



Connectivity of *Avicennia marina* populations within a proposed marine transboundary conservation area between Kenya and Tanzania

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ABSTRACT

Threatened ecosystems such as intertidal mangrove forests often span political boundaries and require cross-border conservation planning initiatives. Population connectivity is key to establish transboundary collaborative actions. In this study, we assessed genetic diversity and connectivity of mangrove populations in a proposed transboundary conservation area (TBCA) between Kenya and Tanzania, where human demography exerts increasing pressure on biodiversity and ecosystem services. East African mangrove ecosystems comprise a complex pattern of estuaries and coastal bays, with *Avicennia marina* as a major mangrove component. Our main objective was to test a hypothesis of overall migration directionality reflecting regional ocean surface current flows. Fourteen microsatellite markers in 670 *A. marina* trees revealed no overall significant difference in allele or gene diversity levels between populations but showed an overall effect of geographic distance with a gradient of admixed gene pools. Migration tests and Approximate Bayesian computations supported a customized stepping-stone model of overall south to north migration with bidirectional gene flow and admixture between adjacent bays near the Kenya-Tanzania border. Observed patterns of gene flow suggest an important effect of large rivers and connections via creeks. Our results indicate that relevance for conservation and management of mangroves areas may remain largely within a hydrological connectivity context of each bay, despite prevailing genetic estimates reflecting historically well-connected mangroves between bays. For sustainable management, populations must be considered complementary and not redundant. Hence, transboundary regions must primarily adhere to local contemporary conservation and management, and not solely rely on the assumption of strong regional connectivity built historically.

1. Introduction

Mangrove forests are highly productive ecosystems that provide a broad range of valuable ecosystem services (Barbier et al., 2011; Lee et al., 2014). Structurally complex and often densely rooted, mangroves provide a spawning and nursery habitat for marine species, and play a vital role in sustaining the production in coastal fisheries (Manson et al., 2005). For example, they provide an important refuge for corals from thermal stress and ocean acidification (Yates et al., 2014; Camp et al., 2016), and as a nursery habitat, may strongly increase the biomass of reef fish (Mumby et al., 2004; Mumby, 2006). Globally, some 210 million people inhabit coastal sites within 10 km of mangrove forest of

which many benefit from mangrove-associated fisheries (Hutchison et al., 2014). It has been suggested that mangrove tourism attracts hundreds of millions of visitors annually (Spalding and Parrett, 2019). As a physical structure, mangroves also protect coastlines and coastal communities against erosion, flood and storms by reducing hydrokinetic energy (Danielsen et al., 2005; Zhang et al., 2012) and have been considered as a more sustainable, cost-effective and ecological alternative to conventional coastal defense engineering (Cheong et al., 2013; Temmerman et al., 2013). Mangroves also have a large capacity for carbon sequestration and play a major role in the oceanic and global carbon cycle (Duarte et al., 2005; Alongi, 2014; Ezcurra et al., 2016). It has been estimated that mangroves on average store three to five times

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more carbon per unit area than other forest types (Donato et al., 2011).

Increasing human population and activities, such as agriculture, aquaculture, and coastal and urban development, have resulted in large-scale deforestation and increased fragmentation of mangroves globally (Richards and Friess, 2016; Thomas et al., 2017; Bryan-Brown et al., 2020). Mangrove loss and fragmentation affect human livelihoods, biodiversity, and ecosystem functioning (Polidoro et al., 2010; Carugati et al., 2018; Estoqué et al., 2018), may influence coastal and marine productivity through altered nutrient fluxes (Twilley, 1988), and are likely to also impact other ecosystems such as seagrass beds and coral reefs with which they are often interlinked (Carr et al., 2017). Mangroves are threatened by climate change, including changes in precipitation and temperature regimes, increased storm frequency and intensity, and fluctuations in sea level (Ward et al., 2016; Lovelock et al., 2015, 2017).

In Tanzania and Kenya, it has been estimated that mangrove area has decreased by 18% and 8%, respectively, between 1980 and 2005 (FAO, 2007), with a more recent mangrove loss estimate along the Kenyan coast of 18% between 1985 and 2010 (Kirui et al., 2013). The mangrove systems in Vanga (Kenya) and Tanga (Tanzania) experience among the greatest loss and degradation rates in the region, estimated at 27 and 14.5 ha yr⁻¹, respectively (Mungai et al., 2019). These trends are driven mainly by human activities such as overharvesting for poles, timber, fuelwood and charcoal, pollution, conversion to other land uses such as solar salt works and aquaculture, human settlement, as well as climate change effects (UNEP, 2014; Bosire et al., 2016). Besides the direct effects on the size and quality of the local habitat patch, habitat loss may alter habitat connectivity and hence impact local and regional ecosystem productivity, functioning and stability (Thompson et al., 2017).

The importance of these coastal habitats and marine systems for local communities and global economy has boosted the formulation and implementation of conservation strategies worldwide. Today, there are above 17,000 marine protected areas (MPAs), covering roughly 27 million km² or 7.5% of the ocean (UNEP-WCMC and IUCN, 2020). These areas consist of “clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values.” (Day et al., 2012). In Kenya and Tanzania, there are 28 MPAs, managed by local and national governments (Marine Conservation Institute, 2020), most of them encompassing mangrove biotopes. Mangrove protection may result in an immediate reduction in household income, but it has been demonstrated that all wealth classes are likely to benefit from the long-term sustainability gains in shrimping and fishing that result from mangrove protection (McNally et al., 2011). Conservation efforts may also reduce carbon emissions (Miteva et al., 2015; Pendleton et al., 2012), increase carbon sequestration rates (Zarate-Barrera and Maldonado, 2015), support (local) fisheries (Aburto-Oropeza et al., 2008), and may help increase the abundance and diversity of coral reef fish populations (Mumby et al., 2004; Serafy et al., 2015; Nagelkerken et al., 2002, 2017). Additionally, besides its role in climate regulation and food security, the conservation and sustainable use of mangroves can contribute to reducing poverty and poverty-driven emigration (UNEP, 2014).

The effectiveness and resilience of MPAs depends on ecological processes such as biological connectivity, which may export propagules that help replenish other populations, important in conserving biodiversity (Palumbi, 2003). As a result, connectivity has been incorporated into marine reserve planning and conservation prioritization (Olds et al., 2013; Weeks, 2017), increasingly so since 2007 (Balbar and Metaxas, 2019). In mangroves, the exchange of propagules (seedlings) between populations is determined by the additive effect of coastal and oceanographic processes (e.g., river flow, waves, tides, near-shore and open-ocean currents, as well as wind energy) and species-specific dispersal traits (Van der Stocken et al., 2019). Estimating patterns of connectivity remains challenging, but genetic approaches and modeling allow to

discern historical or potential gene flow between populations over large distances (Bryan-Brown et al., 2017). Population genetics of mangrove tree species such as *Rhizophora* of which the propagules exhibit a potential for long-distance dispersal may reflect rather recent migration events between estuaries (Wee et al., 2020). Additionally, local bidirectional gene flow of *Rhizophora* was found within large estuaries (Ngeve et al., 2017). Genetic structure and differentiation among estuaries however may reflect historical instead of recent dispersal (Chablé Iuit et al., 2020), especially for mangrove species with propagules of somehow lesser potential for dispersal as in e.g. *Avicennia alba* (Wee et al., 2020) or *Avicennia marina* (Do et al., 2019). Connectivity should not be assumed from dispersal features alone, but also depends on variables such as geographic distance and habitat discontinuities (Binks et al., 2018).

