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Research

Human-mediated dispersal redefines mangrove biogeography in the Anthropocene

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Introduction of species by humans breaks down biogeographic boundaries and results in the homogenization of species composition, yet empirical tests of this impact in marine forest ecosystems are still scarce. Large-scale planting aimed at reversing losses of mangroves has been the dominant strategy for mangrove restoration adopted by many organizations in the past decades, but there is a lack of quantitative understanding of the impacts of such large-scale plantings on mangrove biogeography. Here we used data collected before and after large-scale planting to compare the species richness and compositional similarities among 72 mangrove sites over a biogeographic scale (18–28°N) in China. After the large-scale planting, 15 of the mangrove species spread toward the higher latitudes, reflecting the geographical barriers of the mangrove plants have been broken. Local species richness of mangrove increased by 44.82% and biogeographic compositional similarity of mangroves increased by 13.33%, reflecting large-scale introduction and planting increase local diversity of mangrove but enhance biological homogenization. The dispersal limitation of mangrove communities reduced by 11.1%, which indicates that the community assemblage process of mangrove changed obviously. Worryingly, two alien species, *Sonneratia apetala* and *Laguncularia racemosa*, have dispersal across the biogeographic scale studied, reflecting an increase in the risk of biogeographic invasion. It is expected that biological homogeneity and species invasion will further influence the functional biogeography of mangroves. Our results highlight that mangrove biogeography is defined by human activities in the Anthropocene.

Keywords: Anthropocene, biogeographic invasion, biological homogenization, dispersal release, mangrove biogeography, massive introduction

Introduction

Natural biogeographic barriers cause dispersal limitation of species, which shapes 'classical' biogeographic patterns with increased dissimilarity in the community with increasing geographic distances (Nekola and White 1999, Thuiller et al. 2005, Alvarez-Noriega et al. 2020). In the Anthropocene, humans play a central role in shaping geology and ecology (Crutzen and Stoermer 2000, Steffen et al. 2016, Lee-Yaw et al.



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2019, Shoshitaishvili 2021). The Anthropocene theory suggests that human activities such as species introductions, artificial transplantations, trade and travel have facilitated breaching of natural biogeographic barriers, which results in species establishment in locations far away from their native range (Helmus et al. 2014, Capinha et al. 2015, Ellis 2015, Lundgren et al. 2018, Lee-Yaw et al. 2019). Ultimately, the ‘classical’ biogeographic patterns break down and novel biogeographic patterns emerge (Darling and Carlton 2018, Bernardo-Madrid et al. 2019, Sales et al. 2019). Artificial transplantations have intensified in frequency as a mean to restore damaged ecosystems across the globe and between geographic regions, which accelerates the speed at which plant species spread and colonize suitable areas across the globe and within the geographic regions (Malhi et al. 2014, Edwards et al. 2019). Ultimately, such interventions increase the local species richness and contribute to the homogenization of communities at both global and regional biogeographic scales (Dornelas et al. 2014, Fricke and Svenning 2020). A large number of theoretical studies suggest that with the breakdown of dispersal barriers, species and communities will progressively occupy their potential niches and expand their biogeographic distribution (Nekola and White 1999, Holt et al. 2013, Capinha et al. 2015). This dispersal release is expected to accelerate the speed of community homogenization among biogeographic regions (McKinney and Lockwood 1999, Olden 2006, Fricke and Svenning 2020).

Mangroves comprise a community of terrestrially derived coastal plants that provide key services and benefits to people (Ronnback 1999, Kathiresan and Bingham 2001, Donato et al. 2011, Lee et al. 2014). It is estimated that 2.1% of global mangroves have been lost between 2000 and 2016 at an average annual rate of 0.13% (Goldberg et al. 2020). Another estimation revealed that mangrove forests in southeast Asia between 2000 and 2012 were lost at an average annual rate of 0.18% (Richards and Friess 2016). These findings suggest that aquaculture, urbanization, coastal landfill, pollutions and climate changes are considered to be the driving forces of the mangrove lost (Duke et al. 2007, Richards and Friess 2016, Goldberg et al. 2020). Because of the recognized importance of mangroves, a set of actions have been taken internationally to rescue mangroves (Lee et al. 2019). Plantations play a dominant role in mangrove restoration projects (Ellison 2000). Efforts by individual nations and large international initiatives to protect or restore the mangroves have effectively reduced the loss of global mangrove area in recent years (Lee et al. 2019, Goldberg et al. 2020). For instance, China initiated a set of mangrove reforestation projects since the early 1990s, which resulted in the introduction of number of mangrove species and their spread around the southeast coast (18–28.3°N) (Ren et al. 2009, Wang et al. 2020). The total area of mangrove forests in China changed from ~22 000 ha in 2001 to ~30 000 ha in 2019 (Wang et al. 2020). Due to the large-scale planting, some native and/or alien species have spread across biogeographic barriers (Ren et al. 2009, Capinha et al. 2015). Despite the increase in mangrove area, knowledge of the effect of human

interventions such as artificial transplantation on the biogeographic pattern of mangroves is still lacking.

