Oceanographic connectivity explains the intra-specific diversity of mangrove forests at global scales

Lidiane P. Gouvêa[a,1] (ID), Eliza Fragkopoulou[a] (ID), Kyle Cavanaugh[b], Ester A. Serrão[a] (ID), Miguel B. Araújo[c,d] (ID), Mark John Costello[e] (ID), E. H. Taraneh Westergerling[f,g] (ID), and Jorge Assis[a,e,1] (ID)

The distribution of mangrove intra-specific biodiversity can be structured by historical demographic processes that enhance or limit effective population sizes. Oceanographic connectivity (OC) may further structure intra-specific biodiversity by preserving or diluting the genetic signatures of historical changes. Despite its relevance for biogeography and evolution, the role of oceanographic connectivity in structuring the distribution of mangrove's genetic diversity has not been addressed at global scale. Here we ask whether connectivity mediated by ocean currents explains the intra-specific diversity of mangroves. A comprehensive dataset of population genetic differentiation was compiled from the literature. Multigenerational connectivity and population centrality indices were estimated with biophysical modeling coupled with network analyses. The variability explained in genetic differentiation was tested with competitive regression models built upon classical isolation-by-distance (IBD) models considering geographic distance. We show that oceanographic connectivity can explain the genetic differentiation of mangrove populations regardless of the species, region, and genetic marker (significant regression models in 95% of cases, with an average R-square of 0.44 ± 0.23 and Person's correlation of 0.65 ± 0.17), systematically improving IBD models. Centrality indices, providing information on important stepping-stone sites between biogeographic regions, were also important in explaining differentiation (R-square improvement of 0.06 ± 0.07, up to 0.42). We further show that ocean currents produce skewed dispersal kernels for mangroves, highlighting the role of rare long-distance dispersal events responsible for historical settlements. Overall, we demonstrate the role of oceanographic connectivity in structuring mangrove intra-specific diversity. Our findings are critical for mangroves' biogeography and evolution, but also for management strategies considering climate change and genetic biodiversity conservation.

mangrove forests | genetic differentiation | ocean currents | oceanographic connectivity | biophysical modelling

The distribution of intra-specific genetic diversity can be structured by demographic processes that enhance or limit effective population sizes (1, 2). For instance, historical climate change fluctuations and conservation strategies can create refugial areas of long-term persistence where populations were allowed to accumulate higher and rarer genetic diversity (3), compared to where unsuitable climatic conditions or human-induced disturbances led to bottlenecks and drift (4, 5). Population connectivity can further structure the distribution of intra-specific diversity. For coastal species like mangrove forests, the regional patterns of oceanographic currents can restrict dispersal and gene flow, leading to the formation of highly structured populations that hold the signatures left by historical changes (6).

Mangroves are halophytic plants that form ecosystems with exceptionally high ecological and socioeconomic value (7) across tropical and subtropical coastlines, with distribution ranges typically restricted by low temperatures and reduced precipitation (8). The dispersal ecology of the approximately 80 species of mangroves (18 plant families) includes buoyant seeds, seedlings, and fruits (hereafter referred to as propagules; (9) that exhibit contrasting floating periods, from several days to months (10), which can strongly determine the scales of population connectivity and gene flow. However, the role of oceanographic connectivity in the distribution of intra-specific diversity of mangroves has not been well defined. Most studies to date have used isolation by distance models (11, 12) under the major assumption of higher genetic differentiation with increasing geographic distance (13), or illustrative maps of ocean currents to describe population connectivity (14). These approaches can't capture the complexity of tidal, topographic, and wind-driven oceanographic processes (15), which produce asymmetric (directional) gene flow between populations (14) with high temporal and spatial variability. Additionally, the relationship between ocean currents

Significance

Among the multiple drivers shaping the intra-specific diversity (i.e., genetic diversity) of mangrove forests, the role of connectivity driven by ocean currents has not been well defined at global scales, despite its potential role in regulating population gene flow. Using biophysical modeling and empirical genetic data, we show that oceanographic connectivity can explain population genetic differentiation in mangroves, regardless of the species, region, and genetic marker, overcoming classical approaches based on geographic distance. Ocean currents can either create barriers that isolate populations and increase differentiation levels or promote long-distance dispersal responsible for first settlements and broadscale biogeographical patterns. These findings are relevant for mangroves' biogeography and evolution, as well as management strategies considering climate change and genetic biodiversity conservation.

[1]To whom correspondence may be addressed. Email: lidi_pel@hotmail.com or jorgemfa@gmail.com.

and population dispersal is not linear, but rather positively skewed (16, 17), which is in line with mangrove's strong genetic structure found across species' distribution ranges (18).

More realistic estimates of oceanographic connectivity can be produced with biophysical modeling and Lagrangian simulations (17). These frameworks, mimicking the dispersal behavior of propagules advected by ocean currents, can provide estimates of connectivity (10) that generally match the expectations of independent genetic data (17, 19, 20). Studies on mangroves are still underrepresented, with oceanographic connectivity only estimated at regional scales and considering few species, namely *Rhizophora mucronata* (14), *R. mangle* (12, 21), *Laguncularia racemose* and *R. racemosa* (12, 21, 22), and *Avicennia* species (23, 24), precluding broad conclusions on the subject. One additional study using biophysical modeling provided key insights on the global dispersal and connectivity patterns of mangroves, yet it did not consider independent data to support conclusions (e.g., population genetic differentiation data and species-specific floating periods) (10).

We aim to fill this knowledge gap by asking whether oceanographic connectivity shapes the intra-specific diversity of mangrove forests at global scales. Simulations of oceanographic connectivity were performed with a biophysical model running across the global distribution of mangroves and tested against empirical genetic data compiled from the available literature. Overall, we hypothesize that oceanographic connectivity can better explain population genetic differentiation compared to more simplistic approaches based on isolation-by-distance (IBD) models, as previously found for other ecological groups (17, 25). We integrated graph theory (i.e., network analyses) to consider asymmetric multigenerational stepping-stone connectivity (17), and for the first time, centrality indices accounting for the effect of particular populations promoting gene flow across large water masses. Our results, supporting the role of oceanographic connectivity in mangrove's diversity, have high relevance for biogeography, evolution, and climate change ecology (18), as well as for the new conservation targets of the post-2020 Global Biodiversity framework, which endorses the conservation of genetic diversity of wild populations, as well as the establishment of well-connected networks of protected areas (26, 27).