In this study, we aim at better understanding the patterns of connectivity within a proposed transboundary conservation area (TBCA; hatched area in Fig. 1) along the coast of Kenya and Tanzania (MPRU/KWS, 2015). The TBCA area comprises an approximately 100 km long coastal stretch, oriented broadly southwest-northeast. We collected samples from 12 *Avicennia marina* populations located along the coastal stretch covered by the TBCA, and use a suite of genetic analyses allowing to identify population genetic diversity and structure, and reveal patterns of migration. Our main objective was to test a hypothesis of overall directionality reflecting regional current flows. We therefore considered densely vegetated transects within a stretch of extensive and putatively well-connected mangroves, located on a shelf alongside a very strong northward ocean current through the Pemba Channel (Transboundary region of Tanzania and Kenya). Specific aims were (1) to analyze the genetic diversity and structure of *A. marina* sites; (2) to estimate patterns of connectivity between estuaries; and (3) to test specific hypotheses of demographic history and on migration directionality under panmixia, source-sink or stepping-stone models. To ensure a high resolution of genotyped individuals, we developed new primers for polymorphic microsatellite markers using source material from the study area. The outcome from this study will provide insight into the general patterns of mangrove population connectivity in the region, the physical processes driving dispersal, and highlight populations that are isolated, interconnected or may represent important propagule sources or sinks.

2. Materials and methods

2.1. Study sites and sampling methods

The TBCA and sampling sites are located along the East African coast, near the border of Tanzania and Kenya (Fig. 1). Meteorological conditions in our study region, and hence oceanographic processes, are influenced by the annual migration of the Inter-Tropical Convergence Zone (ITCZ) driving seasonality of the northeast and southwest monsoon (McClanahan, 1988). Surface ocean currents in the region are influenced predominantly by the northward flowing East Africa Coastal Current (EACC) (Schott et al., 2009). The direction of the EACC is not reversed by the reversing wind direction during the northeast monsoon season and part of it turns northwest at latitude 4°S, entering the Pemba Channel (Fig. 1; Semba et al., 2019). The direction of the Pemba Channel Current (PCC; Fig. 1) is predominantly northward but may be occasionally southward during the northeast monsoon season (Semba et al., 2019).

We opted for a design of replicate transects in dense mangrove sites of *A. marina* populations. These populations were from adjacent estuarine areas. A total of 670 *A. marina* individual trees were sampled from 12 sites (transects) in 6 estuaries of the proposed TBCA reaching from Tanga Bay in Tanzania towards Gazi Bay in Kenya (Fig. 1). Maximum distance between sites of *A. marina* was approximately 83 km (great-circle distance between KEN-1A and TAN-6B, computed using the haversine formula). Transects were broad linear, 20 m wide and 100 m in length each and the number of sampled mangrove trees ranged from

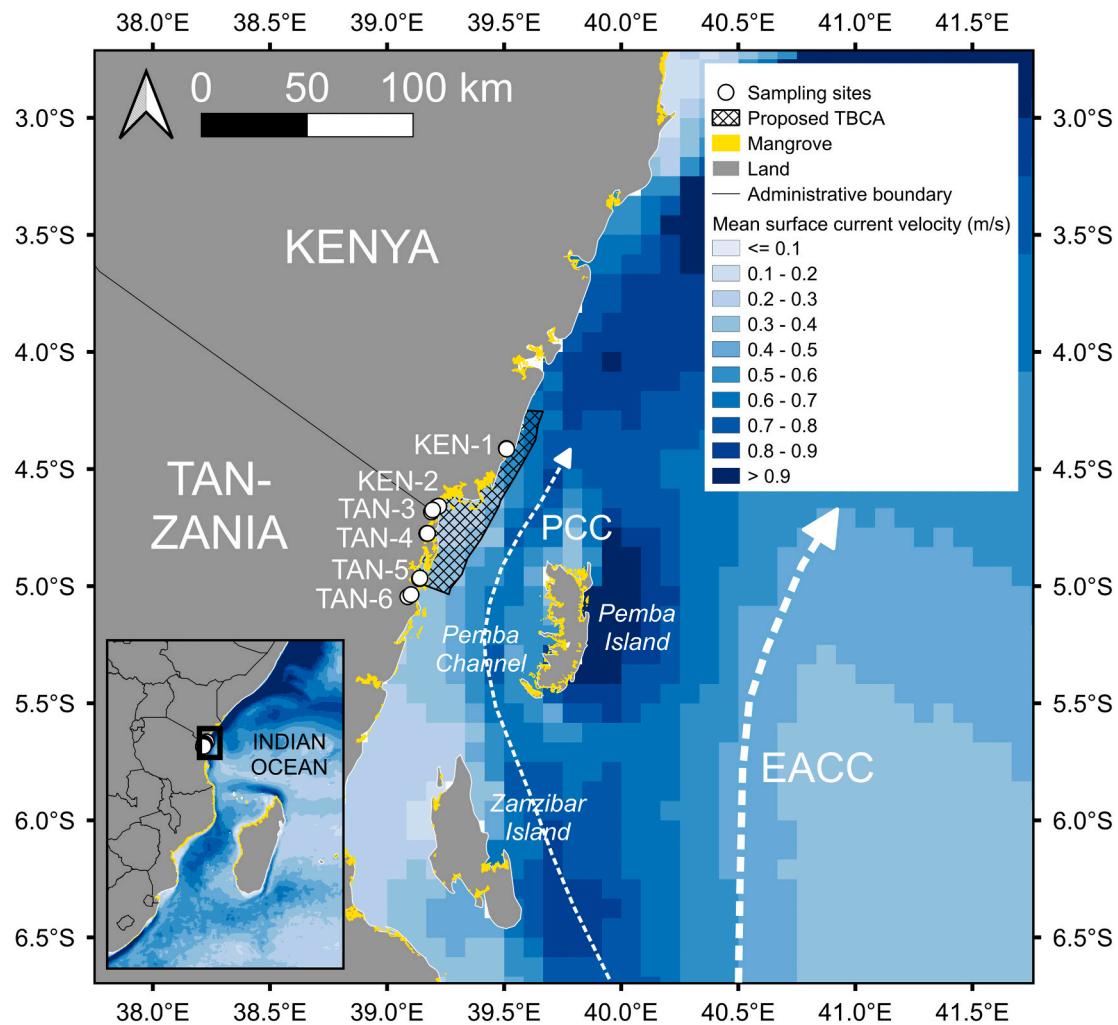


Fig. 1. Map showing the 12 *Avicennia marina* sample locations (white dots) from six different estuaries (KEN-1 to TAN-6) along the Kenya-Tanzania coastline. The sample sites are located within the boundaries of a proposed Marine Transboundary Conservation Area (TBCA; hatched area), characterized by vast stretches of mangrove forest (yellow polygons; Bunting et al., 2018). Blue tones denote mean present (2000–2014) sea surface current velocities downloaded from the Bio-ORACLE dataset (<https://www.bio-oracle.org/>; Assis et al., 2018). Dotted lines indicate the Pemba Channel Current (PCC) which branches off the East African Coastal Current (EACC) at latitude 4°S (Semba et al., 2019). Land and administrative boundaries from the Natural Earth database (www.naturalearthdata.com). Map created using the QGIS 3.10.10 software (www.qgis.org). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

34 to 64 per transect. GPS coordinates were taken at the starting point of each transect. The distance between each subsequent sample within the densely vegetated transects varied between 2 m and 5 m such that a suite of neighbouring trees was included. Most of the trees were adult (3 to 5 m height), only few young established trees (2 to 5 years) were sampled. We discarded patches of seedlings or juveniles to avoid any effect of sibling dominance on the kinship values. Two bright green leaves were collected per individual, dried in open air and preserved in paper envelopes with silica gel for transportation and handling within 1 month.