Here we report the results of a large-scale analysis comparing the biogeographic patterns of coastal mangrove forests before and after dispersal by humans in China. China initiated the first large-scale planting of mangroves in a 10-year mangrove reforestation project in the early 1990s (Ren et al. 2009, Wang et al. 2020). We collected species lists of introduced mangroves, defined as established species originating from human introductions, after 1990. Based on data available from the local forestry and ocean bureau system and field investigations, we collected species occurrence data at 72 sites across 11 degrees of latitude (18–28°N) where mangroves are distributed in China (Supporting information). For simplicity, range before human intervention is defined as locations where the mangrove species occurred before 1990.

Methods

Our study was conducted in 72 coastal sites across 11 degrees of latitude (18–28°N) in China, representing their present geographic distribution (Supporting information). Since 1990, China has invested significant resources in mangrove protection and restoration, mainly through large-scale afforestation (Ren et al. 2009, Wang et al. 2020). Therefore, species established before 1990 are identified as original species (i.e. species distribution before human-mediated dispersal), while those established after 1990 are considered as introduced species (i.e. species distribution after human-mediated dispersal). In this study, established species are defined as species that can grow naturally in coastal regions without artificial care, such as growing in a greenhouse. Extinction species are defined as species that have disappeared from the original distribution sites during our investigation. The species list method is a useful way to study biogeography (Capinha et al. 2015). We gathered the species list of each site mainly by field investigation (Supporting information). We also collected species occurrence data from the local government department (e.g. forestry and/or marine sector), with the literature also as a supplement. More information is presented in the Supporting information.

We quantified the number of species in two ways: 1) using only the original data, i.e. the latitudinal trends of species occurrence and richness before human-mediated dispersal – the original distribution; 2) using both original data and data on introduction – the current distribution. We performed simple linear regression based on Spearman’s correlation to probe the relationship between species richness (number of species) and latitude both before and after human planting (Beaugrand et al. 2002). Based on the species richness data, we used kriging interpolation to represent the species richness on the coast (Ter Steege et al. 2003). The difference of species richness between before and after human planting was analyzed by a permutation test in R, ver. 4.0. 2 (Anderson 2001, <www.r-project.org>).

Bray–Curtis similarity was used to indicate the similarity of mangrove species lists among any two local sites based on species lists based on 1) the original species distributions; 2) the current distributions (Capinha et al. 2015). The biogeographic pattern of mangrove species composition was visualized using non-metric multidimensional scaling (NMDS) based on Bray–Curtis similarity (Dixon 2003). Analysis of similarity (ANOSIM) was used to evaluate differences in species compositions among 10 locations at different latitudes (Dixon 2003). We also performed ANOSIM to test differences in mangrove composition between the original and current species lists. To reveal how (linear or non-linear) the compositional similarity of mangrove changed after human planting, we ran a generalized additive model (GAM) on compositional similarity before and after human planting (Elith et al. 2006, Ferrier et al. 2007, Murase et al. 2009). We compared the degrees of freedom (DF) of the GAM model between before and after the human planting. $DF=1$ suggests linear effects on mangrove composition; $DF > 1$ indicates non-linear effects on mangrove community structure (Guisan et al. 2002). The deviance explained (DE) of the GAM model indicates the mutual explanation rate of two communities before and after human planting (Guisan et al. 2002, Ferrier et al. 2007). Therefore, the degree of change in composition after human planting was calculated by 1-DE.

A null model based on Monte Carlo simulations of species matrix was performed to detect co-occurrence patterns of the mangrove species (random or non-random) (Gotelli and McCabe 2002). The null model was run in R, ver. 4.0.2 (<www.r-project.org>) to test whether the mangrove community structure was non-random (i.e. non-randomly aggregated or segregated) or random occurrence. The *C*-score (i.e. checkerboard score) was used as a metric of co-occurrence of mangrove species. The observed *C*-score was calculated and compared with the *C*-scores calculated for 5000 randomly assembled null models, estimating the probability that the observed (O) index was larger or smaller than the expected value (E) by chance (Gotelli and McCabe 2002). $O > E$ indicates negative co-occurrence (i.e. species are non-randomly segregated, resulting in less co-occurrence), whereas $O < E$ reflects positive co-occurrence (i.e. environmental filtering might cause community with similar species composition to be non-randomly aggregated). $O=E$ for *C*-score indicates random co-occurrence.

To test whether and how (non-randomly aggregated, or non-randomly segregated or random) the biogeographic pattern of mangroves varied with human-mediated dispersal, we calculated the standardized effect size (SES) for the presence/absence matrix using the following equation (Gotelli and McCabe 2002, Lessard et al. 2012):

$$SES = (I_{obs} - I_{sim}) / \varepsilon_{sim}$$

where I_{obs} indicates the observed value, I_{sim} is the mean simulated value and ε_{sim} is the standard deviation of simulated indices (Gotelli and McCabe 2002). The null hypothesis is

that the average $SES=0$ and that 95% of the I_{obs} will fall between 2 and -2 (Gotelli and McCabe 2002). A mean $SES > 2$ for the *C*-score indicates that mangrove species are non-randomly segregated, whereas a $SES < -2$ suggests that the mangrove species are non-randomly aggregated. The direction of the SES value (higher or lower than the expected null) is interpreted as over-dispersion or under-dispersion, and its magnitude represents the strength of the signal of the segregated or aggregated assemblages (Gotelli and McCabe 2002).