Results

The systematic literature search listed 540 potential studies, from which 43 reported genetic differentiation data for mangroves. These studies resulted in 59 datasets covering 20 species of the most common genera (*Avicennia, Bruguiera, Sonneratia*, and *Rhizophora*; *SI Appendix*, Table S1) and life strategies, i.e., viviparous and cryptoviviparous (9), 7 molecular markers, and 691 populations (*SI Appendix*, Table S1) spanning across the known distribution of mangrove forests (i.e., Indo-West Pacific and Atlantic-East Pacific; Fig. 1). On average, 11.71 ± 7.16 populations were sampled per study (range between 4 and 38 populations), with an average genetic differentiation of 0.31 ± 0.17 (range between 0.01 and 0.68, although estimates cannot be compared between studies, species or genetic marker). The average and maximum distance recorded between sampled populations per study were 1,361.51 ± 1,273.02 km and 12,149.20 km, respectively (*SI Appendix*, Table S1).

The biophysical model released a total of 21,891,914 particles from 11,989 source and sink sites over the 5-y period. These particles resulted in 6,106,904 connectivity events (average of 8.37 ± 29.68 per site) linking 561,247 pairs of sites. Longer propagule duration (PD) periods, i.e., up to 180 d, resulted in larger traveled distances. This pattern spanned an average distance of 55.12 ± 63.70 km with 10 d of propagule duration to 715.44 ± 765.59 km with 180 d (maximum of 10,582.96 km; Figs. 2 and 3). The number of connectivity events also increased with propagule duration, from 4,539,045 to 6,106,904 (Fig. 3). The probability of connectivity and dispersal distances showed a positively skewed relationship, regardless of the propagule duration (Fig. 2). Mapping betweenness centrality allowed identifying important hubs for stepping-stone connectivity. For reduced PD, connectivity hubs were mostly distributed along the coastlines of the western Atlantic and the Indo-West Pacific regions, while for increased PD, hubs were distributed in key islands and offshore regions that bridge distant populations (e.g., between continents) and along the Indo-West Pacific region (Fig. 3).

Isolation by distance models (IBD) were significant for 72.88% of the linear regression models (significant *P* values in 43 out of 59 models), with an average R-square of 0.33 ± 0.21 and a Person's correlation of 0.55 ± 0.18 (Fig. 3 and *SI Appendix*, Table S1 and Supplement 2, (30)). Multigenerational stepping-stone oceanographic connectivity (OC) estimates considering centrality indices were significant for 94.91% of the linear regression models (significant *P*-values in 56 out of 59 models), with an average R-square of 0.44 ± 0.23 (up to 0.97) and a Person's correlation of 0.65 ± 0.17 (Fig. 3 and *SI Appendix*, Table S1 and Supplement 2, (30)). The remaining non-significant models had marginal *P* values ranging between 0.06 and 0.08 (*SI Appendix*, Table S1). All individual comparisons between IBD and OC models at the study, species, and genetic marker levels are presented in Supplement 2 (30).
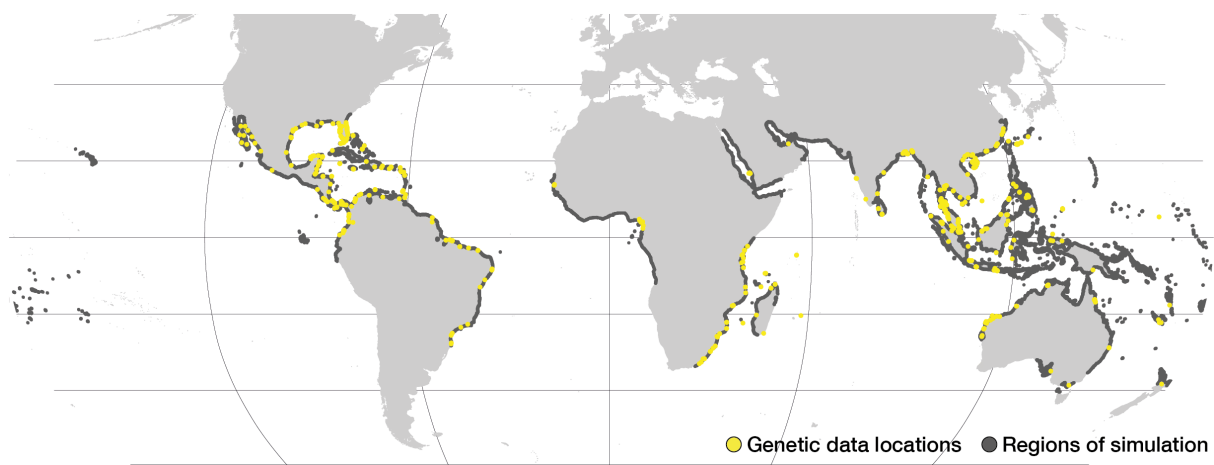
Fig. 1. Global distribution of mangrove forests (dark contour; updated by UNEP-WCMC; version 1.4, March 2021; 28) where the biophysical modelling simulated oceanographic connectivity, and populations sampled for genetic differentiation data (yellow circles).
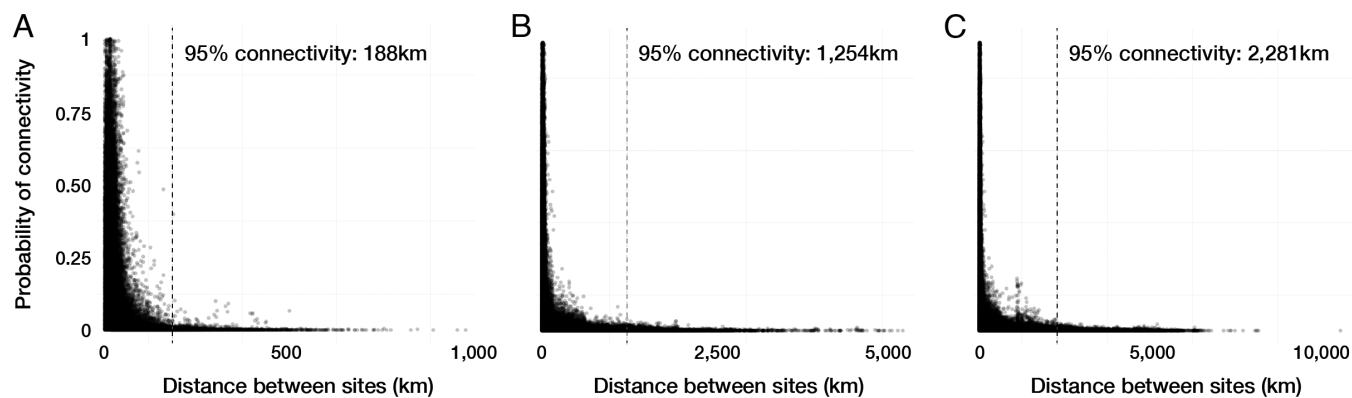
Fig. 2. Probability of connectivity as a function of potential dispersal distance (km) inferred with biophysical modeling for (*A*) 10 d, (*B*) 70 d and (*C*) 180 d of propagule duration (10 d represent the minimum, 70 d the average and 180 d the 90th percentile of mangrove propagule duration; inferred by (29) to the closest 10th day). Black circles in *A–C* represent all connectivity events between pairs of sources and sink sites.