2.2. DNA extraction and microsatellite analysis

DNA was extracted from 20 to 30 mg of dried leaf tissue with the E.Z.N.A. SP Plant DNA Mini kit (Omega Bio-tek, Norcross, GA, USA) protocol for dried samples. New microsatellite markers were developed for this study by next generation sequencing (NGS), using source material from Gazi Bay within the TBCA (Triest et al., 2020). An Illumina paired-end library was constructed and sequenced using the Illumina HiSeq platform at Macrogen (Seoul, Republic of Korea).

We used SSR_pipeline (Miller et al., 2013) to search the NGS data for microsatellites (SSR = simple sequence repeats or microsatellites). Out

of 19.3 million 100 bp paired end reads, 1.4 million pairs were successfully joined by the module joinseqs. The module SSR_search found 5178 dinucleotide SSRs with at least ten repeats, 362 trinucleotide SSRs with at least 8 repeats and 227 tetranucleotide SSRs with at least 6 repeats. We used Batchprimer3 (You et al., 2008) to design primers and 56 primer-pairs were selected for synthesis on basis of number of repeats and expected fragment length. Six of these markers were added to eight previously developed markers by Maguire et al. (2000) and Geng et al. (2007) to form one single multiplex polymerase chain reaction (PCR) for this study (online Appendix Table A1). One forward or reverse primer of each pair was fluorescence-labelled with one of 4 different dye-labels (6FAM/VIC/NED/PET) and mixed in a primer mix at 0.2 μM each. Multiplex PCR reactions consisted of 6.25 μl master mix (Qiagen Multiplex PCR), 1.25 μl primer mix, 2.5 μl H₂O and 2.5 μl of genomic DNA, making a total volume of 12.5 μl.

PCR was performed in a thermal cycler (Bio-Rad MyCycler) with the following conditions: an initial denaturation of 95 °C for 15 min followed by 35 cycles of 30 s denaturation at 95 °C, 90 s annealing at 57 °C and 80 s elongation at 72 °C followed by a final extension of 30 min at 60 °C. PCR products were separated on an ABI3730XL sequencer (Macrogen, Seoul, Korea) and allele sizes were determined with

GeneMarker V2.60 (SoftGenetics LLC, State College, USA). Independent replicates for allele scoring by three researchers ensured consistent interpretation.

2.3. Statistical analysis of genetic data

Prior to population and individual-based data analysis we tested for genotypic disequilibrium, potential null alleles and overall resolution of the selected fourteen microsatellite markers in *A. marina*. A linkage test between all pairs of loci (1000 permutations) gave no genotypic disequilibrium at the 0.05 level using FSTAT (v.2.9.3) (Goudet, 2001). No scoring errors or large allele dropouts were indicated using MICRO-CHECKER (Van Oosterhout et al., 2004). The probability of identity (PI), namely whether two individuals could share an identical multilocus genotype by chance using GenAlEx (v.6.5; Peakall and Smouse, 2012), gave a cumulative probability of identity for all polymorphic loci in each site of 2.1×10^{-6} to 6.9×10^{-8} thereby providing ample resolution, even for siblings, potentially present in our subsequent sampling design, that reached a PI of 1.1×10^{-3} to 8.8×10^{-4} (online Appendix Fig. A1).

Basic population genetic variables were measured for each site: total number of alleles (A), mean number of alleles (A_M), effective number of alleles (A_E), allelic richness (A_R) for 34 diploid samples i.e., the lowest sample size of KEN-2B (Table 1), observed heterozygosity (H_O), unbiased expected heterozygosity (H_E) and population inbreeding coefficient (F_{IS}) using FSTAT and GenAlEx. The genetic structure among sites (F_{ST}), inbreeding within sites (F_{IS}) and overall inbreeding (F_{IT}) was calculated via AMOVA- F_{ST} at 999 random permutations using GenAlEx v.6.5. Overall gene flow Nm was roughly estimated from F_{ST} under assumption of an island migration model. Pairwise genotypic differentiation (F_{ST}) was used to produce a PCoA and together with a pairwise geographic Euclidean distance to perform a Mantel test using 1000 permutations in GenAlEx (v.6.5). A more precise test at population level using F_{ST} and five distance classes of 1, 10, 40, 60, 84 km was performed using a similar amount of pairwise comparisons and 1000 permutations with SPAGeDi 1.5a (Hardy and Vekemans, 2002). These distance classes represent threshold values instead of a full linear regression of a Mantel test. The overall F_{LJ} kinship coefficient (Loiselle et al., 1995) for all sites of *A. marina* was estimated for five maximum distance classes at 0.3, 1, 2, 5 and 15 km (mean distances were ln transformed: -1.40, -0.05, 0.27, 1.18, 2.41) using SPAGeDi 1.5a and considering the whole sample as a reference and considering an equal number of pairs for each distance class. An assignment of individuals to their 'self' population or to another population was done with the 'leave-one-out' option in GenAlEx.

A Bayesian clustering analysis at individual level was carried out in STRUCTURE version 2.3.4 (Pritchard et al., 2000) using an admixture model with correlated allele frequencies. The model ran 10 iterations for

each K value from 1 to 12; the burn-in period was 50,000 with 500,000 Markov chain Monte Carlo (MCMC) repeats. The optimal K was inferred with the ΔK statistic (Evanno et al., 2005) and LnPK using Structure Harvester (Earl and von Holdt, 2012) calculated with StructureSelector (Li and Liu, 2018). The software BARRIER 2.2 (Manni et al., 2004) was used to detect the location of sharp genetic changes between neighbouring populations on basis of one overall pairwise F_{ST} matrix and 14 pairwise F_{ST} matrices of every microsatellite locus allowing a maximum of one barrier per matrix.

Migrate-n (Beerli, 2006; Beerli and Palczewski, 2010) was used to estimate the mutation-scaled population sizes (Theta) and immigration rates (M). The Brownian model was tested locus by locus along with the product of all distributions of all loci. Uni- and bidirectional historical migration/expansion models were tested. Uniform prior distribution settings (min, max, delta) were as follows for Theta = 0.0, 10.0, 0.1 and for M = 0.0, 100, 10.0. The number of recorded steps was 10^6 at a sampling frequency of 10^3 after an initial burn-in. The effective number of immigrants per generation (Nem) was calculated as $[Theta \times M] / 4$ (Kennedy et al., 2016). Specific hypotheses testing on directionality were considered in panmixia, source-sink or stepping-stone models for the migration between six mangrove estuaries of the coastal shelf area situated alongside the Pemba Channel. The most seaward sites were considered (KEN-1B, KEN-2B, TAN-3B, TAN-4B, TAN-5B), except for Tanga Bay where the more landward site was considered (TAN-6A). This was done to avoid any prior effect from the inbred TAN-6B (seaward) site. In the latter, six out of fourteen loci showed a shortage of heterozygotes which is a within-site phenomenon of non-random mating, not necessarily reflecting among-site relationships. The Brownian motion mutation model within each case was adopted for a subsample of 20 individuals in a transect, following the abovementioned settings, computing two replicate chains (with different seed), and using the Bezier thermodynamic integration (Beerli and Palczewski, 2010) for calculation of the Bayes factors from marginal likelihoods giving model probabilities.