Results

The original distribution data set represented a subset of 24 species over a 9-degree latitudinal range comprising 484 occurrence records (Supporting information). The current distribution data set contained 578 occurrence records spread across a 11-degree latitudinal range, with a total of 26 species. Our introduced species data set contained 94 occurrence records spread across an 11-degree latitudinal range for a total of 18 species (Supporting information). The extinction species data set included 54 records spread across 8°, for a total of 10 species.

We found that species richness significantly increased after human planting (permutation test, p -value=0.01; Supporting information). Before large-scale artificial planting, the latitudinal distribution of mangroves in China ranged from 18 to 27.3°N and most of the species (>10) were distributed in latitudes lower than 20°N (Fig. 1a). After the artificial planting, the mangroves extended beyond 27.3–28.3°N and most of mangroves (>10 species) occurred up to 25°N (Fig. 1b). The biogeographic patterns of species richness (latitudinal trend of the number of species) between before and after human-mediated dispersal were significantly different (permutation test, $p=0.01$). The slope and intercept of the linear regressions after human-mediated dispersal were greater than those before human-mediated dispersal (SMATR test, $p < 0.05$; Fig. 1c).

Results show that the similarity of mangrove communities showed clear latitudinal trends both before and after human-mediated dispersal (Supporting information). More importantly, the geographical distribution of mangrove species after human-mediated dispersal was significantly different from those before human-mediated dispersal (Global $R=0.52$, $p=0.001$; Fig. 2a), suggesting that the distribution ranges of mangroves after human-mediated dispersal was greater than those before human-mediated dispersal (Fig. 2a). The similarity of mangrove community composition increased after human-mediated dispersal (Fig. 2b). Moreover, the GAM analysis showed that mangrove composition exhibited a clear non-linear relationship before and after human-mediated dispersal ($df=8.15$, $p < 0.001$, Fig. 2c). About 70% of the variation of the compositional similarities after dispersal mediated by humans could be explained by mangrove composition before human-mediated dispersal, i.e. about 30% of the variation of mangrove compositions was created by humans and environmental changes (Fig. 2c).