Comparing Akaike information criterion (AIC) values between approaches showed that 100% of the OC models (considering centrality) explained more variability in genetic differentiation data than the IBD. This resulted in an average gain in R-square of 0.18 ± 0.16 (up to 0.76) and in Person's correlation of 0.21 ± 0.19 (up to 0.78; Fig. 4). The same general patterns were held when PD was varied to capture the uncertainty (*SI Appendix,* Table S3). The use of centrality indices enhanced the goodness of fit of 100% of the models, by an average R-square of 0.05 ± 0.07 (up to 0.42; *SI Appendix,* Table S1; Supplement 4, (30)).

Discussion

The global distribution of intra-specific diversity of mangrove forests can be explained by multigenerational stepping-stone oceanographic connectivity, regardless of the species, region, or genetic marker. The modeling approach, accounting for the temporal and spatial complexity of oceanographic processes, as well as key ecological dispersal traits, improved the ability to explain genetic differentiation when compared to more simplistic, yet widely used isolation by distance models. The integration of centrality indices derived from graph theory showed the potential role of particular sites as hubs for connectivity (Fig. 3), which may bridge populations across large water masses, facilitating gene flow and therefore reducing genetic differentiation levels.

The biophysical modeling based on high-resolution ocean circulation data coupled with graph theory showed how taxon-specific traits may strongly impact the potential for population dispersal, as well as the overall levels of genetic differentiation (*SI Appendix,* Fig. S1). Mangrove species have contrasting dispersal periods (29) that can result in oceanographic connectivity events at scales differing by more than one order of magnitude (from an average of 55.12 km to 715.44 km between 10 and 180 d of propagule duration). The number of population connectivity events also increased with dispersal potential, a result that is somewhat expected in biophysical modeling simulation connectivity of advected passive particles (31). However, the relationship between increasing dispersal periods and potential connectivity did not show a linear relationship, but rather a positively skewed one, independently of the propagule duration considered, which can result in connectivity events of up to 10,582 km. This is in line with theoretical dispersal kernels (32), as well as empirical evidence suggesting that mangrove propagules do not tend to disperse far away from source locations (10, 11), yet rare long-distance dispersal events can occur, as proposed across the Atlantic (33, 34), Indian (35), and Pacific Oceans (33, 35). These

general traits of mangroves' dispersal ecology may be key in driving intra-specific biodiversity levels. While limited dispersal potential explains the strong genetic structure found across species distribution ranges (36), the rare events at larger scales must be crucial during the first colonization of distant habitats (10).