The demographic history of divergence and admixture between *A. marina* populations was carried out on thirteen microsatellites considered as a single group with dinucleotide repeats, using the approximate Bayesian computation (ABC) approach implemented in DIYABC version 2.0 (Cornuet et al., 2014). We conducted a model with the same six populations as used in Migrate-n. Based on the latter outcome, we specifically conceptualized three scenarios (Fig. 2) of demographic history along the coast of Tanzania and Kenya. For this model building, the populations were ranked from south to north as follows: N1 (TAN-6), N2 (TAN-5), N3 (TAN-4), N4 (TAN-3), N5 (KEN-2) and N6 (KEN-1). Scenario 1 represented a South to North stepping-stone whereas scenario 2 a north to south stepping-stone migration route. Scenario 3 included an admixture of N3 (TAN-4) from its neighbouring

Table 1

Location details and population genetic variables of *Avicennia marina* sites within a proposed transboundary marine protected area along the coast between Kenya and Tanzania. N: number of genotyped samples; A: number of alleles; A_M : mean number of alleles; A_E : effective number of alleles; A_R : allelic richness at k = 34 diploid individuals; H_O : observed heterozygosity; H_E : expected gene diversity; F_{IS} : within-population inbreeding coefficient (with *** at $p < 0.001$; * at $p < 0.05$ significance level).

Site	Location	Latitude	Longitude	N	A	A_M	A_E	A_R	H_O	H_E	F_{IS}
KEN-1A	Gazi Bay	04° 24' 43.1 S	039° 30' 34.9 E	53	48	3.4	2.1	3.3	0.411	0.436	0.066
KEN-1B	Gazi Bay	04° 24' 52.5 S	039° 30' 38.4 E	61	46	3.3	2.2	3.1	0.421	0.446	0.063
KEN-2A	Vanga Bay	04° 39' 42.1 S	039° 12' 46.1 E	60	46	3.3	2.0	3.1	0.425	0.427	0.013
KEN-2B	Vanga Bay	04° 39' 30.7 S	039° 13' 15.0 E	34	46	3.3	2.0	3.3	0.397	0.427	0.086
TAN-3A	Jasini estuary	04° 40' 57.7 S	039° 11' 23.5 E	62	43	3.1	1.9	2.9	0.336	0.404	0.177*
TAN-3B	Jasini estuary	04° 40' 28.9 S	039° 11' 40.6 E	57	52	3.7	2.0	3.5	0.381	0.424	0.112*
TAN-4A	Moa Bay	04° 46' 30.0 S	039° 10' 11.4 E	59	51	3.6	2.2	3.5	0.450	0.479	0.068
TAN-4B	Moa Bay	04° 46' 29.4 S	039° 10' 22.1 E	60	57	4.1	2.3	3.9	0.464	0.474	0.030
TAN-5A	Kwale Bay	04° 58' 05.6 S	039° 08' 19.2 E	64	45	3.2	1.9	3.0	0.362	0.371	0.031
TAN-5B	Kwale Bay	04° 57' 55.8 S	039° 08' 25.7 E	54	48	3.4	2.1	3.3	0.376	0.431	0.137*
TAN-6A	Tanga Bay	05° 02' 42.5 S	039° 05' 20.4 E	53	52	3.7	2.3	3.6	0.400	0.471	0.159*
TAN-6B	Tanga Bay	05° 02' 10.3 S	039° 06' 08.5 E	53	48	3.4	2.2	3.3	0.298	0.459	0.359*
Overall				670	73	3.5	2.1	3.8	0.393	0.437	0.118***

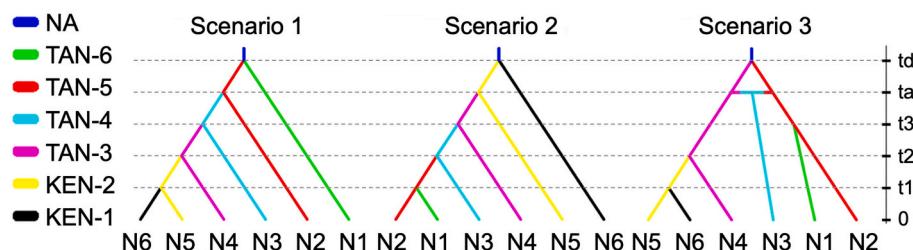


Fig. 2. The three scenarios tested for an approximate Bayesian computation (ABC) model implemented in DIYABC version 2.0. Six populations with effective population sizes N1 to N6 correspond with TAN-6 to KEN-1. Scenario 1 represents a unidirectional stepping-stone from south to north; scenario 2 is a unidirectional stepping-stone from north to south and scenario 3 includes an admixture within a unidirectional stepping-stone from south to north. NA is the ancestral effective population size and t# represent subsequent time events (not drawn to scale). Scenario 3 gave the highest probability and scenario 2 was very unlikely.

populations N4 (TAN-3) and N2 (TAN-5). Comparison of these scenarios will allow us to conclude whether an admixture is involved or not for *A. marina* mangroves within the proposed TBCA region. In all scenarios, t# represents the time scale measured in number of generations (largest numbers refer to oldest events) and N# represented the effective size of the corresponding populations during the indicated time period. We used default prior values for all parameters, except for the maximum population size and maximum values of time scale (25,000 instead of 10,000 default values) based on the outcome of the preliminary test runs of prior distributions. Summary statistics of 123 variables (mean number of alleles, mean gene diversity, mean allele size variance, F_{ST} , classification index and $(d\mu)^2$ distance) were considered for each population or pairwise comparison of samples. One million simulation data were run for each scenario and the most-likely scenario was obtained from a comparative assessment of their posterior probabilities. The goodness-of-fit was checked through a principal component analysis (PCA) using the 'model checking' option. The posterior distribution of parameters (N# and t#) was estimated.

3. Results

3.1. Genetic diversity and inbreeding

In 12 sites of 6 *A. marina* mangrove estuaries along the 84 km coastal stretch, the total number of alleles observed in the considered fourteen loci was 73 (43–57), with a mean number of alleles (A_M) ranging from 3.1–4.1, an effective number of alleles (A_E) from 1.9–2.3 and an adjusted allelic richness (A_R) from 2.9–3.9 (Table 1). The overall observed heterozygosity ($H_O = 0.393$) was slightly lower than the expected heterozygosity ($H_E = 0.437$). The within population inbreeding (mean $F_{IS} = 0.118$) ranged from 0.013 to 0.359 and was significant ($p < 0.05$) for five sites (Table 1). Population TAN-6B had six loci (out of fourteen) that showed heterozygote shortage that we interpreted as the result of non-random mating instead of null alleles.

3.2. Genetic differentiation between sites

Avicennia marina along the coastal stretch showed an overall AMOVA- $F_{IT} = 0.177$, $F_{ST} = 0.067$ and $F_{IS} = 0.118$, though with all these low values at $p = 0.001$ (Table 2). Within the region, 82% of *A. marina* genetic variation came from within individuals whereas 7% was among the sites, giving a roughly estimated overall gene flow of Nm well above one (Table 2). Pairwise differentiation ranged from 0.009 for sites in

close vicinity to 0.143 between estuaries (online Appendix Table A2). A PCoA showed a gradient along the first axis due to inbreeding in some sites, although *A. marina* individuals clustered as a single cloud (online Appendix Fig. B2).