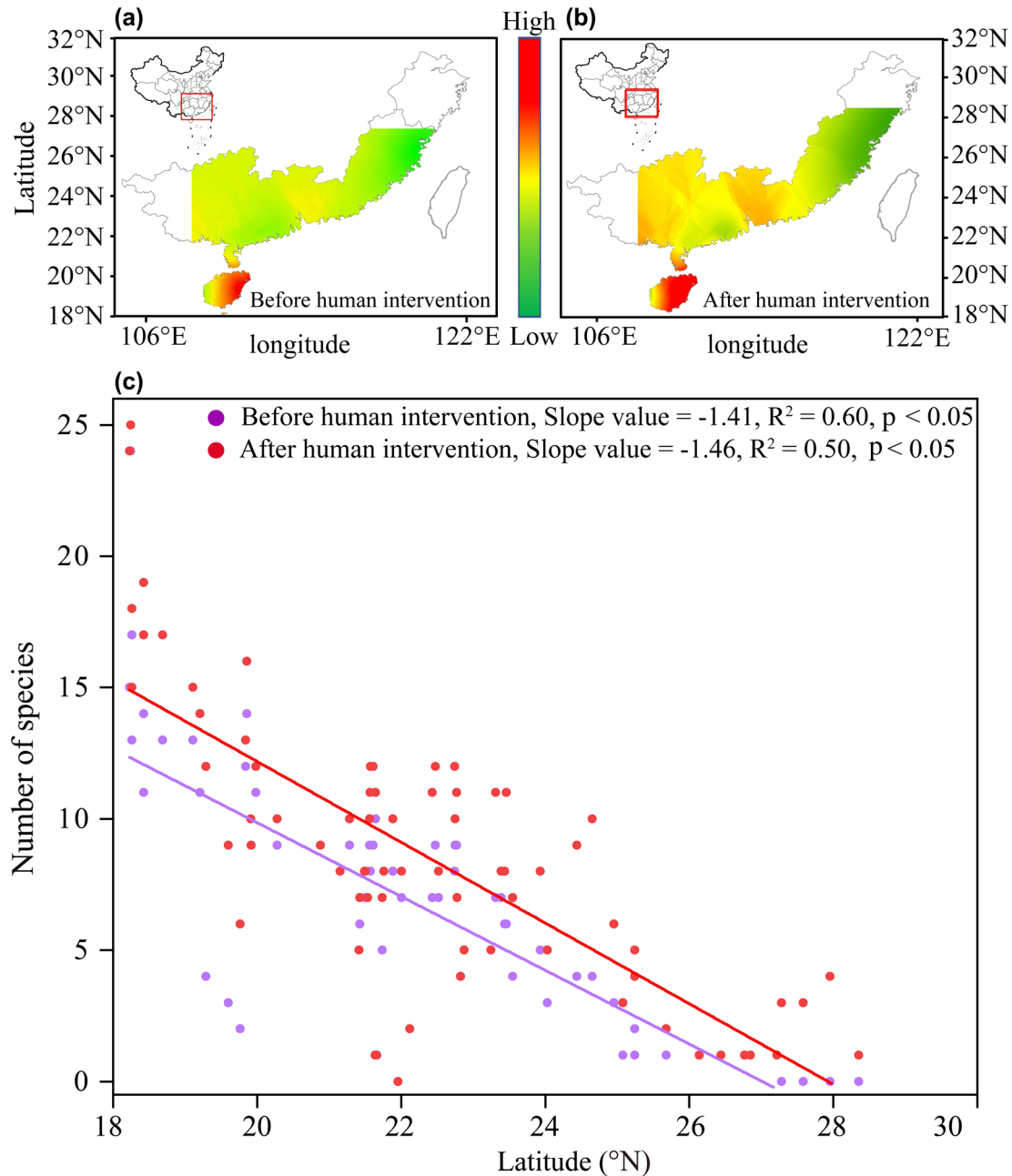


Figure 1. Biogeographic pattern of mangrove species richness. Map of species richness before (a) and after (b) dispersal by humans. Latitude trends of species richness before and after dispersal by humans (c).

The observed C -scores (Checkerboard score) were greater than those predicted by null models both before and after human planting (Supporting information), but the mean SES of mangrove composition after the dispersal by humans was lower than that before human-mediated dispersal (permutation test, $p < 0.001$; Supporting information). These findings indicate that human planting reduced the strength of non-random patterns of mangrove segregation at a biogeographic scale. Furthermore, the compositional similarities of communities both before and after human planting distinctly decreased with increasing geographic distance (Mantel test, Spearman's $r < 0$; $p < 0.01$; Fig. 3a), indicating that dispersal

limitations largely controlled the biogeographic patterns of mangroves both before and after human-mediated dispersal. The GAM results show that the non-linear effects of dispersal limitation increased (df-value increased from 5.75 to 6.75; Fig. 3b–c) but the strength of spatial limitation reduced (DE decreased from 32.3% to 21.2%; Fig. 3b–c) after planting.

Discussion

Humans have emerged as a strong force reshaping global ecology (Ellis 2015). Here, we demonstrate through a case study

