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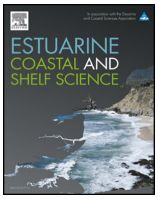

Migrant pool model of dispersal explains strong connectivity of *Avicennia officinalis* within Sundarban mangrove areas: Effect of fragmentation and replantation

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ABSTRACT

The ability of mangrove trees to reproduce and disperse in highly dynamic tidal environments is reflected in the contemporary genetic diversity and structure of their populations. Resilience and establishment may occur through either local recruitment (propagule pool model) or over longer distances with mixed origins (migrant pool model), thereby affecting the connectivity between natural populations. Anthropogenic activities such as encroachment and fragmentation or from mitigating reforestation could cause strategy switches and thus the connectivity and genetic structure of populations. In this study, we considered *Avicennia officinalis*, a dominant component of the Sundarban mangrove forest in Bangladesh to estimate dispersal dynamics over various distances within estuaries. A total of 423 individuals of *A. officinalis,* distributed over thirteen sites in the Sundarbans were sampled at both large and fine-scaled spatial level, the latter for comparison of natural and dense with fragmented sites. Up to 62 alleles showed a comparable level of allele diversity and gene diversities at both juvenile and adult life stages, assuming overall high levels of outcrossing. Significant inbreeding levels and high kinship values were solely observed at a reforested *A. officinalis* site. Genetic variables revealed high levels of connectivity between sites at close vicinity, with only a weak structure over larger geographic distances, between natural core Sundarban and coastal edge populations. Kinship coefficients were mostly low though significant up to several kilometers along estuarine branches, thereby suggesting propagule dispersal beyond each site. A fine-scaled analysis of kinship levels estimated for fragmented and natural forest plots along both sides of a river revealed that fragmentation induced higher kinship levels over 25–50 m distance, whereas dense natural populations were composed of less related individuals at shortest distances. *A. officinalis* populations might stay resilient through a mixture of unrelated propagules, clearly adhering a migrant pool model in natural sites and propagule pool model in fragmented sites. A poor gene diversity of planted trees might jeopardize the sustainability of mangrove plantation practices. Furthermore, high levels of diversity and connectivity indicated that the core Sundarban populations are a relevant source of germplasm in afforestation programmes.

1. Introduction

The deltaic Sundarban mangrove forest covers the plains that were formed by the continuous input of fertile alluvial deposits of the Ganges, Brahmaputra and Meghna rivers. Its rich floral and faunal diversity is therefore intricately linked to the ever-changing hydrodynamics in the Ganges Delta (Gopal and Chauhan, 2006). Surface elevation and small topographic changes have a strong influence on mangrove species distribution (Leong et al., 2017). Despite the rapid shoreline modification or disturbances and natural calamities, the considerable resilience of mangrove forest is remarkable over timescales due to the fast recruitment ability, which is a pioneer-phase characteristics of life-history traits (Alongi, 2008), whenever establishment is allowed. Regardless the vast area of the Sundarbans and a limited net loss of mangrove forest, the changes and turnover of deforestation and reforestation is considerable and resulted in degradation (Giri et al., 2007). The constant influx of fertile deposits has also been the main reason for the intensive human encroachment on the

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Sundarban ecosystem with subsequent degradation of its resources (Islam and Wahab, 2005). In general, exploitation of resources and habitat loss may result in the loss of genetic diversity by reducing the effective population sizes, which further highlights the necessity of integrated management schemes (Ledig, 1992; Ratnam et al., 2014). Genetic diversity and population structure knowledge is considered as crucial information for afforestation and for genetic resource conservation of mangrove trees (Maguire et al., 2000b; Giang et al., 2003; Arnaud-Haond et al., 2006; Homer, 2009; Salas-Levia et al., 2009; Céron-Souza et al., 2012; Islam et al., 2012; Zhang et al., 2015; Mori et al., 2015; Triest et al., 2018). The genetic diversity of a population reveals both the recent and past reproductive and dispersal dynamics (Assis et al., 2013), where the genetic composition of established juveniles reflect the most recent processes (Van Geert et al., 2008). Comparison of adults with juveniles or considering life strategies with asynchronous reproductive output (e.g. spawning period, surface current mobility of eggs and hatchlings) is often used in fish population genetic structure (Pacheco-Almanzar et al., 2017) and likewise, propagules of mangrove trees experience a floating period over various distances, at the dispersal stage. Conceptually, the source of colonizers could either follow a migrant pool model, where its colonizers originate from a pool of different but still highly connected demes - resulting in low differentiation despite multiple sources - or a propagule pool model, where colonizers come from a restricted pool of an already differentiated origin population, thereby giving high differentiation (Slatkin, 1977). Explorative studies can apply such simplistic models whereas detailed processes can be explained better with metapopulation models. Contemporary migration rates of *Rhizophora racemosa* from West Africa, indicated that colonization of a large Cameroonian river channel may have occurred following a propagule pool model, including indications of a most likely propagule source, whereas most populations of large estuaries follow the migrant pool model (Ngeve et al., 2016). A recent study of *Avicennia officinalis* L. populations along both sides of the Ganges in Bangladesh revealed that wide rivers may act as physical barriers and affected historical gene flow (Triest et al., 2018).