A Mantel test resulted in an overall isolation-by-distance ($y = 0.0007x + 0.0344$; $R^2 = 0.37$ at $p = 0.006$) over 84 km (Fig. 3a). A more detailed isolation-by-distance test (Fig. 3b) of pairwise population differentiation (F_{ST}) over five distance classes (end points in km) showed significant lower differentiation within the shortest considered distance up to 1 km ($p < 0.001$) and a significantly higher than average differentiation beyond 40 km ($p < 0.05$). The kinship value (F_{IJ}) decreased significantly over the full distance (slope $b = -0.0084$ at $p < 0.001$), with higher kinship values than average at maximum 0.3 km (mean ln value = -1.40; $p < 0.001$) and up to a maximum distance of 1 km (mean ln value = -0.05; $p < 0.05$) (Fig. 3c).

A BARRIER analysis showed minor breaks due to isolation-by-distance between KEN-1 and KEN-2, slight inbreeding of TAN-4, and more elevated inbreeding in TAN-6B (Fig. 4a). A Bayesian clustering analysis of individual *A. marina* trees performed in STRUCTURE indicated a gradient of very admixed clusters (Fig. 4b). Delta K was very low for most inferred clusters and reached a marginally higher value at $K = 5$ (Fig. 4c), referring to a regional substructure of KEN-1 and TAN-6 versus a large mixed group. The LnPK reaches a plateau from $K = 5$ onwards (Fig. 4d). However, this $K = 5$ value must be regarded as an estimation only relevant for a coastal stretch of the WIO with limited cases of assignment of every individual to but a single gene pool. The assignment of individuals resulted in 49% to the 'self' population.

3.3. Gene flow and migration rates

Specific testing (Migrate-n) of gene flow directionality between mangrove estuaries located along the 84 km coastal stretch, indicated that panmixia, bidirectional and unidirectional stepping-stone models (from south to north as well as from north to south), and various source-sink models appeared less likely than a customized stepping-stone model that considered a south to north migration as well as a regional bidirectionality between KEN-2B, TAN-3B and TAN-4B (Table 3 and Fig. 5). Highest estimated gene flow values were from TAN-5B towards TAN-4B ($Nem = 2.14$) and from TAN-3B towards TAN-4B ($Nem = 1.76$) thereby indicating the site TAN-4B of Moa Bay as a sink rather than a source. Lowest gene flow estimates were southwards from KEN-2B towards TAN-3B ($Nem = 0.16$) indicating a lesser influence of a southward migration over this short distance within the Vanga Bay.

Table 2

Summary of AMOVA and F-statistics of *Avicennia marina* sites within a proposed transboundary marine protected area along the coast between Kenya and Tanzania. (df: degrees of freedom, % Est.Var.: estimated variance).

<i>A. marina</i>	df	SS	MS	Est. Var.	%	F-statistics	p-Value
Among populations	11	313,823	28,529	0.225	7%	$F_{ST} = 0.067$	0.001
Among individuals	658	2290,216	3,481	0.366	11%	$F_{IS} = 0.118$	0.001
Within individual	670	1841,000	2,748	2,748	82%	$F_{IT} = 0.177$	0.001
Total	1339	4445,040		3,339	100%	$Nm = 3.5$	

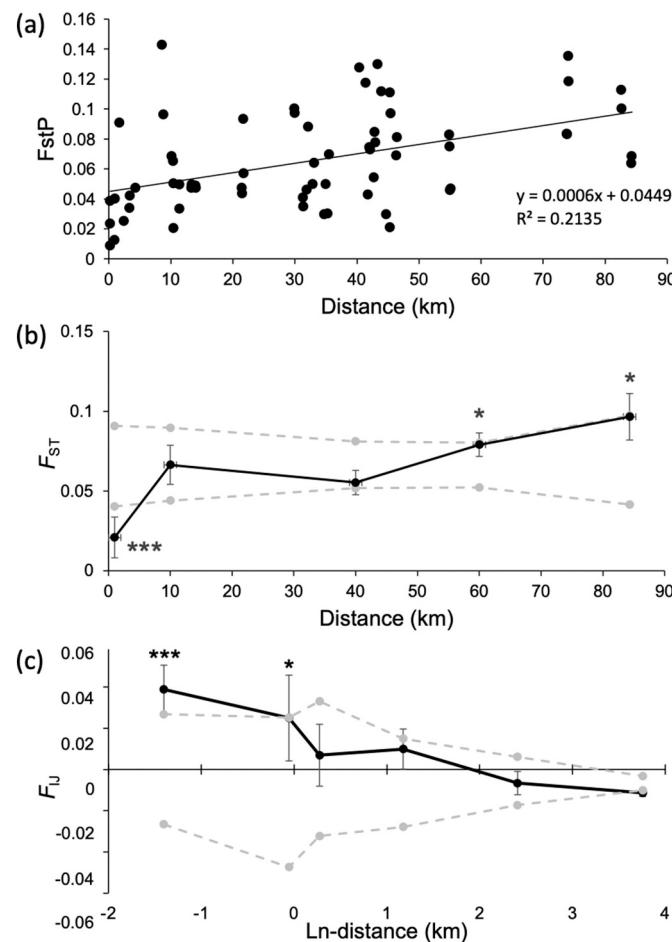


Fig. 3. Isolation-by-distance of *Avicennia marina* sites with (a) an overall Mantel test with positive regression of pairwise genetic differentiation F_{STP} ; (b) a Mantel test over five distance classes; (c) Spatial autocorrelation of *Avicennia marina* individuals showing higher kinship values (F_{IS}) at the shortest distances. *** $p < 0.001$; * $p < 0.05$; dotted grey lines represent upper and lower confidence intervals at 95%.

Comparing the three scenarios of the ABC approach, the highest value of posterior probability (0.635) and 95% confidence interval (CI: 0.602–0.669) was obtained for scenario 3 (Fig. 2), namely a stepping-stone migration history from south to north including a regional admixture of N3 (TAN-4). This probability value and CI did not overlap with the 95% CI of the other stepping-stone scenarios from which the north to south scenario appeared most unlikely (online Appendix Table B1). Absence of significant differences between observed and simulated data in many of the 123 summary metrics, besides for the mean number of alleles, (online Appendix Table B2) and the positioning of the observed data within the clustered cloud of simulated data of the PCA (online Appendix Fig. B1), revealed that the selected scenarios fitted the observed data. The median values of the effective population sizes of scenario 3 ranged from 9010 to 15,700 (Table 4) and median divergence times were estimated as 1140 to 3430 generations (Table 4). The ABC simulation indicated *A. marina* populations of Kenya as being established more recently than those of Tanzania. Considering an approximate generation time of about 20 years for *A. marina*, though with much potential overlap between generations, the divergence times along this stretch of the East African coastline could be rather recent and roughly from early Holocene.

4. Discussion

In this study, we examined the genetic diversity and structure of *A. marina* populations within a proposed transboundary conservation area (TBCA) between Kenya and Tanzania, along a southwest-northeast oriented coastal stretch of approximately 100 km. Overall, our results indicated limited difference in allelic or gene diversity and consequently high levels of connectivity between sites. Both Migrate-n analysis and approximate Bayesian computations provide evidence for gene flow predominantly from south to north, but with bidirectional gene flow and admixture in the central part of our study area. These findings support our main hypothesis that the genetic structure and the inferred dispersal directionality reflect the dominant surface water flow directionality in the region, but indicate that near-shore currents associated with river outflow and tidal creeks (Triest et al., 2020) may play an important role in the persistence of local connectivity.