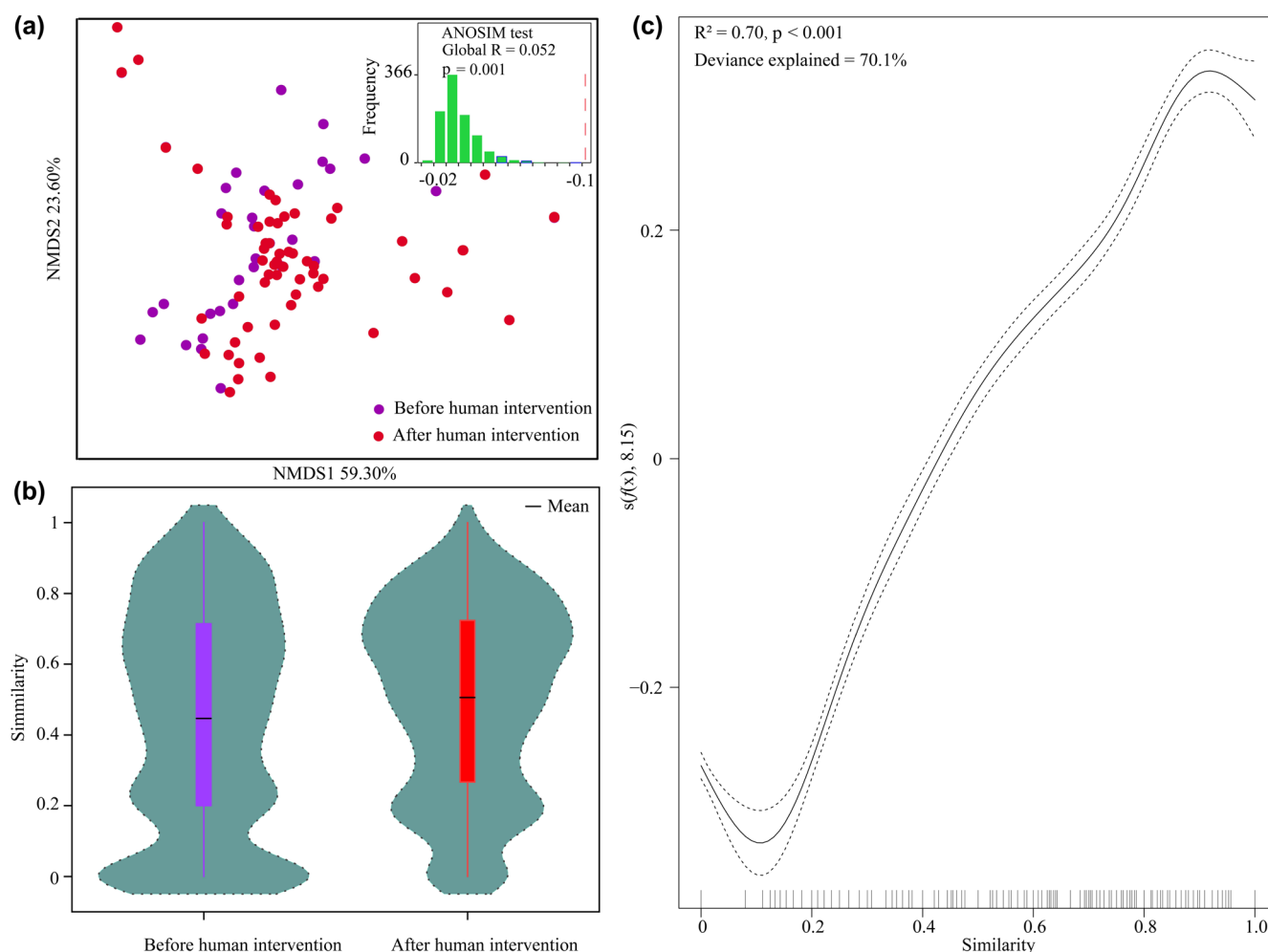


Figure 2. Compositional similarities of mangroves in China. Non-metric multidimensional scaling (NMDS) ordination based on Bray–Curtis similarity before and after dispersal assisted by humans (a). Violin plot of compositional similarity before and after dispersal by humans (b). Based on generalized additive model (GAM), non-linear relationship of compositional similarities between before and after dispersal assisted by humans (c).

in China that human-mediated dispersal (large-scale artificial planting and species introduction) has changed the biogeographic pattern of mangroves over a large spatial scale. Our results suggest that species introduction has already resulted in a modified biogeographic pattern of coastal mangroves. Furthermore, alterations in mangrove biogeography may be greater if exotic species are introduced. Species introductions triggered number of effects, including poleward expansions of mangroves, increase in local species richness, homogenization of communities on a biogeographic scale and dispersal release of species composition, which collectively eroded the strength of the segregated pattern of mangrove species associations at biogeographic scale. This shift highlights the effects of humans on the biogeography of mangroves.

Human-mediated dispersal broke down the biogeographic barriers of species

Theoretically, dispersal is a critical process that determines the geographic distribution of a species. Dispersal as a process

dominates the colonization and establishment of species in new habitats and unoccupied niches (Nekola and White 1999). Large-scale surveys have achieved significant advances in evaluating the dispersal of coastal and marine biota (Van der Stocken et al. 2019a, 2019b). These studies suggest that the spatial dispersal of marine taxa such as mangroves is controlled by natural barriers, including climatic discontinuity, sea-level rise, geomorphology, tide regime, mesoscale eddies, the timing of reproduction, fecundity and body size (Van der Stocken et al. 2019a, Wang et al. 2019). Notwithstanding, human activities (e.g. trade, travel and species introductions) have been breaching natural barriers to dispersal, resulting in an increasing number of species colonizing and establishing in locations far away from their native range (Capinha et al. 2015, Alvarez-Noriega et al. 2020). Our findings suggest that 15 of the mangrove species in China spread toward the higher latitudes after the human-mediated dispersal (Supporting information), including *Kandelia obovata*, *Rhizophora stylosa*, *Bruguiera sexangula*, *Bruguiera gymnorrhiza*, *Bruguiera sexangula* var. *rhynchoptetala*, *Excoecaria agallocha*, *Lumnitzera racemosa*,

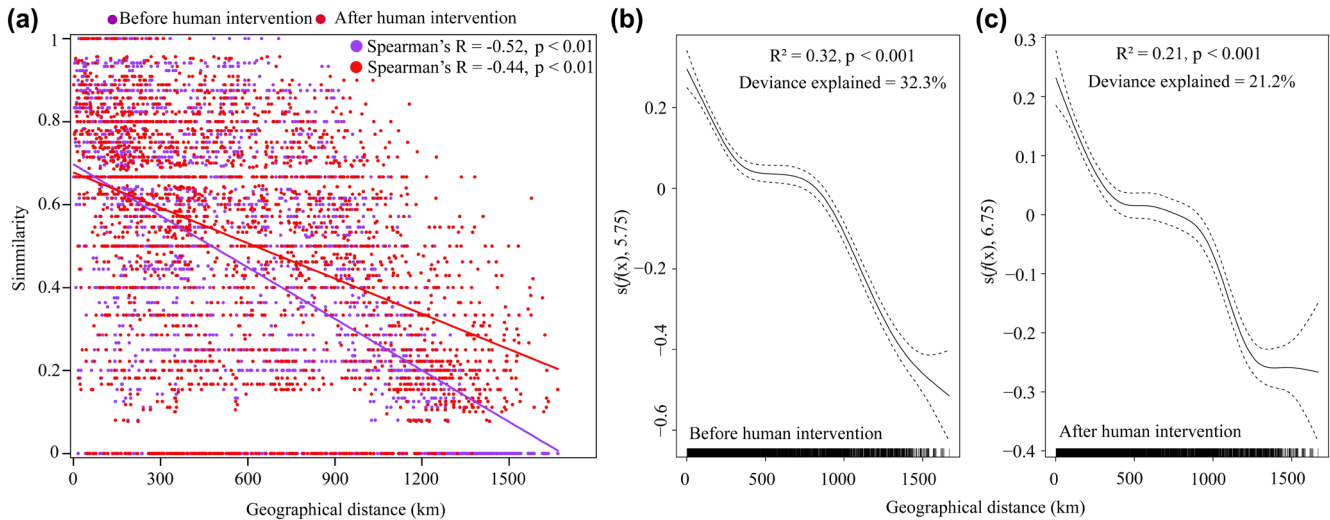


Figure 3. Relationship between compositional similarities of mangrove and geographic distances. Spearman's rank correlations between the Bray–Curtis dissimilarity of mangrove communities and geographic distance (a). Based on generalized additive model (GAM), non-linear relationship between the Bray–Curtis dissimilarity of mangrove communities and geographic distance before (b) and after (c) dispersal by humans.

