectivity in the seagrass *Halodule wrightii*. *Mar. Ecol. Prog. Ser.* **567**, 95–107 (2017).
19. Short, F. T. *et al.* *Seagrasses. The Wetland Book: II: Distribution, Description and Conservation*. (Springer, 2016).
20. Green, E. P., Short, F. T. & Frederick, T. *World Atlas of Seagrasses*. (University of California Press, 2003).
21. Larkum, A. W. D., Orth, R. J. & Duarte, C. M. *Seagrasses: Biology, Ecology and Conservation*. 1–691. <https://doi.org/10.1007/978-1-4020-2983-7> (2006).
22. Nordlund, L. M. *et al.* Seagrass ecosystem services—What's next?. *Mar. Pollut. Bull.* **134**, 145–151 (2018).
23. Waycott, M. *et al.* Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proc. Natl. Acad. Sci.* **106**, 12377–12381 (2009).
24. Micheli, F., Bishop, M. J., Peterson, C. H. & Rivera, J. Alteration of seagrass species composition and function over two decades. *Ecol. Monogr.* **78**, 225–244 (2008).
25. Jordà, G., Marbà, N. & Duarte, C. M. Mediterranean seagrass vulnerable to regional climate warming. *Nat. Clim. Change* **2**, 821–824 (2012).
26. Ackerman, J. D. Sexual reproduction of seagrasses: Pollination in the marine context. in *Seagrasses: Biology, Ecology and Conservation*. 89–109 (Springer, 2007).
27. Ruiz-Montoya, L., Lowe, R. J. & Kendrick, G. A. Contemporary connectivity is sustained by wind and current-driven seed dispersal among seagrass meadows. *Mov. Ecol.* **3**, 1–14 (2015).
28. Sumoski, S. E. & Orth, R. J. Biotic dispersal in eelgrass *Zostera marina*. *Mar. Ecol. Prog. Ser.* **471**, 1–10 (2012).
29. Tol, S. J. *et al.* Long distance biotic dispersal of tropical seagrass seeds by marine mega-herbivores. *Sci. Rep.* **7**, 1–8 (2017).
30. Schupp, E. W. & Fuentes, M. Spatial patterns of seed dispersal and the unification of plant population ecology. *Ecoscience* **2**, 267–275 (1995).
31. Den Hartog, C. & Kuo, J. Taxonomy and biogeography of seagrasses. in *Seagrasses: Biology, Ecology and Conservation*. 1–23 (Springer, 2007).
32. Darnell, K. M., Booth, D. M., Koch, E. W. & Dunton, K. H. The interactive effects of water flow and reproductive strategies on seed and seedling dispersal along the substrate in two sub-tropical seagrass species. *J. Exp. Mar. Bio. Ecol.* **471**, 30–40 (2015).
33. McMillan, C. Seed reserves and seed germination for two seagrasses, *Halodule wrightii* and *Syringodium filiforme*, from the western Atlantic. *Aquat. Bot.* **11**, 279–296 (1981).
34. Hall, L. M., Hanisak, M. D. & Virnstein, R. W. Fragments of the seagrasses *Halodule wrightii* and *Halophila johnsonii* as potential recruits in Indian River Lagoon, Florida. *Mar. Ecol. Prog. Ser.* **310**, 109–117 (2006).