In this study, we focus on the local structure of *A. officinalis* in the natural dynamic Sundarban forest (Bangladesh) keeping in mind the extensive and intensive human exploitation activities in the sampling area and the hydrochorous dispersal of *A. officinalis* seedlings. A screening of the genetic diversity on different geographic scales can represent an effective tool to assess and subsequently manage the influence of human encroachment on the health status of the Sundarban mangrove forest. *A. officinalis* is a major constituent of this 4366 km^2 mangrove forest (Iftekhar and Saenger, 2008; Giri et al., 2011) and widely used in reforestation programmes in Bangladesh since 1966 (Rahman et al., 2010). The effectiveness of such restoration initiatives includes selection of suitable sites, quality checks of planting material and post-establishment monitoring (Rahman et al., 2010). Especially the hydrological suitability of a potential mangrove replantation site is an essential parameter that is often overlooked (Lewis III, 2005) and generally results in very low survival rates of planted seedlings (Ellison, 2000; Primavera and Esteban, 2008; Samson and Rollon, 2008). A focus on restoring natural processes and prerequisites for natural colonization are often a more efficient way to go forward (Lewis III, 2005) and maintain resilience. Along the Chittagong coastline, large-scale plantation schemes were undertaken in Bangladesh since 1966 (Rahman et al., 2010) and some of forested stands characterized by similar aged trees did show significant levels of inbreeding that might originate from the use of siblings and related propagules taken from similar mother trees (Triest et al., 2018).

Restoration of mangrove populations is a key aspect in any sustainable management programme, where artificial reforestation through planting of seedlings may alter the evolutionary continuum as it enables human-induced selection of a favorable gene pool (White et al., 2007). *A. officinalis* is a cryptoviviparous mangrove that disperses itself through buoyant hydrochorous propagules (Tomlinson, 1986). Because of *Avicennia*'s protandrous flower-developing mechanism, a wide range of mating systems, from selfing over biparental inbreeding up to high levels of outcrossing, can be expected (Aluri, 1990; Raju et al., 2012). Estimated outcrossing rates of different *Avicennia* species often suggest such a mixed mating system (Maguire et al., 2000b; Arnaud-Haond et al., 2006; Céron-Souza et al., 2012; Nettel et al., 2013; Mori et al., 2015; Hermansen et al., 2015). High outcrossing rates lead to increased genotypic diversity, which might facilitate the adaptability of a species to new areas (Proffitt and Travis, 2014). *Avicennia*'s mixed mating system may minimize the effect of population substructure and biparental inbreeding (Nettel et al., 2013). Mixed mating is suggested to be an evolutionary adaptation linked to their pioneer species strategy, as it allows for a special type of self-pollination (geitonogamy, involving pollen from other flowers of same tree) or by close relatives (Vallejo-Marín and Uyenoyama, 2004; Mori et al., 2015). Progeny thus can be ensured even when starting from a few founders. Besides sexual reproduction, a few studies demonstrated a possibility of vegetative reproduction through clonal growth of stems in several mangrove species. *A. marina* (*in vitro,* Alatar et al., 2015), *A. germinans* (*in situ,* Carmona et al., 2012) and *A. officinalis* (Das et al., 1997; Govindan and Kathiresan, 2015) showed potential for clonal propagation. We emphasize on 'potential', because even the *in situ* experiments applied root growth inducing hormones among other experimental manipulations. As far as we know, no clonal propagation has been experimentally demonstrated in *Avicennia* under natural conditions, though Tsuda and Ajima (1999) reported that *A. officinalis* is able to sprout again after harvesting, which could enable trunks to persist under the heavy exploitation for fuel wood and timber.

Within the wide Ganges delta, considering mangrove areas of Chittagong and Sundarban, a moderate level of genetic differentiation of *A. officinalis* populations was found over these distances up to 265 km (Triest et al., 2018). A genetic structure could be explained by both geographic distances and the presence of many large estuarine, North-South oriented, rivers as physical barriers (Triest et al., 2018). In mangroves, dispersal distance and directionality of propagules is predominantly determined by tidal river or ocean currents and by wind action (Van der Stocken et al., 2013, 2015a). Nonetheless, the dense root system of mangroves may obstruct the dispersal of propagules before leaving the site, thereby promoting dispersal over short distances (Van der Stocken et al., 2015b). Restricted pollen and non-random propagule dispersal may result in a fine-scaled genetic structure (FSGS) of juveniles established near adult mother trees (Céron-Souza et al., 2012; Mori et al., 2015; Ngeve et al., 2017a). Because only a very weak isolation-by-distance under a continuous distribution model was observed for *A. officinalis* within the Sundarban core region (Triest et al., 2018), we now further hypothesized that there would be ample gene flow over short distances, if not hampered by wide rivers acting as East-West barriers. Individual-based FSGS analyses allow to interpret and infer distances over which related cohorts of propagules might have established within a given plot and contemporary present as adult trees. It can be hypothesized that in the case of exposed, open, naturally flooded mangrove habitats there would be no or less spatial structure because of random mixed propagule migration across a particular plot, whereas varying degrees of anthropogenic pressures, mainly from encroachment, could lead to founders of local origin and show significant FSGS (Ngeve et al., 2017a). Mangrove areas bordering local villages, settlements and agricultural areas are subject to habitat fragmentation, and supposed to restrict the dispersal distance of propagules.

Our previous study on *A. officinalis* dealt with a genetic differentiation of two gene pools revealed over large geographic distances (hundreds of kilometers) or across wide rivers as potential barriers but also highlighted a smooth isolation-by-distance and ample gene flow within the diversity hotspot of the core Sundarbans (Triest et al., 2018). Further unraveling dispersal strategy and distances within the Sundarban gene pool of *A. officinalis* can be approached by comparing