Acanthus ilicifolius, *Aegiceras corniculatum*, *Avicennia marina*, *Xylocarpus granatum*, *Sonneratia caseolaris*, *Sonneratia hainanensis*, *Sonneratia alba* and *Sonneratia gulngai*. The poleward extensions of *K. obovata*, *A. corniculatum* and *E. agallocha* have reached 28.4°N latitude, which was a significant change (spread toward the higher latitude at distances of 1.1–4.5-degree latitudinal range) for these species. In China, *K. obovata*, *A. corniculatum* and *E. agallocha* are limited (by natural dispersal) in regions south of 27.3, 25.1 and 23.9°N, respectively (Li and Lee 1997, Chen et al. 2009, Wang et al. 2020). The poleward limit of mangrove plants is broadly set by the 20°C winter seawater isotherm (Duke 1992, 2017, Ellison et al. 1999). The theoretical and empirical research has suggested that climate warming will associate with shifts in the distributions of plant species toward higher latitudes (Chen et al. 2011) and decreased frequency of extreme cold event has resulted in the consequence of poleward extension of mangrove (Cavanaugh et al. 2014, Osland et al. 2017). Therefore, global warming and low temperature in winter may be the main factors affecting the expansion of current mangroves.

In this study, we highlight that human-mediated dispersal caused a consequence of the poleward extension of mangroves. On the one hand, compared with natural dispersal, mangrove plants can be more easily spread to high latitudes through artificial introduction. This easily breaks down the various biogeographic barriers (e.g. tide, environmental pollution and short-term vitality) in the process of mangrove immigration, and then even may result in successful colonization of some species under climate warming (Supporting information) (Hickling et al. 2006, Chen et al. 2009). On the other hand, the artificial introduction may break down the eco-physiological barriers of mangroves. For the successful colonization and establishment of mangroves at the local site (especially in high latitudes), a set of ecological domestications (e.g. low-temperature or/and high-salinity acclimation) by artificial selection may be carried out

before introduction (Supporting information), which would break down the eco-physiological barriers of mangroves (Larson et al. 2014, Ellis 2015). Additionally, the ecological domestication of mangroves will further occur in the introduction site after introduction.

Niche theory and meta-community theory suggest that species will occupy their potential environmental niche and develop resistance genes adapted to the local special environment when the geographic dispersal barriers are removed (Leibold et al. 2004, Giehl and Jarenkow 2012). Therefore, this human-mediated poleward expansion is triggering not only niche expansion but also other effects such as domestication of the resistant gene/species for cold resistance (Slatyer et al. 2013). Similar range extension is exemplified by the anole lizards, which broke through island barriers through human-aided transport and spread around the Caribbean islands (Helmus et al. 2014). Human transport also caused the breakdown of the 'classical' biogeographic regions of gastropods, resulting in changing global distributions (Capinha et al. 2015). In addition, a recent study focused on the introduction of aquatic non-indigenous species has suggested that over the past 50 years, on average one aquatic non-indigenous species broke its natural barrier under the influence of human activities every 8.4 days (Bailey et al. 2020). These findings suggest that human-mediated dispersal (including trade, travel and species introductions) have caused the breakdown of the 'classical' biogeographic regions that are largely determined by dispersal barriers and historical factors such as continental drift or paleoclimates (Young 2014, Capinha et al. 2015, Duke et al. 2017).

Human-mediated dispersal of exotic species increases the risk of invasion at biogeographic scale

The deliberate and accidental human-mediated dispersal is the main driving force that contributed to the dramatic

increase in global plants, animals and microbes over the past hundreds of years (Ellis 2015, Darling and Carlton 2018). Deliberate biotic introductions have resulted in adverse ecological invasions (Mack et al. 2000, Seastedt 2015). Two exotic species *Sonneratia apetala* and *Laguncularia racemosa* were deliberately introduced into China in the 1980s and began to spread widely as an afforestation species since 1990 (Ren et al. 2009, Wang et al. 2020). Currently, *S. apetala* and *L. racemosa* have spread throughout the southeast coast of China by a combination of human introduction and natural spread (Supporting information). The populations of these exotic species are sufficiently large that covers more than 3800 ha (He et al. 2018, Wang et al. 2020). Still, these species have not yet been defined as invasive in mangrove ecosystems in China (Ren et al. 2009, Wang et al. 2020).