35. Digiantonio, G., Blum, L., McGlathery, K. & Waycott, M. Genetic mosaicism and population connectivity of edge-of-range *Halodule wrightii* populations. *Aquat. Bot.* **161**, 103161 (2020).
36. Alberto, F. *et al.* Genetic differentiation and secondary contact zone in the seagrass *Cymodocea nodosa* across the Mediterranean-Atlantic transition region. *J. Biogeogr.* **35**, 1279–1294 (2008).
37. Assis, J. *et al.* Ocean currents shape the genetic structure of a kelp in southwestern Africa. *J. Biogeogr.* **49**, 822–835 (2022).
38. Assis, J. *et al.* Past climate changes and strong oceanographic barriers structured low-latitude genetic relics for the golden kelp *Laminaria ochroleuca*. *J. Biogeogr.* **45**, 2326–2336 (2018).
39. Gouvêa, L.P., Fragkopoulou, Cavanaugh, K., E., Serrão, E. A., Araújo, M.B., Costello, M.J., Taraneh, W., Assis, J. Oceanographic connectivity explains the intraspecific diversity of mangrove forests at global scales. *Proc. Natl. Acad. Sci.* (2023) (**in press**).
40. Harwell, M. C. & Orth, R. J. Long-distance dispersal potential in a marine macrophyte. *Ecology* **83**, 3319–3330 (2002).
41. van Tussenbroek, B. I. *et al.* The biology of *Thalassia*: paradigms and recent advances in research. *Seagrasses Biol. Ecol. Conserv.* **51**, 409–439 (2007).
42. van Dijk, J. K., van Tussenbroek, B. I., Jiménez-Durán, K., Márquez-Guzmán, G. J. & Ouborg, J. High levels of gene flow and low population genetic structure related to high dispersal potential of a tropical marine angiosperm. *Mar. Ecol. Prog. Ser.* **390**, 67–77 (2009).
43. Renner, S. Plant dispersal across the tropical Atlantic by wind and sea currents. *Int. J. Plant Sci.* **165**, S23–S33 (2004).
44. Putman, N. F. *et al.* Simulating transport pathways of pelagic Sargassum from the Equatorial Atlantic into the Caribbean Sea. *Prog. Oceanogr.* **165**, 205–214 (2018).
45. Wang, M. *et al.* The great Atlantic Sargassum belt. *Science* (80-) **365**, 83–87 (2019).
46. Witherington, B., Hiram, S. & Hardy, R. Young sea turtles of the pelagic Sargassum-dominated drift community: Habitat use, population density, and threats. *Mar. Ecol. Prog. Ser.* **463**, 1–22 (2012).
47. Salter, M. A., Rodríguez-Martínez, R. E., Álvarez-Filip, L., Jordán-Dahlgren, E. & Perry, C. T. Pelagic Sargassum as an emerging vector of high rate carbonate sediment import to tropical Atlantic coastlines. *Glob. Planet. Change* **195**, 103332 (2020).
48. Moser, M. L. & Lee, D. S. Foraging over Sargassum by western North Atlantic seabirds. *Wilson J. Ornithol.* **124**, 66–72 (2012).
49. Heck, K. L. & Valentine, J. F. Plant-herbivore interactions in seagrass meadows. *J. Exp. Mar. Bio Ecol.* **330**, 420–436 (2006).
50. Figuerola, J., Green, A. J. & Santamaría, L. Comparative dispersal effectiveness of wigeongrass seeds by waterfowl wintering in south-west Spain: Quantitative and qualitative aspects. *J. Ecol.* **90**, 989–1001 (2002).
51. Tol, S. J., Jarvis, J. C., York, P. H., Congdon, B. C. & Coles, R. G. Mutualistic relationships in marine angiosperms: Enhanced germination of seeds by mega-herbivores. *Biotropica* **53**, 1535–1545 (2021).
52. Lanyon, J. M. & Marsh, H. Digesta passage times in the dugong. *Aust. J. Zool.* **43**, 119–127 (1995).
53. Brand, S. J., Lanyon, J. M. & Limpus, C. J. Digesta composition and retention times in wild immature green turtles, *Chelonia mydas*: A preliminary investigation. *Mar. Freshw. Res.* **50**, 145–147 (1999).
54. Patrício, A. R. *et al.* Green Turtles Highlight Connectivity Across a Regional Marine Protected Area Network in West Africa. *Front. Mar. Sci.* **9**, 1 (2022).
55. Patrício, A. R. *et al.* Dispersal of green turtles from Africa's largest rookery assessed through genetic markers. *Mar. Ecol. Prog. Ser.* **569**, 215–225 (2017).
56. Hernández, A. L. M. & van Tussenbroek, B. I. Patch dynamics and species shifts in seagrass communities under moderate and high grazing pressure by green sea turtles. *Mar. Ecol. Prog. Ser.* **517**, 143–157 (2014).
57. Tsiamis, K. *et al.* Marine benthic algal flora of Ascension Island, South Atlantic. *J. Mar. Biol. Assoc. UK* **97**, 681–688 (2017).