Comparing the inferred patterns of oceanographic connectivity against empirical genetic data per species, study, and genetic marker corroborated our main hypothesis. Connectivity estimates explained genetic differentiation in nearly all tests performed (95%), and, compared to isolation by distance models, the approach improved the explanatory power by an average R-square of 0.18 ± 0.16 (up to 0.76) and Person's correlation of 0.21 ± 0.19 (up to 0.77). This result builds upon existing studies performed with a limited number of species and regions (18, 21, 37). Such an improvement in modeling genetic differentiation likely resulted from considering the combined effect of realistic oceanographic features (17, 38), the directionality of ocean currents (16), and the potential for stepping-stone connectivity (17). On the one hand, fronts, eddies, and bifurcations generate oceanographic barriers that can isolate neighboring populations (39) and increase their genetic differentiation (16, 17), as verified for *Rhizophora* species considered in our models in regions of Southeast Asia (14), Eastern Africa (22), Western Indian Ocean (39), and South America (12). On the other hand, the directionality of ocean currents can further play a role in the relative degree of gene flow, by promoting either unidirectional or bidirectional connectivity between pairs of populations (16, 40). Multigenerational stepping-stone connectivity is also key while performing comparisons against genetic data, because differentiation levels reflect both colonization and gene flow events acting across large temporal scales, and direct oceanographic transport between sampled populations is very unlikely. Finally, our analyses also considered the add-on effect of centrality indices, which improved all models explaining genetic data (average R-square of 0.06 ± 0.07, and maximum of 0.42). Regions of high centrality provided information about particular sites functioning as stepping-stones between populations and with a higher degree of reachability (41, 42), which may promote gene flow and reduce genetic differentiation levels [i.e., hubs for genetic connectivity (43)]. Conversely, regions of lower centrality are linked to dispersal barriers and, therefore, genetic discontinuities (16). Mapping centrality allowed verifying that the Indo-West Pacific concentrates most hubs for stepping-stone connectivity, matching mangroves' hotspot of interspecific diversity (3), and that islands and offshore regions are key for long-distance dispersal events, bridging populations of species with longer dispersal periods.
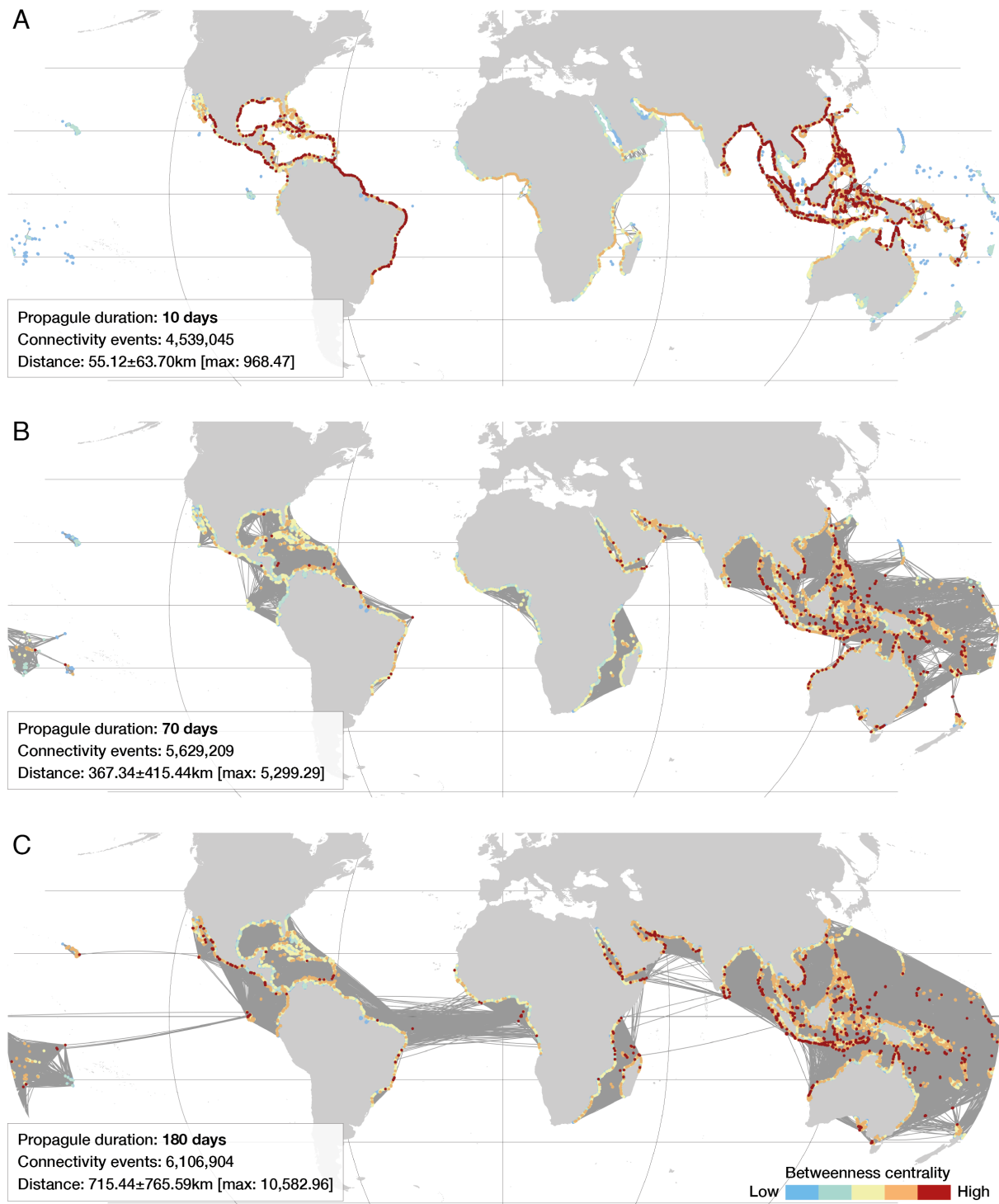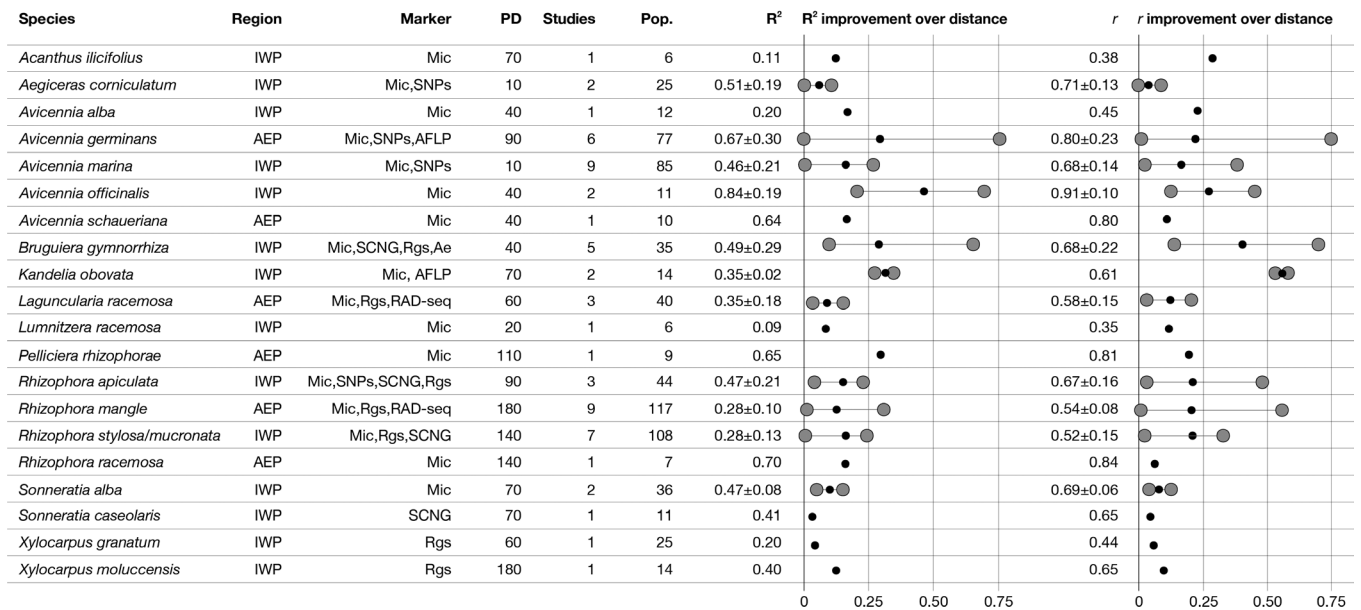
Fig. 3. Connectivity of mangrove forests at global scale inferred with biophysical modeling for (*A*) 10 d, (*B*) 70 d and (*C*) 180 d (10 d represent the minimum, 70 d the average and 180 d the 90th percentile of mangrove propagule duration; inferred by (29) to the closest 10th day with information available on *SI Appendix, Table S2*). Betweenness centrality is mapped to depict important hubs for stepping-stone connectivity. Information on the distance traveled, probability of connectivity and number of connectivity events are also shown.