Here, we try to discuss whether these exotic mangroves are possible to become invasive species based on the three classical phases of the process of invasion: introduction, naturalization and invasive (Richardson et al. 2000). The processes are defined as follows (Richardson et al. 2000): Introduction indicates that a species has been transported by human activities across a major geographical barrier; Naturalization only starts when barriers are overcome and do not limit the natural survival of individuals and regular reproduction; Invasion means that introduced plants produce reproductive offspring in areas distant from sites of introduction. At the stage of naturalization, the population size is sufficiently large that it will not be extinction due to environmental stochastic changes (Richardson et al. 2000). At the stage of invasion, the distance and time of species natural dispersal is generally >100 m over <50 years (Richardson et al. 2000).

In the past three decades, *S. apetala* has overcome the biogeographical barrier and spread throughout the southeast coast of China by a combination of human introduction and natural spread from 18°N to 28.4°N latitude (Supporting information). *L. racemosa* has similarly spread in latitudes between 18°N and 25.4°N (Supporting information). These exotic species have reproduced naturally and their populations are sufficiently large that covers more than 3800 ha in China (He et al. 2018, Wang et al. 2020). Obviously, with the help of humans, these exotic mangroves have passed the introduction stage and successfully entered the stage of naturalization in the past three decades. Previous studies that focus on the naturalization of *S. apetala* on Qi'ao Island have also confirmed this view (Chen et al. 2014). *S. apetala* and *L. racemosa* successfully naturalized in China might be via high trait plasticity (Fazlioglu and Chen 2020). Therefore, the time from introduction to naturalization of these exotic mangroves (*S. apetala* and *L. racemosa*) might be less than 30 years, which is much smaller than the mean time (149 years) from introduction to recorded naturalization of plants in northern Australia (Caley et al. 2008). These alien mangroves seem to be developing on the road of invasion at an alarming rate. This is contributed by human activities and their high plasticity and adaptability to environmental changes (Fazlioglu and Chen 2020).

However, deciding whether these exotic mangroves should be labeled 'naturalized, noninvasive' or 'invasive' can still be problematic. On the one hand, in the Zhangjiang estuary, a few seedlings of *S. apetala* have been observed in a site that is 13.6 km apart from the nearest planted forests with *S. apetala* community (Supporting information). Similar phenomena have also been found in other areas with mangroves distribution in China such as Zhanjiang, Yangjiang (Guangdong), Shenzhen, Kaozhou Bay and Dongzhai Bay (Supporting information). These mean that the propagules of *S. apetala* and *L. racemosa* can spread over long distances to establish naturally by wind, waters and animals in the past three decades, which is consistent with the definition of invasion. Importantly, the distance and time of these alien species natural dispersal is generally >100 m over <30 years, which is also consistent with the definition of invasion (Richardson et al. 2000).

On the other hand, the network analysis verifies that large-scale introduction of these exotic species reduced the modularization of the biogeographical network of mangroves in China (Supporting information), reflecting the stability of mangrove ecosystem reduced and ecosystem vulnerability increases with the introduction of exotic species (Grilli et al. 2016, Mo et al. 2021). Therefore, these exotic species may further erode the stability of mangrove ecosystem and then might enhance ecosystem vulnerability by a combination of human introduction and natural spread. Ecosystems with high vulnerability and low stability are more vulnerable to invasion (Romanuk et al. 2009, Grilli et al. 2016). Previous studies have verified that the plasticity of these exotic mangroves was greater than those of native species in China (Fazlioglu and Chen 2020), reflecting that these exotic mangroves might be more successful in competition with native species under the changing world (Ren et al. 2009, Fazlioglu and Chen 2020). Additionally, the allelopathy of these exotic mangroves may reduce the germination rate of seeds belonging to native mangrove species (Chen et al. 2020b, Fazlioglu and Chen 2020) and reduce biodiversity (e.g. microbial communities and benthic communities) in mangrove ecosystem (Yu et al. 2020), which weaken or even deprive mangrove ecosystem functioning and service such as carbon sequestration (Peng et al. 2016, Lee et al. 2019, Yu et al. 2020). Based on the framework of functional biogeography, which is defined as the analysis of the patterns, causes and consequences of the geographic distribution of functional diversity (Violle et al. 2014), this is bound to affect the functional biogeographic pattern of the mangrove ecosystem. This is might be a biogeographical ecological consequence of these alien species that large-scale planting by humans. Although some contributions debate that these species do not invade native mangroves (Chen et al. 2014), the living of the alien mangroves begins to have detectable ecological consequences, which is the point at the change from 'naturalized, noninvasive' to 'invasive' (Richardson et al. 2000). Therefore, these exotic mangroves (i.e. *S. apetala* and *L. racemosa*) may be moving toward the invasion at an unknown rate.

Furthermore, ongoing global changes (e.g. rising temperature, changed precipitation and increased CO₂) are

expected to increase species invasion risk (Mack et al. 2000, Bradley et al. 2010, Seastedt 2015). Therefore, the speeds from naturalization to invasion of these exotic species are expected to accelerate under the combined effects of global changes and artificial introductions, and therefore lead to risk of invasions. Deliberately introduced species by humans over large geographic scales may therefore lead to risk of invasions that change the biogeography of species groups and even alter the functional biogeography.