58. Marcovaldi, M. A. *et al.* Recaptures of tagged turtles from nesting and feeding grounds protected by Projeto Tamar-Ibama, Brazil. in *Proceedings of the 19th Annual Symposium on Sea Turtle Biological Conservation NOAA Technical Memorandum NMFS-SEFSC*. Vol. 443. 164–166 (2000).
59. Avise, J. C. Molecular population structure and the biogeographic history of a regional fauna: A case history with lessons for conservation biology. *Oikos* **63**, 62–76 (1992).
60. Briggs, J. C. *Global Biogeography* (Elsevier, 1995).
61. GiachiniTosetto, E., Bertrand, A., Neumann-Leitão, S. & Nogueira Júnior, M. The Amazon River plume, a barrier to animal dispersal in the Western Tropical Atlantic. *Sci. Rep.* **12**, 537 (2022).
62. Volk, D. R., Konvalina, J. D., Floeter, S. R., Ferreira, C. E. L. & Hoffman, E. A. Going against the flow: Barriers to gene flow impact patterns of connectivity in cryptic coral reef gobies throughout the western Atlantic. *J. Biogeogr.* **48**, 427–439 (2021).
63. de Meirelles, A. C. O., Carvalho, V. L. & Marmontel, M. West Indian manatee *Trichechus manatus* in South America: Distribution, ecology and health assessment. in *Advances in Marine Vertebrate Research in Latin America*. 263–291 (Springer, 2018).
64. Chambault, P. *et al.* Connecting paths between juvenile and adult habitats in the Atlantic green turtle using genetics and satellite tracking. *Ecol. Evol.* **8**, 12790–12802 (2018).
65. Arnaud-Haond, S. *et al.* Genetic structure at range edge: Low diversity and high inbreeding in Southeast Asian mangrove (*Avicennia marina*) populations. *Mol. Ecol.* **15**, 3515–3525 (2006).
66. Nguyen, X.-V. & Jutta, P. Assessment by microsatellite analysis of genetic diversity and population structure of *Enhalus acoroides* from the coast of Khanh Hoa Province, Vietnam. *Acta Oceanol. Sin.* **38**, 144–150 (2019).
67. Jiang, K., Tsang, P.-K.E., Xu, N.-N. & Chen, X.-Y. High genetic diversity and strong differentiation in dramatically fluctuating populations of *Zostera japonica* (Zosteraceae): Implication for conservation. *J. Plant Ecol.* **11**, 789–797 (2018).
68. Phan, T. T. H., De Raeymaeker, M., Luong, Q. D. & Triest, L. Clonal and genetic diversity of the threatened seagrass *Halophila beccarii* in a tropical lagoon: resilience through short distance dispersal. *Aquat. Bot.* **142**, 96–104 (2017).
69. Tanaka, N., Demise, T., Ishii, M., Shoji, Y. & Nakaoka, M. Genetic structure and gene flow of eelgrass *Zostera marina* populations in Tokyo Bay, Japan: Implications for their restoration. *Mar. Biol.* **158**, 871–882 (2011).
70. Yu, S. *et al.* Population genetic structure of the threatened tropical seagrass *Enhalus acoroides* in Hainan Island. *China. Aquat. Bot.* **150**, 64–70 (2018).
71. Reusch, T. B. H., Ehlers, A., Hämmerli, A. & Worm, B. Ecosystem recovery after climatic extremes enhanced by genotypic diversity. *Proc. Natl. Acad. Sci.* **102**, 2826–2831 (2005).
72. Crutsinger, G. M. *et al.* Plant genotypic diversity predicts community structure and governs an ecosystem process. *Science* (80-) **313**, 966–968 (2006).
73. Van Dijk, J. K. & van Tussenbroek, B. I. Clonal diversity and structure related to habitat of the marine angiosperm *Thalassia testudinum* along the Atlantic coast of Mexico. *Aquat. Bot.* **92**, 63–69 (2010).
74. Bricker, E., Calladine, A., Virnstein, R. & Waycott, M. Mega clonality in an aquatic plant—A potential survival strategy in a changing environment. *Front. Plant Sci.* **9**, 435 (2018).
75. Eckert, C. G., Samis, K. E. & Loughheed, S. C. Genetic variation across species' geographical ranges: The central-marginal hypothesis and beyond. *Mol. Ecol.* **17**, 1170–1188 (2008).
76. Tilquin, A. & Kokko, H. What does the geography of parthenogenesis teach us about sex?. *Philos. Trans. R. Soc. B Biol. Sci.* **371**, 20150538 (2016).
77. Araújo, A. & Campredon, P. Banc d'Arguin (Mauritania). in *The Wetland Book: II: Distribution, Description, and Conservation*. 1319–1332 (Springer, 2016).
78. Chefaoui, R. M. *et al.* Predicted regime shift in the seagrass ecosystem of the Gulf of Arguin driven by climate change. *Glob. Ecol. Conserv.* **32**, e01890 (2021).