Despite the general agreement found between oceanographic connectivity and population genetic differentiation, our models were not significant in 3 out of the 59 tests (yet *P*-values were marginally significant), and even in those that were significant, not all variability was explained (~43% variability explained, on average), most likely due to the effect of additional drivers not related to present-day oceanographic processes. For instance, the direction and intensity of ocean currents could have changed in the past (44), shaping distinct gene flow patterns and barriers to

dispersal (e.g., the Central American Isthmus) that could have left a strong imprint in the distribution of intra-specific diversity (45). Alongside population connectivity, genetic diversity can also be structured by past demographic processes. The sea-level fluctuations during glacial-interglacial cycles of the Quaternary might have repeatedly shifted mangroves' distribution, also influencing genetic diversity (2). More recently, ongoing climate changes (24, 46) and human-induced disturbance (47, 48) may have also impacted genetic levels owing to population size

Species	Region	Marker	PD	Studies	Pop.	R²	R² improvement over distance	r	r improvement over distance
Acanthus ilicifolius	IWP	Mic	70	1	6	0.11		0.38	
Aegiceras corniculatum	IWP	Mic,SNPs	10	2	25	0.51±0.19		0.71±0.13	
Avicennia alba	IWP	Mic	40	1	12	0.20		0.45	
Avicennia germinans	AEP	Mic,SNPs,AFLP	90	6	77	0.67±0.30		0.80±0.23	
Avicennia marina	IWP	Mic,SNPs	10	9	85	0.46±0.21		0.68±0.14	
Avicennia officinalis	IWP	Mic	40	2	11	0.84±0.19		0.91±0.10	
Avicennia schaueriana	AEP	Mic	40	1	10	0.64		0.80	
Bruguiera gymnorrhiza	IWP	Mic,SCNG,Rgs,Ae	40	5	35	0.49±0.29		0.68±0.22	
Kandelia obovata	IWP	Mic, AFLP	70	2	14	0.35±0.02		0.61	
Laguncularia racemosa	AEP	Mic,Rgs,RAD-seq	60	3	40	0.35±0.18		0.58±0.15	
Lumnitzera racemosa	IWP	Mic	20	1	6	0.09		0.35	
Pelliciera rhizophorae	AEP	Mic	110	1	9	0.65		0.81	
Rhizophora apiculata	IWP	Mic,SNPs,SCNG,Rgs	90	3	44	0.47±0.21		0.67±0.16	
Rhizophora mangle	AEP	Mic,Rgs,RAD-seq	180	9	117	0.28±0.10		0.54±0.08	
Rhizophora stylosa/mucronata	IWP	Mic,Rgs,SCNG	140	7	108	0.28±0.13		0.52±0.15	
Rhizophora racemosa	AEP	Mic	140	1	7	0.70		0.84	
Sonneratia alba	IWP	Mic	70	2	36	0.47±0.08		0.69±0.06	
Sonneratia caseolaris	IWP	SCNG	70	1	11	0.41		0.65	
Xylocarpus granatum	IWP	Rgs	60	1	25	0.20		0.44	
Xylocarpus moluccensis	IWP	Rgs	180	1	14	0.40		0.65	

0   0.25   0.50   0.75   0   0.25   0.50   0.75

Fig. 4. Improvement in modeling performance by including oceanographic connectivity, considering the average propagule duration (PD) of each species (to the closest 10th day, with information available on *SI Appendix*, Table S2), over isolation by distance. Modeled species, region, genetic marker, propagule duration, number of studies, sampled populations (at the 8.5 km spatial resolution of the biophysical model), average of linear regression (R^2) and Pearson´s correlation (r) of oceanographic connectivity, and the average (black circles) and minimum and maximum (gray circles) difference of R-square and Person's correlation coefficient between oceanographic connectivity (considering centrality indices) and isolation by distance models. For results without centrality indices, please refer to *SI Appendix*, Table S1. Regions of mangrove occurrence in each study are abbreviated as IWP (Indo West Pacific) and AEP (Atlantic East Pacific). Genetic markers are shown as Mic (Microsatellite), Rgs (rubisco gene and spacers), SCNG (single-copy nuclear gene), SNPs (single nucleotide polymorphisms), RAPD (random amplified polymorphic DNA), AFLP (amplified fragment length polymorphism), and Ae (Allozyme).

reductions in the face of unfavorable niche conditions or by founder effects at the leading edge of new colonizations (49). Alternative means of dispersal, such as wind and insect-driven pollination (21, 50), and human-induced reforestation (51), can also shape the distribution of genetic diversity in ways (i.e., distance and direction) that may contrast with those from the prevalent oceanographic currents. Finally, the available genetic data compiled by systematic search of the literature did not cover all mangrove species (20 out of ~80 species), and the genetic markers used could have also biased the estimates of population differentiation. For instance, some markers like mitochondrial DNA have reduced resolution and can be prone to selecting specific genotypes (52), potentially confounding the actual degree of population connectivity.

Overall, our biophysical modeling shows that oceanographic connectivity explains the population differentiation of mangrove forests at global scales. This is of high relevance not only for biogeography and evolution (15, 29, 31) but also for climate change ecology since ocean currents can modify the link between climate change and biogeographical shifts (53, 54). The future persistence and expansion of mangrove populations, as well as their gene pools, may become a process primarily dependent on the regional patterns of ocean currents, which may facilitate or hinder distributional shifts depending on their agreement with temperature, precipitation (53, 55, 56) and salinity changes (57). Global conservation strategies can also benefit from our findings. The highlighted importance of stepping-stone processes and central populations acting as hubs for gene flow can pave the way for future research pinpointing priority conservation areas for mangroves under the post-2020 global biodiversity framework [e.g., high-betweenness hot spots; (58, 59), a new framework that targets the conservation of genetic diversity of wild populations, as well as the establishment of well-connected networks of protected areas (27)].

Methods

Biophysical Modeling and Graph Theory. Simulations of oceanographic connectivity between populations of mangrove forests were produced at global scales with a biophysical modeling framework (Supplement 5; (41, 60)) previously validated against genetic and demographic data for numerous coastal species of different ecological groups (e.g., fish, invertebrates, and macroalgae; (16, 17, 54, 61)). In this framework, passive particles representing mangrove propagules were advected in a virtual ocean by the patterns of daily ocean currents data derived from the Hybrid Coordinate Ocean Model (HYCOM), a high-resolution hindcast of the northward and eastward components of ocean currents (spatial resolution: 0.08°, approx. 6 to 9 km), which can resolve complex oceanographic processes such as ocean eddies filaments, fronts, and meandering currents (38).