Human-mediated dispersal increased biogeographical homogenization

Although biotic homogenization may result in global or regional loss of species, local α diversity (e.g. species richness) may stay constant or even increase as invaders replace or coexist with natives (McKinney and Lockwood 1999, Olden 2006). Our results suggest that human-mediated species introductions significantly increased local species richness and resulted in the homogenization and dispersal release of species composition at a biogeographic scale. These suggest that human-assisted dispersal of species especially exotic species has sparked widespread changes in the biogeographical distribution of mangroves. This modification may result in two consequences: range expansions of introduced species (including exotic species and some native common species) and range contractions of local species (e.g. rare and endangered species) (Olden et al. 2004, Olden 2006). Therefore, the gradual replacement of specific local mangroves forms by generalist mangroves (i.e. including exotic mangroves and some native common species) in space and time and therefore results in 'mangrove homogenization'. Similar evidence shows that human-mediated species introductions homogenized the African and Eurasian mammalian biogeographic regions and the global invertebrate distribution (Capinha et al. 2015). Recent studies have also shown decreased dissimilarity in community composition across member taxa in various biotic groups (Olden et al. 2004, Fricke and Svenning 2020). A consensus views that human-mediated species introductions have already resulted in substantial biotic intermixing and contributed to the turnover of species composition and biotic homogenization (Young 2014, Capinha et al. 2015).

Additionally, biotic homogenization will result in a consequence of range contractions of some local species specifically rare and endangered species (based on the definition from the International Union for Conservation of Nature, IUCN). Indeed, we found that the population size of *Lumnitzera littorea* in the wild reduced greatly from 359 in 2006 to 12 in 2015 in the context of the continuous expansion of introduced species and the increasing pressure on the climate and environment (Supporting information). The wild populations of some mangrove species (e.g. *Rhizophora lamarkii*, *Sonneratia hainanensis* and *Sonneratia ovata*) are less than 50 around the coastal in China, which is increasing the risk of being replaced by other species (Supporting information). Niche vacancies caused by the population decline and locally extinct species will provide opportunities for the

establishment of other species (Seastedt 2015, Sanchez-Bayo and Wyckhuys 2019, Chen et al. 2020a). These changes in species composition usually lead to the development of novel ecosystems.

Implications for the restoration and conservation of global mangroves

The simplistic, piecemeal and short-sighted large-scale planting that resulted in human-mediated dispersal of mangroves has boosted mangrove areas in China since 1990 (Lee et al. 2019, Wang et al. 2020). However, this rapid reversal of the trend in aggregate mangrove area influenced important biogeographical processes, which is an important reference for the restoration and conservation biogeography of global mangroves. In this study, large-scale planting (human-mediated dispersal) indeed increased local species richness of mangroves and resulted in 15 of the mangrove species spread toward the higher latitudes and then changed the biogeographical pattern of mangroves in China. On the surface, this is a welcome turnaround in mangrove biogeographical conservation because local diversity and geographical ranges of mangroves have increased.

However, this turnaround poses potential risks to the biogeographical pattern of mangroves since it might be at the expense of sacrificing local endangered species, increasing biogeographic homogeneity and increasing the risk of species invasion. In the past three decades, 15 common local species and 2 exotic species contributed to the increasing of mangrove areas and the changing of mangrove biogeographical patterns via large-scale planting in China. The available living spaces of mangroves in the intertidal zone are very limited due to the impact of hypoxia stress caused by tidal (Lovelock et al. 2015). In the limited living spaces, the large-scale planting of common species and exotic species will seize the spatial niche of some local endangered species, and then squeeze the survival spaces of endangered species, which may eventually lead to the extinction of these species. Therefore, excluding the restoration of rare and endangered local species and blindly large-scale planting common and exotic species to increase local species richness and mangrove areas should be marked as short-sighted approaches (Lee et al. 2019).

Additionally, the functional biogeography of mangrove ecosystems is diverse because of their differences in geomorphologic and diversity settings in the geographical distributions (Lee et al. 2014, Duke 2017). Large-scale monospecific plantations lack the environmental complexity and species diversity at a biogeographical scale that underpins the functional biogeography of mangrove ecosystems (Friess et al. 2019). Worse still, in the past three decades, the plantations of exotic species (i.e. *S. apetala* and *L. racemosa*) account for more than 50% of the total plantation areas in China (i.e. cover >3800 ha) (He et al. 2018, Wang et al. 2020), which eroded the biogeographical network stability of mangroves. These alien species have successfully passed the naturalization stage and are moving toward the invasion stage. If global planting is accepted as an excuse for the introduction

of exotic species like in China, a world with invasive mangroves and even a world without functional mangroves could quickly materialize (Lee et al. 2019).

Currently, reversing global mangrove loss has become a global target. In this study, human actions such as large-scale planting directly influence the biogeographical pattern of mangroves. Therefore, a restoration program with a biogeographical framework should be considered to conserve global mangroves in the future. The restoration of rare and endangered species should be considered in the framework. Before a comprehensive assessment of ecological effects, be cautious or avoid using exotic species for large-scale planting.

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Data are available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.dr7sqv9zv>> (Chen et al. 2021).

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