4.1. Genetic diversity and inbreeding

We found very similar levels of allele and gene diversity in *A. marina* populations, especially for those near the Kenya-Tanzania border, the central part of our study area. Genetic diversity was always lower than expected under a Hardy-Weinberg equilibrium, in particular for one southernmost and few northernmost Tanzania populations. Such lowered levels of heterozygosity may be generally attributed to different processes such as genetic drift, restricted gene flow, inbreeding, or a combined result from limited population size and even favoring homozygotes through selection (Arnaud-Haond et al., 2006). Our analysis suggests, however, that this unbalance is due to a local inbreeding effect as often became apparent in populations of *Avicennia* species (Hermansen et al., 2015; De Ryck et al., 2016; Do et al., 2019). Inbreeding values in sites of the TBCA mostly were low or non-significant, except for a moderately high value ($F_{IS} = 0.137$ to 0.359, $p < 0.05$) in the southernmost Tanzania populations Tanga (TAN-6A and TAN->6B) and Kwale (TAN-5B), and ($F_{IS} = 0.112$ to 0.177, $p < 0.05$) in Jasini (TAN-3A and TAN-3B). These higher inbreeding levels most likely are not caused by strict self-pollination but may originate from outcross pollination restricted to few adjacent flowering mangrove trees and subsequent establishment of a propagule cohort within very short distance of 10–30 m as was detected with fine-scaled analysis for some *A. marina* populations of Gazi Bay (Triest et al., 2020) and in northern Vietnam (Do et al., 2019) and of 50–100 m for *Avicennia germinans* in Northwestern Mexico (Millán-Aguilar et al., 2016).

High levels of relatedness may also be indicative for the effects of past and ongoing mangrove habitat disturbance and depletion in a region (Arnaud-Haond et al., 2006). Anthropogenic disturbances such as mangrove cutting typically result in areal decline and increased fragmentation of mangrove habitat (Thomas et al., 2017; Bryan-Brown et al., 2020). This may reduce genetic diversity (DiBattista, 2008), and hence, theoretically impact the genetic robustness and long-term viability under changing environmental conditions (Frankham, 1995). It has been suggested that less genetically diverse mangroves may suffer much greater destruction from sea level changes compared to mangrove populations with higher genetic diversity (Guo et al., 2017) although this is difficult to demonstrate. Since mangroves provide habitat to a wide range of animal species and support adjacent ecosystems, their decline and loss, regardless of genetic deterioration, may have effects that cascade on these interlinked communities.

4.2. Overall high level of connectivity

AMOVA, pairwise F_{ST} , PCoA, STRUCTURE and BARRIER analysis all indicate low genetic differentiation between populations, and hence good connectivity between populations throughout the TBCA. For example, 82% of *A. marina* genetic variation was attributed to differences within individuals, and only 7% to differences between

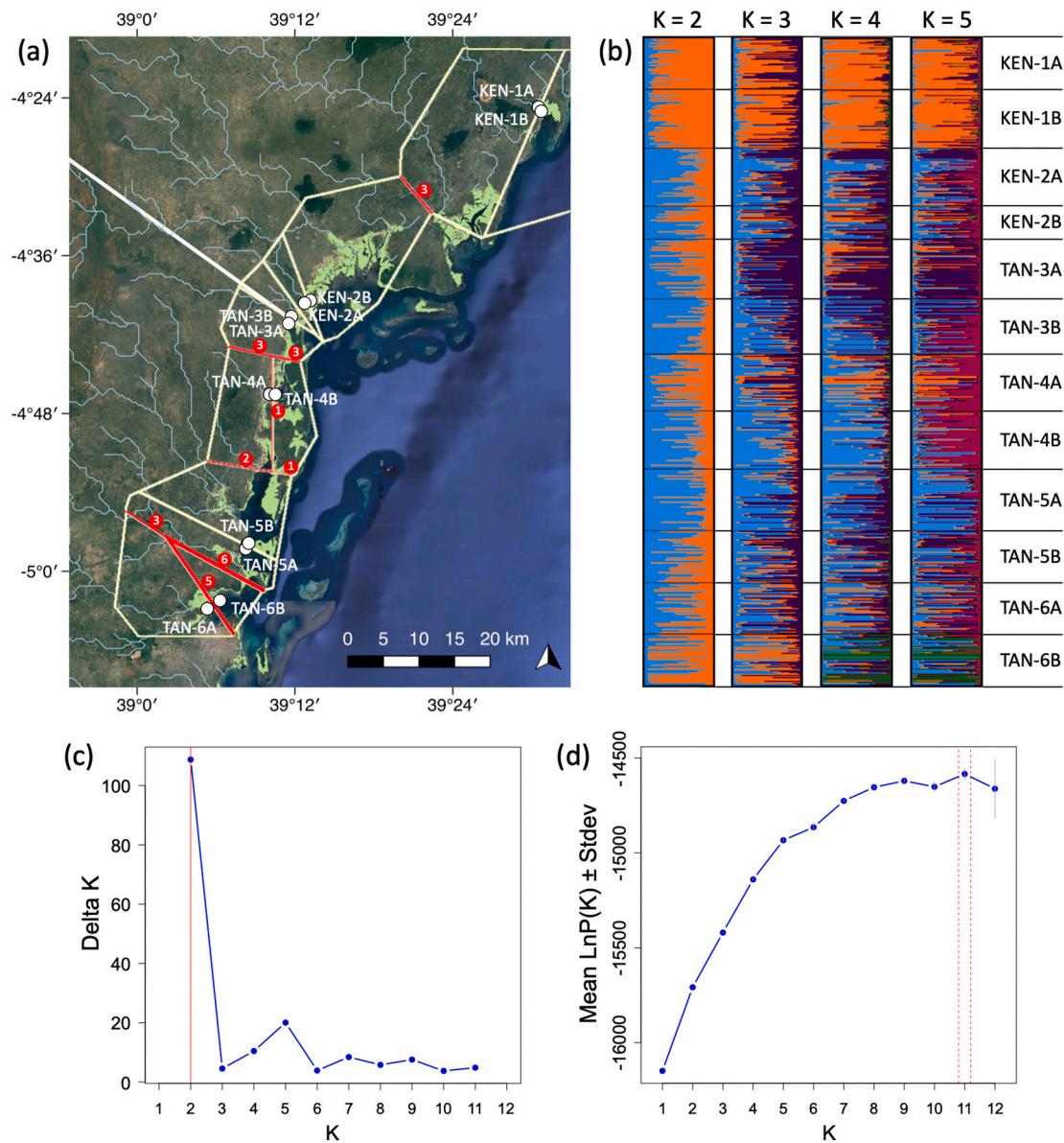


Fig. 4. (a) Map of study area and sample locations (white dots) with an overlay of first barriers (red lines on map) between neighbouring sites. Thickness of the red lines and associated numbers (red dots on map) indicate the relative importance of each gene flow barrier. (b) Barplots of Bayesian clustering analysis (STRUCTURE at $K = 2$, $K = 3$, $K = 4$ and $K = 5$), with ΔK (c) and $\text{LnP}(K)$ (d) graphs, are north-south oriented. Abbreviations of sample locations are denoted in Table 1. Background map created with QGIS 3.10.10 (www.qgis.org), using data from Natural Earth (www.naturalearthdata.com) and the Global Mangrove Watch database (mangrove polygons; Bunting et al., 2018). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

populations. Overall, populations appeared to be well connected from Tanga (TAN-6) to Vanga (KEN-2) with only a single exception of a site in Tanga, due to inbreeding causing a local break. Most importantly, significant relatedness between populations were found up to maximum 1 km (usually only within the much shorter transect) and slight but non-significant genetic differentiation occurred within a distance less than 40 km. Significant relatedness at local scales and the lack of IBD over distances of 40 km is consistent with previous findings that demonstrated high within-patch gene flow and potential oceanic dispersal over tens of kilometers (Clarke, 1993). Significant levels of genetic differentiation over distances exceeding 40 km most likely reflects the effect of the >40 km unsampled distance, and the potential of the Kisite sandbank, located in front of KEN-2, to interfere with and impede hydrochorous propagule transport, between KEN-1 (Gazi) and all other populations. Such IBD beyond 40 km was obtained from the integrative F_{ST} method, however Migrate-n models ignore this gap and show an

elevated gene flow between each site throughout the considered TBCA.