The simulations run across the global distribution of mangrove forests [as inferred from (28) and updated by The United Nations Environment Programme World Conservation Monitoring Centre (UNEP-WCMC); version 1.4, March 2021] for the 5-y period between 2015 and 2019. Individual particles were released on a daily basis from source sites located 8,5 km apart (matching the resolution of the HYCOM model) and were allowed to drift on the ocean surface (mangrove propagules are buoyant and can remain on the ocean surface (62) for up to 180 d (90th percentile of mangrove propagule duration; 29) until they eventually ended up on sink sites, or got lost in the open ocean. The position of individual particles was determined hourly by bilinear interpolation over the velocity fields to smooth trajectories. All trajectories were aggregated to produce matrices of the pairwise probability of connectivity between the source and sink sites by dividing the number of particles released from site i that reached site j, by the total number of particles released from site i. Graph theory was used to capture asymmetrical multigenerational stepping-stone connectivity between sites (31, 41). The graph nodes were structured by the source and sink sites and the edges by the average probability of connectivity per year, i.e., to account for the inter-annual variability of oceanographic patterns (43). Floyd–Marshall's algorithm found the shortest paths between sites by minimizing the sum of log-transformed probabilities, and their stepping-stone probabilities were determined with a product function (17, 63).

The directionality of oceanographic currents was considered using the index proposed by (16), under the assumption of bidirectionally connected populations having higher gene flow and, therefore, lower genetic differentiation compared to unidirectionally connected populations. Additionally, centrality graph-based indices were determined to consider their potential role in population connectivity (41), namely betweenness and closeness centrality. Betweenness centrality measured the influence of each node on the overall population connectivity, identifying stepping-stones linking nodes and aggregating the overall network (i.e., clusters), while closeness centrality measured the reachability of each node by the length of the shortest path between that node and all other nodes (42). Sites with higher betweenness and/or closeness centrality may promote higher levels of gene flow across populations and therefore reduce genetic differentiation (42).

Testing the Role of Oceanographic Connectivity. Genetic differentiation data for mangrove forests were compiled through a systematic search of the literature. The Web of Science platform was accessed in December 2022 with the search criteria "genetic diversity and mangrove*" or "genetic differentiation and mangrove*" or "phylogeography and mangrove*". The studies resulting from the search were reviewed (main article and *SI Appendix*), and only those reporting estimates of pairwise population genetic differentiation were selected. Information about the sampled species, the location (coordinates) of populations, the number of individuals sampled per population, the molecular markers used in genetic analyses and the pairwise differentiation matrices were retained. These data were then revised based on up-to-date taxonomic information. Specifically, *Pelliciera rhizophorae* data were separated into *P. rhizophorae* and *Pelliciera benthamii* (64) according to the known distribution of each species, while the data of *Rhizophora stylosa* refer to *R. stylosa/mucronata,* as these two were grouped into a single species (65).

Because genetic differentiation data cannot be compared, statistical tests exploring the role of oceanographic connectivity were performed individually per species, study, and genetic marker. Three competing linear regression models were performed per dataset by fitting genetic differentiation against 1) a null model of isolation by shortest marine distance between populations (i.e., excluding landmasses), 2) a multigenerational stepping-stone oceanographic connectivity model based on probability estimates, and 3) a multigenerational stepping-stone oceanographic connectivity model considering the role of betweenness and closeness centrality. Pairwise genetic differentiation levels were averaged whenever two or more sampled populations fell within a site (i.e., from where the biophysical modeling runs; sites located 8.5 km apart). Oceanographic connectivity per species was obtained by restricting the outputs of the biophysical model to the known PD of each species (*SI Appendix*, Table S2). This information was averaged whenever the same species had multiple PD periods reported in the literature, and for species with no PD reported, the average PD of the genus was considered (*SI Appendix*, Tables S1 and S2; 66). Datasets were discarded whenever the number of observations was below eight (i.e., pairs of connected populations), following recommendations for linear regression (Supplement 2 and 3; (30, 67)).

Betweenness and closeness centrality were considered in the regression models as the average of each pair of sampled populations.

The improvement in explaining genetic data by adding oceanographic connectivity was determined with the AIC, the goodness of fit (adjusted R-square), and Pearson's correlation coefficient (Fig. 3).

A sensitivity analysis (*SI Appendix*, Table S3) showed how the uncertainty of PD estimates did not influence the capacity of the biophysical modelling to explain population genetic differentiation. This analysis was performed per study, species, and genetic marker by testing the improvement of adding oceanographic connectivity when using additional PD values around the average PD of species. In particular, ± 30 PD days (10-d steps) were considered, as this is the average difference found in the literature for multiple PD periods reported for the same species (*SI Appendix*, Table S2).

All analyses were performed in R (R Development Core Team, 2018) using the R packages "bigmemory," "data.table," "dismo," "doparallel," "geosphere," "gstat," "igraph," "raster," and "vegan." The source code for biophysical modeling is available in Supplementary Information 5 (60).

Data, Materials, and Software Availability. Supplementary Information 2, 3, and 4 described in the *Methods* and *Results* section are openly available in Figshare (30). The source code for biophysical modeling (Supplement 5) may be accessed on GitHub (60).

Author affiliations: ᵃCCMAR–Center of Marine Sciences, University of the Algarve, 8005-139 Faro, Portugal; ᵇDepartment of Geography, University of California, Los Angeles, CA 90095; ᶜDepartment of Biogeography and Global Change, National Museum of Natural Sciences, CSIC-Spanish National Research Council, 28806 Madrid, Spain; ᵈRui Nabeiro Biodiversity Chair, MED–Mediterranean Institute for Agriculture, Environment and Development, University of Évora, 7000 Évora, Portugal; ᵉFaculty of Bioscience and Aquaculture, Nord Universitet, 1490 Bodø, Norway; ᶠDepartment of Biological Sciences, University of Bergen, 5020 Bergen, Norway; and ᵍInstitute of Marine Research, 5817 Bergen, Norway