79. Becheler, R., Diekmann, O., Hily, C., Moalic, Y. & Arnaud-Haond, S. The concept of population in clonal organisms: Mosaics of temporally colonized patches are forming highly diverse meadows of *Zostera marina* in Brittany. *Mol. Ecol.* **19**, 2394–2407 (2010).
80. Michot, T. C. *et al.* *Impacts of Hurricane Mitch on Seagrass Beds and Associated Shallow Reef Communities Along the Caribbean Coast of Honduras and Guatemala*. (US Department of the Interior, US Geological Survey, 2002).
81. Byron, D. & Heck, K. L. Hurricane effects on seagrasses along Alabama's Gulf Coast. *Estuaries Coasts* **29**, 939–942 (2006).
82. van Tussenbroek, B. I., Barba Santos, M. G., Van Dijk, J. K., Sanabria Alcaraz, S. N. M. & Téllez Calderón, M. L. Selective elimination of rooted plants from a tropical seagrass bed in a back-reef lagoon: A hypothesis tested by hurricane Wilma (2005). *J. Coast. Res.* **24**, 278–281 (2008).
83. Gallegos, M. E., Merino, M., Rodriguez, A., Marbà, N. & Duarte, C. M. Growth patterns and demography of pioneer Caribbean seagrasses *Halodule wrightii* and *Syringodium filiforme*. *Mar. Ecol. Prog. Ser.* **109**, 99–104 (1994).
84. Elso, M. Z., Manent, P., Luque, A., Ramdani, M. & Robaina, R. R. Genetic description and remote sensing techniques as management tools for *Zostera noltii* seagrass populations along the Atlantic Moroccan coast. *J. Coast. Res.* **33**, 78–87 (2017).
85. Alotaibi, N. M., Kenyon, E. J., Cook, K. J., Börger, L. & Bull, J. C. Low genotypic diversity and long-term ecological decline in a spatially structured seagrass population. *Sci. Rep.* **9**, 1–11 (2019).
86. Campanella, J. J. *et al.* Clonal diversity and connectedness of turtle grass (*Thalassia testudinum*) populations in a UNESCO biosphere reserve. *Aquat. Bot.* **123**, 76–82 (2015).
87. Jahnke, M. *et al.* Patterns and mechanisms of dispersal in a keystone seagrass species. *Mar. Environ. Res.* **117**, 54–62 (2016).
88. Larkin, P., Schonacher, T., Barrett, M. & Paturzzio, M. Development and characterization of microsatellite markers for the seagrass *Halodule wrightii*. *Conserv. Genet. Resour.* **4**, 511–513 (2012).
89. Alberto, F. MsatAllele_1.0: An R package to visualize the binning of microsatellite alleles. *J. Hered.* **100**, 394–397 (2009).
90. Van Oosterhout, C., Hutchinson, W. F., Wills, D. P. M. & Shipley, P. MICRO-CHECKER: Software for identifying and correcting genotyping errors in microsatellite data. *Mol. Ecol. Notes* **4**, 535–538 (2004).
91. Bailleul, D., Stoeckel, S. & Arnaud-Haond, S. RClone: A package to identify multilocus clonal lineages and handle clonal data sets in R. *Methods Ecol. Evol.* **7**, 966–970 (2016).
92. R Development Core Team. *R: A Language and Environment for Statistical Computing*. (R Foundation for Statistical Computing, 2021).
93. Arnaud-Haond, S., Duarte, C. M., Alberto, F. & Serrão, E. A. Standardizing methods to address clonality in population studies. *Mol. Ecol.* **16**, 5115–5139 (2007).
94. Stoeckel, S., Porro, B. & Arnaud-Haond, S. The discernible and hidden effects of clonality on the genotypic and genetic states of populations: Improving our estimation of clonal rates. *Mol. Ecol. Resour.* **21**, 1068–1084 (2021).
95. Belkhir, K., Borsa, P., Chikhi, L., Raufaste, N. & Bonhomme, F. GENETIX 4.05, Logiciel Sous Windows TM Pour la Génétique des Populations. (1996).
96. Stoeckel, S. & Masson, J.-P. The exact distributions of FIS under partial asexuality in small finite populations with mutation. *PLoS ONE* **9**, e85228 (2014).
97. Reichel, K., Masson, J.-P., Malrieu, F., Arnaud-Haond, S. & Stoeckel, S. Rare sex or out of reach equilibrium? The dynamics of FIS in partially clonal organisms. *BMC Genet.* **17**, 1–16 (2016).
98. Falush, D., Stephens, M. & Pritchard, J. K. Inference of population structure using multilocus genotype data: Linked loci and correlated allele frequencies. *Genetics* **164**, 1567–1587 (2003).
99. Earl, D. A. STRUCTURE HARVESTER: A website and program for visualizing STRUCTURE output and implementing the Evanno method. *Conserv. Genet. Resour.* **4**, 359–361 (2012).
100. Besnier, F. & Glover, K. A. ParallelStructure: AR package to distribute parallel runs of the population genetics program STRUCTURE on multi-core computers. *PLoS One* **8**, 70651 (2013).
101. Jombart, T. *et al.* Package 'adegenet'. *GitHub Repositories*. <https://github.com/thibautjombart/adegenet>. Accessed 11 Nov 2021 (2018).
102. Assis, J. *et al.* Oceanographic conditions limit the spread of a marine invader along southern African shores. *PLoS One* **10**, e128124 (2015).
103. Buonomo, R. *et al.* Habitat continuity and stepping-stone oceanographic distances explain population genetic connectivity of the brown alga *Cystoseira amentacea*. *Mol. Ecol.* **26**, 766–780 (2017).
104. Nicastro, K. R. *et al.* Congruence between fine-scale genetic breaks and dispersal potential in an estuarine seaweed across multiple transition zones. *ICES J. Mar. Sci.* **77**, 371–378 (2020).
105. Haklay, M. & Weber, P. Openstreetmap: User-generated street maps. *IEEE Pervasive Comput.* **7**, 12–18 (2008).
106. Assis, J. *et al.* Weak biodiversity connectivity in the European network of no-take marine protected areas. *Sci. Total Environ.* **773**, 145664 (2021).
107. Ntuli, N. N. *et al.* Rejection of the genetic implications of the “abundant centre hypothesis” in marine mussels. *Sci. Rep.* **10**, 1–12 (2020).