Estimated gene flow directionality within the proposed TBCA is from south to north. This is consistent with the northward surface current flow through the Pemba Channel, which is controlled by the East African Coastal Current (EACC), and with coral reef connectivity patterns observed by Mayorga-Adame et al. (2017), using individual based models coupled with ocean circulation models and assuming passive particles (i.e., comparable to passive mangrove propagule dispersal). The EACC is an extension of the Northeast Madagascar Current (NEMC) and flows northward throughout the year (Swallow et al., 1991). Drifter trajectories showed that upon approaching Pemba Island from the south, part of the EACC turns northwest and enters the Pemba Channel (Semba et al., 2019). Semba et al. (2019) also reported that southeasterly winds increase current speeds through the Pemba Channel during the southeast monsoon (min: 0.04 m/s, max: 1.73 m/s, mean \pm SD: 0.83 ± 0.44 m/s; $N = 197$), while reversing winds during the northeast monsoon

Table 3

Comparison of migration models on gene flow directionality for *Avicennia marina*, between mangrove estuaries located along a 84 km coastal stretch of the Pemba Channel (Kenya, Tanzania). The model with highest support is highlighted in grey. Connected populations with $><$ referring to bidirectional and $>$ or $<$ to unidirectionality.

Coastal shelf area	Model	Directionality	Bezier log marginal-likelihood	Model choice	Model probability
Full model	Panmixia	All	-939 888.63	8	0
N  S	Stepping-stone	Bidirectional	-556 964.31	6	0
N  S	Stepping-stone	Unidirectional from south to north: $6 > 5 > 4 > 3 > 2 > 1$	-381 357.54	4	0
N  S	Stepping-stone	Unidirectional from north to south: $1 > 2 > 3 > 4 > 5 > 6$	-381 347.33	3	0
N  S	Stepping-stone	Unidirectional from south to north and bidirectional for sites $2 <> 3 <> 4$	-258 861.65	1	1
N  S	Stepping-stone	Unidirectional from south to north and bidirectional for sites $3 <> 4$	-266 798.18	2	0
N  S	Source-Sink	Sites 2, 3 and 4 as source	-664 658.35	7	0
N  S	Source-Sink	Sites 2, 3 and 4 as sink; sites 5 and 6 as source	-456 991.40	5	0

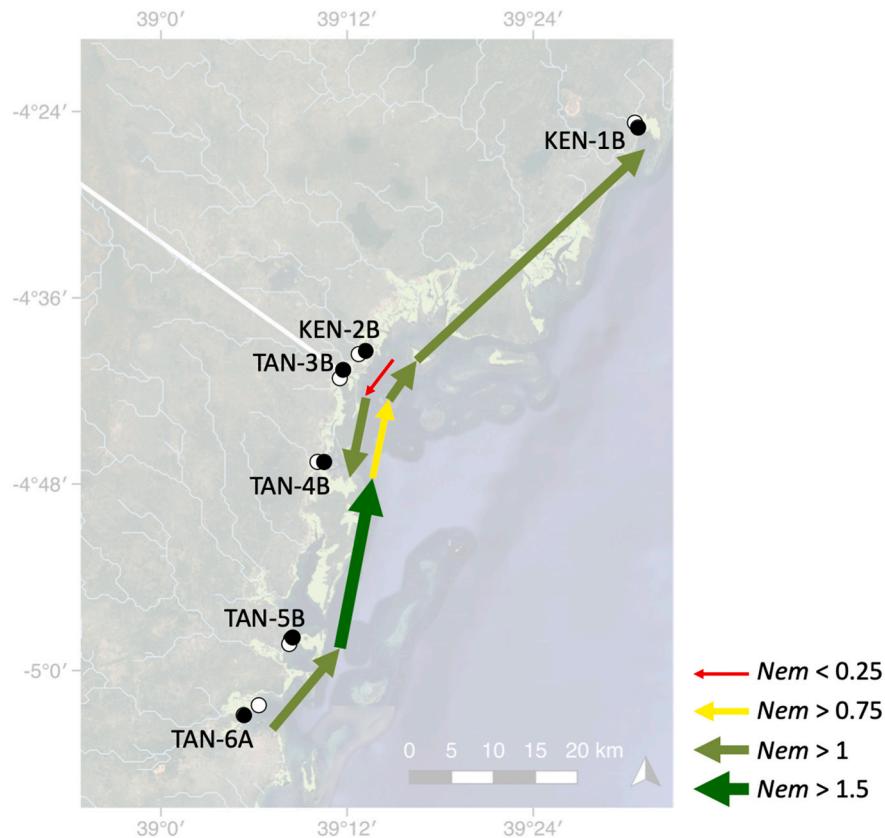


Fig. 5. Study area and sample locations (black and white dots) with indication of gene flow estimates following a custom migration model including uni- and bidirectionality. Sample sites considered for this analysis (black dots) consist of the most seaward sites, except for Tanga Bay where the more landward site was considered (TAN-6A) to avoid any prior effect from the inbred TAN-6B (seaward) site. Background map created with QGIS 3.10.10 (www.qgis.org), using data from Natural Earth (www.naturalearthdata.com) and the Global Mangrove Watch database (mangrove polygons; [Bunting et al., 2018](#)).

may reduce the speed of the northward surface current (min: 0.05 m/s, max: 1.34 m/s, mean \pm SD: 0.56 ± 0.31 m/s; $N = 51$). For propagules reaching open water, it would take about 1 month or 1 day, respectively, to travel 100 km considering these minimum and maximum flow rates. Data regarding mangrove propagule buoyancy and viability is scarce

and incomplete, but reported values suggest that *A. marina* propagules can remain afloat and viable in water for about two weeks to several months (Rabinowitz, 1978; Clarke, 1993; Clarke et al., 2001). These time spans would allow for connectivity between populations in our study region, as suggested by the relatively high gene flow among most

Table 4

Estimated divergence parameters for scenario 3 (unidirectional stepping-stone from south to north including admixture as shown in Fig. 2) and their 95% confidence interval based on the logistic estimate of DIYABC. N#: Effective population size; t#: time scale measured in number of generations. Numbers N1–N6 refer to populations ranked from south to north, with NA as ancestral population; t1–t3 refer to increasingly older events, with td as oldest divergence; ta refers to admixture with an admixture rate ra.