1. I. Cerón-Souza et al., Contrasting demographic history and gene flow patterns of two mangrove species on either side of the Central American Isthmus. Ecol. Evol. **5**, 3486–3499 (2015).
2. J. A. Mantiquilla, M. S. Shiao, H. C. Shih, W. H. Chen, Y. C. Chiang, A review on the genetic structure of ecologically and economically important mangrove species in the Indo-West Pacific. Ecol. Genet. Genomics **18**, 100078 (2021).
3. A. K. Banerjee et al., Setting the priorities straight–species distribution models assist to prioritize conservation targets for the mangroves. Sci. Total Environ. **806**, 150937 (2022).
4. R. Granado, L. C. P. Neta, A. F. Nunes-Freitas, C. M. Voloch, C. F. Lira, Assessing genetic diversity after mangrove restoration in Brazil: Why is it so important? Diversity **10**, 27 (2018).
5. R. Zhang et al., Population subdivision promoted by a sea-level-change-driven bottleneck: A glimpse from the evolutionary history of the mangrove plant Aegiceras corniculatum. Mol. Ecol. **31**, 780–797 (2022).
6. X. Li et al., Re-evaluation of phylogenetic relationships among species of the mangrove genus Avicennia from Indo-West Pacific based on multilocus analyses. PLoS One **11**, 1–14 (2016).
7. A. Mitra,"Ecosystem services of mangroves: an overview" in Mangrove Forests in India (Springer, Cham, 2020), pp. 1–32.
8. L. P. Gouvêa et al., Global impacts of projected climate changes on the extent and aboveground biomass of mangrove forests. Divers. Distrib. **28**, 2349–2360 (2022).
9. P. B. Tomlinson, The botany of mangroves (Cambridge University Press, ed. 2, 2016), pp. 135-152.
10. T. Van der Stocken, D. Carroll, D. Menemenlis, M. Simard, N. Koedam, Global-scale dispersal and connectivity in mangroves. Proc. Natl. Acad. Sci. U.S.A. **116**, 915–922 (2018).
11. R. M. Binks et al., Habitat discontinuities form strong barriers to gene flow among mangrove populations, despite the capacity for long-distance dispersal. Divers. Distrib. **25**, 298–309 (2018).
12. P. M. Francisco, G. M. Mori, F. M. Alves, E. V. Tambarussi, A. P. de Souza, Population genetic structure, introgression, and hybridization in the genus Rhizophora along the Brazilian coast. Ecol. Evol. **8**, 3491–3504 (2018).
13. F. Rousset, Genetic differentiation and estimation of gene flow from F-statistics under isolation by distance. Genetics **145**, 1219–1228 (1997).

14. A. K. S. Wee et al., Oceanic currents, not land masses, maintain the genetic structure of the mangrove Rhizophora mucronata Lam. (Rhizophoraceae) in Southeast Asia. J. Biogeogr. **41**, 954–964 (2014).
15. M. Jahnke, P. R. Jonsson, Biophysical models of dispersal contribute to seascape genetic analyses. Philos. Trans. R. Soc. B Biol. Sci. **377**, 20210024 (2022).
16. R. Buonomo 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).
17. J. Assis et al., Ocean currents shape the genetic structure of a kelp in southwestern Africa. J. Biogeogr. **49**, 822–835 (2022).
18. T. Van der Stocken, D. Menemenlis, Modelling mangrove propagule dispersal trajectories using high-resolution estimates of ocean surface winds and currents. Biotropica **49**, 472–481 (2017).
19. N. N. Ntuli et al., Rejection of the genetic implications of the "Abundant Centre Hypothesis" in marine mussels. Sci. Rep. **10**, 604 (2020).
20. K. R. Nicastro 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).
21. R. G. J. Hodel et al., Terrestrial species adapted to sea dispersal: Differences in propagule dispersal of two Caribbean mangroves. Mol. Ecol. **27**, 4612–4626 (2018).
22. M. N. Ngeve, T. Vanderstocken, D. Menemenlis, N. Koedam, L. Triest, Contrasting effects of historical sea level rise and contemporary ocean currents on regional gene flow of rhizophora racemosa in eastern atlantic mangroves. PLoS One **11**, 1–24 (2016).
23. G. M. Mori, M. I. Zucchi, A. P. Souza, Multiple-geographic-scale genetic structure of two mangrove tree species: The roles of mating system, hybridization, limited dispersal and extrinsic factors. PLoS One **10**, 1–23 (2015).
24. M. F. Da Silva et al., Geographical and environmental contributions to genomic divergence in mangrove forests. Biol. J. Linn. Soc. **132**, 573–589 (2021).
25. C. Sjöqvist, A. Godhe, P. R. Jonsson, L. Sundqvist, A. Kremp, Local adaptation and oceanographic connectivity patterns explain genetic differentiation of a marine diatom across the North Sea-Baltic Sea salinity gradient. Mol. Ecol. **24**, 2871–2885 (2015).