Acknowledgements

We thank Marta Valente (CCMAR sequencing laboratory) for genotyping samples, Peter Wirtz and Paulo Catry for field sampling and the local staff from all the institutions and countries involved, including PNBA, IBAP and St. Eustatius, for the technical and logistical help. All the study protocol was performed in accordance with relevant national and international guidelines. Samples were collected under license and logistic support of the local authorities at each country during missions of the projects involved. This work was funded by Portuguese National Funds from FCT—Foundation for Science and Technology, through UIDB/04326/2020, UIDP/04326/2020, LA/P/0101/2020, PTDC/BIA-CBI/6515/2020, and fellowships SFRH/BD/138182/2018, SFRH/BSAB/150485/2019, the transitional norm-DL57/2016/CP1361/CT0035, the Individual Call to Scientific Employment Stimulus 2022.00861.CEECIND, project MARAFRICA: AGA-KHAN/540316524/2019, and by a Pew Marine Fellowship to EAS. The sampling collections were supported by projects LuandaWaterFront AGKN-FCT-333191101, by the MAVA Foundation projects ResilienSEA, "Consolidation of sea turtle conservation at the Bijagós, Guinea-Bissau" granted to the Instituto da Biodiversidade e das Áreas Protegidas da Guiné-Bissau (IBAP), "PNBA-site emblématique pour les tortues" granted to the National Park of the Banc d'Arguin, project "Survie des Tortues Marines" PRCM/STM POOOA4/OA9 by PRCM (Partenariat Régional pour la Conservation de la zone côtière et Marine en Afrique de l'Ouest), EU-H20202 854248 (Tropibio), EU-BiodivERsA program, Programa de Pós-Graduação em Ciência para o Desenvolvimento (Fundação Calouste Gulbenkian), FCT scholarship attributed to RLF (SFRH/BD/73947/2010), the Scientific Council of the National Park of the Banc d'Arguin (funded by BACOMAB) and by the BLUE ROUTE project (PT-INNOVATION-0072—Preparing the new OCEAN economy 2030: the blue route of discovery). This study received support from the Portuguese

node of EMBRC-ERIC, specifically EMBRC.PT ALG-01-0145-FEDER-022121 and funding from the European Union's Horizon 2020 research and innovation programme through project Assemble Plus under grant agreement No. 8329.

Author contributions

All authors contributed to the conceptualization of the study and approved the submitted version. E.S., A.T., J.A., and G.P. conceived and designed the study. Laboratory genotyping work was carried out by A.T. The genetic data were analyzed by A.T. and the biophysical modelling was performed by J.A. The manuscript was written by A.T., E.S., and J.A., with all authors contributing to drafts.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1038/s41598-023-36367-y>.

Correspondence and requests for materials should be addressed to A.I.T.

Reprints and permissions information is available at www.nature.com/reprints.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.



Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

© The Author(s) 2023, corrected publication 2023