Parameter	Mean	Median	Mode	Lower CI	Upper CI
N1 (TAN-6)	15,700	15,700	16,100	8800	22,600
N2 (TAN-5)	11,100	10,600	9980	4810	19,300
N3 (TAN-4)	16,400	16,700	16,100	9040	22,800
N4 (TAN-3)	15,500	15,600	15,800	9010	22,200
N5 (KEN-2)	15,000	15,100	15,100	7410	22,800
N6 (KEN-1)	9910	9010	7150	3270	20,000
t1	1520	1140	654	294	3880
t2	3470	3010	2740	1270	7200
t3	4190	3430	2370	1340	9710
ta	3070	2320	1400	628	8370
ra	0.52	0.53	0.55	0.10	0.93
td	4010	2500	1510	621	13,100
NA	1120	528	22	47	4060

populations ($N_{\text{eff}} > 1$). Despite evidence for potential long-distance dispersal (LDD) in *A. germinans* (Dodd et al., 2002; Nettel and Dodd, 2007; Mori et al., 2015), high levels of LDD have been questioned for species in the mangrove genus *Avicennia* and several studies suggest that dispersal in *Avicennia* species is likely restricted to a few tens of kilometers (e.g., Clarke, 1993; Duke et al., 1998; Melville and Burchett, 2002; Van der Stocken et al., 2018; Binks et al., 2018). Binks et al. (2018) found evidence for occasional LDD up to 100 km, which is similar to the distance between the southernmost and northernmost population considered in this study. However, reported maxima of dispersal distances based on release-recapture experiments are limited by the scale of observation. While there is a need for more data regarding the dispersal capacity of this species, available data demonstrates the potential for connectivity between populations across the TBCA, most evidently in a stepping-stone manner though not exclusively. Our result on *A. marina* add to the emerging evidence that *Avicennia* species tend to follow a stepping-stone migration pattern, such as the unidirectional way obtained for *A. alba* in the western part of the Malaysian Peninsula (Wee et al., 2020) and bidirectional ways of *A. germinans* along each of the Caribbean and Pacific coasts of central America (Ochoa-Zavala et al., 2019). The demographic evolution scenarios considered in this study were from a strongly connected mangrove area along the same coastline (De Ryck et al., 2016) and featured by admixed gene pools as shown in our structure analysis, though slightly differentiated for Gazi Bay (KEN-1). ABC tests indicate that the Gazi gene pool (KEN-1), within the context of the currently studied populations, most probably originated through northward directed stepping-stone migration events from an older admixed and more southern located Tanzanian gene pool. All events were estimated at only a few thousand generations ago, reflecting approximately a timeframe of early Holocene, though the latter needs to be thoroughly tested using large-scale phylogeographic studies. We assume that population expansion and large effective population sizes account for the detected patterns along the studied East African coastline.

In the central part of our study area, between populations KEN-2B, TAN-3B and TAN-4B, we found indications of bidirectional gene exchange. This admixture is most likely explained by local hydrological dynamics rather than regional ocean currents that flow northward throughout the year. Despite the reversal of the winds during the northeast monsoon, the water surface currents of the EACC and through the Pemba Channel, are not reversed and continue to flow northward (Semba et al., 2019). More likely, the bidirectional outcome can be explained by the fact that (1) sites 2, 3 and 4 are relatively less exposed to conditions of the open ocean, and (2) there is a direct connection of a

long but narrow creek between TAN-3B and TAN-4B, thereby potentially connecting Vanga Bay with the Moa Bay. The river input appears larger in the Vanga Bay than for the Moa Bay (the latter has creeks, no rivers). The bays are situated on a shelf, with sheltered zones and extensive mangrove areas. Along the inner part of mangrove areas, the connecting creeks and direction of river outflow may play an important local role for persistence of connectivity.

4.3. Conservation relevance in transboundary context

The TBCA across the Kenya-Tanzania border is proposed with a defined outline along a southwest-northeast oriented coastal stretch of roughly 100 km (MPRU/KWS, 2015). The proposal which aligns with the Nairobi Convention under the aegis of the United Nations Environment Programme is currently under negotiation (Teff-Seker et al., 2020, <https://www.unenvironment.org/nairobiconvention/>). The International Union for Conservation of Nature (IUCN) outlines a typology and features of TBCA in general (Vasiljević et al., 2015). This document defines ecological connectivity for transboundary conservation as follows: ‘the movement of species and the occurrence of ecological processes (biological, geochemical and physical) are enabled by the existence of portions of one or more common (shared) ecosystems’, this is: across international borders.

The aforementioned technical policy document (MPRU/KWS, 2015) draws attention to mangroves as one of the eight listed main marine habitats in the Kenya-Tanzania transboundary area. Within mangroves of the Western Indian Ocean particularly, but also throughout its wide range in the Indo-West Pacific, *Avicennia marina* is a foundation species with an eurytopic nature and also with a pioneering potential. In several sites, its presence in landward as well as seaward mangrove zones is remarkable (Bosire et al., 2016). It is not threatened nor declining, its presence is however very much related to functional and pristine mangrove systems, with its share in ecosystem services of the entire system as well as through species-dependent services.

At present restoration and forest management in the transboundary area that we studied is not coordinated. In mangrove system conservation *A. marina* warrants attention, but it is not among the most frequently planted species in restoration or reforestation initiatives. This is due to the greater ease of planting Rhizophoraceae species (whether successfully or not), explaining their popularity (UNEP, 2020). Systematic, science-supported mangrove management, conservation and recovery within the area is mostly apparent in the Kenyan Mikoko Pamoa project of a community-based blue carbon initiative. The sustained presence and population health of *A. marina* depends primarily on natural recruitment, though it can be integrated in coordinated restoration. A detailed protocol for mangrove management and restoration through planting is offered in the guidelines by UNEP (2020). These do not call for genetic conservation and consideration of the genetic structure existing for any of the species including *A. marina*. Yet, the understanding and consideration of the genetic structure and connectivity between populations, if existing, of this foundation and umbrella species of the mangrove system within the proposed TBCA of Kenya and Tanzania contribute to the requirements as intended by IUCN (Vasiljević et al., 2015). Mangrove management must follow the precautionary principle, where genetic diversity offers potential of adaptation to local conditions as well as resilience to environmental change, though as yet it is impossible to provide evidence as to its importance for a slow turn-over long-lived tree species.

From our data on 12 sites in 6 estuaries within the 100 km Kenya-Tanzania coastal stretch, two patterns appear: an effect of geographic distance with a gradient of admixed gene pools among estuaries, with an overall south to north migration pattern (and areas of bidirectional flow), corroborating general expectations from regional ocean surface currents. Such flow is not incompatible with historical colonisation patterns from the early Holocene and it is probably ongoing today. In order to allow for biological spatial processes to take place (sensu

Vasiljević et al., 2015) and to both conserve genetic specificity as well as ecological resilience through connectivity and continued gene flow, the coordinated management plans to be developed within this TBCA must consider the coastal physical accessibility, crucial to propagule flow and successful replenishment or colonisation. Wherever (re)planting is foreseen (and this may expand in view of the carbon offset-related ecosystem services) the use of local planting material of *Avicennia marina* in nurseries must become a guideline in the standard protocols.

CRediT authorship contribution statement

Ludwig Triest: Conceptualization; Data curation; Formal analysis; Funding acquisition; Methodology; Project administration; Supervision; Visualization; Writing - original draft; Writing - review & editing. **Tom Van der Stocken:** Conceptualization; Methodology; Visualization; Writing - original draft; Writing - review & editing. **Tim Sierens:** Investigation; Writing - review & editing. **Emmanuel Kwikweta:** Investigation; Resources; Writing - review & editing. **Mwita M. Mangora:** Supervision; Writing - review & editing. **Nico Koedam:** Conceptualization; Funding acquisition; Methodology; Supervision; Writing - original draft; Writing - review & editing.

Declaration of competing interest

The authors declare no competing interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2021.109040>.

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