26. D. Alagador, J. O. Cerdeira, M. B. Araújo, Climate change, species range shifts and dispersal corridors: An evaluation of spatial conservation models. *Methods Ecol. Evol.* **7**, 853–866 (2016).
27. CBD, First Draft of The Post-2020 Global Biodiversity Framework (UN Convention on Biological Diversity, Montreal, QC, Canada,2021), pp. 1–9.
28. C. Giri *et al.*, Status and distribution of mangrove forests of the world using earth observation satellite data. *Glob. Ecol. Biogeogr.* **20**, 154–159 (2011).
29. T. Van der Stocken *et al.*, A general framework for propagule dispersal in mangroves. *Biol. Rev.* **94**, 1547–1575 (2019).
30. L. P.Gouvêa *et al.*, Oceanographic connectivity explains the intraspecific diversity of mangrove forests at global scales: Supplements from 2 to 4. *Figshare.* https://doi.org/10.6084/m9.figshare.19597318. Deposited 14 April 2022.
31. J. Assis *et al.*, Potential biodiversity connectivity in the network of marine protected areas in Western Africa. *Front. Mar. Sci.* **8**, 1–12 (2021).
32. T. Van Der Stocken *et al.*, The role of wind in hydrochorous mangrove propagule dispersal. *Biogeosciences* **10**, 3635–3647 (2013).
33. K. Takayama, M. Tamura, Y. Tateishi, E. L. Webb, T. Kajita, Strong genetic structure over the American continents and transoceanic dispersal in the mangrove genus Rhizophora (Rhizophoraceae) revealed by broad- scale nuclear and chloroplast DNA analysis. *Am. J. Bot.* **100**, 1191–1201 (2013).
34. J. P. Kennedy *et al.*, Postglacial expansion pathways of red mangrove Rhizophora mangle, in the Caribbean Basin and Florida. *Am. J. Bot.* **103**, 260–276 (2016).
35. E. Y. Lo, N. C. Duke, M. Sun, Phylogeographic pattern of Rhizophora (Rhizophoraceae) reveals the importance of both vicariance and long-distance oceanic dispersal to modern mangrove distribution. *BMC Evol. Biol.* **14**, 83 (2014).
36. S. W. J. Canty *et al.*, Mangrove diversity is more than fringe deep. *Sci. Rep.* **12**, 1695 (2022).
37. Q. Geng *et al.*, Ocean currents drove genetic structure of seven dominant mangrove species along the coastlines of Southern China. *Front. Genet.* **12**, 615911 (2021).
38. E. P. Chassignet *et al.*, The HYCOM (HYbrid Coordinate Ocean Model) data assimilative system. *J. Mar. Syst.* **65**, 42–50 (2007).
39. L. Triest *et al.*, Expansion of the mangrove species Rhizophora mucronata in the Western Indian Ocean launched contrasting genetic patterns. *Sci. Rep.* **11**, 4987 (2021).
40. F. Alberto *et al.*, Isolation by oceanographic distance explains genetic structure for Macrocystis pyrifera in the Santa Barbara channel. *Mol. Ecol.* **20**, 2543–2554 (2011).
41. J. Assis *et al.*, Weak biodiversity connectivity in the European network of no-take marine protected areas. *Sci. Total Environ.* **773**, 145664 (2021).
42. E. Estrada, Ö. Bodin, Using network centrality measures to manage landscape connectivity. *Ecol. Appl.* **18**, 1810–1825 (2008).
43. A. F. Rozenfeld *et al.*, Network analysis identifies weak and strong links in a metapopulation system. *Proc. Natl. Acad. Sci. U.S.A.* **105**, 18824–18829 (2008).
44. L. Caesar, G. D. McCarthy, D. J. R. Thornalley, N. Cahill, S. Rahmstorf, Current Atlantic meridional overturning circulation weakest in last millennium. *Nat. Geosci.* **14**, 118–120 (2021).
45. A. K. S. Wee *et al.*, Genetic structures across a biogeographical barrier reflect dispersal potential of four Southeast Asian mangrove plant species. *J. Biogeogr.* **47**, 1258–1271 (2020).
46. D. A. Friess *et al.*, The state of the World's Mangrove forests: Past, present, and future. *Annu. Rev. Environ. Resour.* **44**, 89–115 (2019).
47. W. Lu, Z. Zou, X. Hu, S. Yang, Genetic diversity and mating system of two mangrove species (Rhizophora apiculata and Avicennia marina) in a heavily disturbed area of China. *Diversity* **14**, 115 (2022).
48. D. Gorman, "Historical losses of mangrove systems in South America from human-induced and natural impacts" in *Threats to Mangrove Forests*, C. Makowski, C. Finkl, Eds. (Coastal Research Library, Springer, Cham, 2018), vol. **25**, pp. 155–171.
49. M. Ochoa-Zavala *et al.*, Reduction of genetic variation when far from the niche centroid: Prediction for mangrove species. *Front. Conserv. Sci.* **2**, 795365 (2022).
50. I. Cerón-Souza, E. Bermingham, W. O. McMillan, F. A. Jones, Comparative genetic structure of two mangrove species in Caribbean and Pacific estuaries of Panama. *BMC Evol. Biol.* **12**, 205 (2012).
51. B. R. Parida, P. Kumar, Mapping and dynamic analysis of mangrove forest during 2009–2019 using landsat–5 and sentinel–2 satellite data along Odisha Coast. *Trop. Ecol.* **61**, 538–549 (2020).
52. S. Arnaud-Haond *et al.*, Assessing genetic diversity in clonal organisms: Low diversity or low resolution? Combining power and cost efficiency in selecting markers. *J. Hered.* **96**, 434–440 (2005).
53. J. Garciá Molinos, M. T. Burrows, E. S. Poloczanska, Ocean currents modify the coupling between climate change and biogeographical shifts. *Sci. Rep.* **7**, 1–9 (2017).
54. J. Assis *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).
55. M. J. Osland *et al.*, Climatic controls on the global distribution, abundance, and species richness of mangrove forests. *Ecol. Monogr.* **87**, 341–359 (2017).
56. R. D. Ward, D. A. Friess, R. H. Day, R. A. Mackenzie, Impacts of climate change on mangrove ecosystems: A region by region overview. *Ecosyst. Heal. Sustain.* **2**, e01211 (2016).
57. T. Van der Stocken, B. Vanschoenwinkel, D. Carroll, K. C. Cavanaugh, N. Koedam, Mangrove dispersal disrupted by projected changes in global seawater density. *Nat. Clim. Chang.* **12**, 685–691 (2022).
58. E. Ser-Giacomi *et al.*, Lagrangian betweenness as a measure of bottlenecks in dynamical systems with oceanographic examples. *Nat. Commun.* **12**, 4935 (2021).
59. D. Abecasis, E. Fragkopoulou, B. Claro, J. Assis, Biophysical modelling and graph theory identify key connectivity hubs in the Mediterranean marine reserve network. *Front. Mar. Sci.* **9**, 1-11 (2023).
60. J. Assis, The source code for biophysical modeling (Supplement 5). *Github.* http://github.com/jorgeassis/biophysicalModelling. Deposited 10 February 2023.
61. M. Klein *et al.*, High interannual variability in connectivity and genetic pool of a temperate clingfish matches oceanographic transport predictions. *PLoS One* **11**, e0165881 (2016).
62. J. Pineda, J. A. Hare, S. Sponaugle, Larval transport and dispersal in the coastal ocean and consequences for population connectivity. *Oceanography* **20**, 22–39 (2007).
63. J. Assis *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).
64. N. C. Duke, A systematic revision of the vulnerable mangrove genus pelliciera (Tetrameristaceae) in equatorial america. *Blumea J. Plant Taxon. Plant Geogr.* **65**, 107–120 (2020).
65. K. Takayama, Y. Tateishi, T. Kajita, Global phylogeography of a pantropical mangrove genus Rhizophora. *Sci. Rep.* **11**, 1–13 (2021).
66. M. Gandra, J. Assis, M. R. Martins, D. Abecasis, Reduced global genetic differentiation of exploited marine fish species. *Mol. Biol. Evol.* **38**, 1402–1412 (2020).
67. D. G. Jenkins, P. F. Quintana-Ascencio, A solution to minimum sample size for regressions. *PLoS One* **15**, e0229345 (2020).