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RESEARCH ARTICLE

Point of (no) return? Vegetation structure and diversity of restored mangroves in Sulawesi, Indonesia, 14–16 years on

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Mangrove forests, benefitting millions of people, experience significant degradation. Global recognition of the urgency of halting and reversing this trend have initiated numerous restoration activities. Restoration success is typically evaluated by estimating mangrove survival and area restored, while diversity and structure of vegetation, as proxies for functional forests, are rarely considered. Here we assess mangrove species richness along sea-landward transects and evaluate restoration outcomes by comparing number of mangrove species, relative species abundance, biomass, diameter, and canopy cover in "Monoculture Reforestation", "Mixed Species Regeneration" and adjacent "Reference" forest stands, 14 (Tiwoho site) and 16 years (Likupang site) after restoration activities took place. In the "Monoculture Reforestation" plots, mangrove diversity and structure still closely reflected the original restoration actions, with only one and two "new" species having established among the originally densely planted "foundation" species. In contrast, the "Mixed Species Regeneration" plots were more similar to the "Reference" plots in terms of tree diameter and canopy coverage, but species number, abundance and biomass were still lower. The trajectory of the "Mixed Species Regeneration" plots suggests their similarity with the "Reference" stands will increase over time, whereas such "smooth" transition is unlikely to happen in the planted "Monoculture Reforestation" stands, in the foreseeable future. Implementing frequent small-scale disturbances in restored forest management would increase stand structure and diversity, accelerating the establishment of a more natural, and likely more functional and resilient forest.

Key words: coastal management, mangrove forest, marine, regeneration, restoration

Implications for Practice

- "Mixed Species Regeneration" areas more closely replicated the structure and diversity of "Reference Forest" than "Monoculture Reforestations" after 14–16 years. This would not have been clear from using conventional methods of assessing tree survival and area restored only.
- When the goal is to bring back diverse, functional forests, the still common practice of planting seedlings of one or two species only, in narrow rows, must be discouraged.
- Creating small gaps in planted monospecific forests could help practitioners to drive plantations into more diverse and resilient mangroves.

Introduction

Mangrove forests are unique tropical and subtropical ecosystems. They offer essential habitat and nursery grounds for commercially important fish and other fauna (Robertson & Duke 1987; Mohamed et al. 2014; Huxham et al. 2017), can sustain the secondary production of fisheries resources (Sandoval et al. 2022), afford firewood, materials for the construction of houses and fishing gear and income (Djamaluddin 2004; Diele et al. 2010; Chow 2018), protect coastlines from erosion (Lee et al. 2014;

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Dasgupta et al. 2019), bioremediate and help mitigate climate change by sequestering carbon (Murdiyarso et al. 2015; Cameron et al. 2019; Jennerjahn 2020). Despite their ecological and economic importance, mangroves have experienced significant degradation and deforestation (Polidoro et al. 2010). In Indonesia, for example, at least 10%, and potentially more than 33% of the country's mangroves have been lost in the last decades (Kusmana 2014; Tosiani 2020; Arifanti et al. 2021). Shrimp aquaculture has been particularly damaging, with some estimates indicating a loss of approximately 800,000 ha of mangrove area in the 30 years following the shrimp pond aquaculture expansion policy (Ilman et al. 2021). Between 1987 and 2002, 123,000 ha of mangroves were legally degraded (Sukardjo 2006) and a range of illegal activities and pressures, including logging, mining, reclamation (Kusmana 2014; Arifanti et al. 2019; Arifanti et al. 2021) and pollution (Pramudji 2001) caused additional losses.

By raising awareness of the manifold negative consequences of mangrove loss, efforts to conserve them, and to rehabilitate or restore degraded mangrove areas have increased across the globe (Kairo et al. 2001; Dale et al. 2014; Feller et al. 2017), giving rise to tentative mangrove conservation optimism (Friess et al. 2020). In fact, restoration/rehabilitation (R/R) projects have nearly tripled in the last 20 years with the majority taking place in Southeast Asia and Brazil (Duarte et al. 2020). The government of Indonesia has boldly committed to restore 600,000 ha of mangroves by 2024, to help mitigate climate change and deliver its Nationally Determined Contribution Targets (adopting the concept of blue carbon), protect coastlines, and to bring back the many other ecosystem services that mangrove forests provide (Kompas 2021; Sidik et al. 2023). As in most other regions (Portillo et al. 2017), the Indonesian government's R/R actions often involve planting of propagules, or seedlings, and mangrove restoration is considered a success if the survival rate is ≥70% (Ministerial Regulation Forestry No. P.70/Menhut-II/2008). However, many mangrove restoration activities have failed, in Indonesia as elsewhere, due to, for example, selection of the wrong species (Alwidakdo et al. 2014; Barnuevo & Asaeda 2018), tidal abrasion/erosion (Alwidakdo et al. 2014), and pests and diseases (Alwidakdo et al. 2014; Makaruku & Aliman 2019). It is thus important that the environmental setting of an area to be restored is firstly adequately assessed (Balke & Friess 2016). Following the principles of ecological mangrove restoration (Lewis 1999), planting should only be conducted when natural propagule supply is absent, and if natural recruitment cannot be aided through hydrological modifications bringing back tidal inundation. Furthermore, when planting is the chosen method for restoration, it is desirable to consider not only area (successfully) replanted as the key metric for success, but also the diversity of the replanted forest (Lee et al. 2019). For example, a recent study has shown how the presence of species with different root structures diversifies habitat conditions. This complexity of the root structure results in a multifunctional ecological habitat (Vorsatz et al. 2021).

Mangrove restoration projects have also failed due to a lack of community involvement at the onset of projects, missing or inappropriate governance structures and misalignment of the objectives of external agents and local stakeholders (Field 1998). Mangrove restoration is often conducted as a "one-off" (Brown 2017; Kodikara et al. 2017; Lee et al. 2019) without adequate documentation and monitoring of success, unlike restoration projects conducted for other ecosystems (Mazón et al. 2019). Moreover, aspects related to diversity, ecological functions and resilience are rarely monitored (Yando et al. 2021).

Here, we assess plant species diversity and forest structure at two restoration sites in Northern Sulawesi, Indonesia, one representing an estuarine and the other a coastal fringe geomorphological setting, to inform future restoration activities. Between 2003 and 2005 degraded former shrimp pond land was restored by local communities at both sites. Different levels of hydrological interventions (none, digging trenches, and opening locks of shrimp ponds) and restoration measures were conducted, the latter involving areas of both monospecific planting in dense rows and a mixed approach of facilitated natural regeneration following initial random planting of several species. We evaluated the success of the different restoration actions taken, going beyond the typically used metrics "area restored," by assessing species diversity and structure of these mangroves relative to the method used to restore them, and how they compare to nearby reference stands 14 or 16 years on. Our study reveals significant differences between the restored sites with implications for future mangrove management strategies.

Methods

Study Area

Two restoration sites of similar age presenting different geomorphological settings were selected, Likupang (16 years old restoration site; 1°40′11.40″N 125°2′13.45″E), a riverine/estuarine low intertidal mangrove and Tiwoho (14 years old restoration site; 1°35′41.57″N 124°50′41.75″E), a coastal fringe mangrove part of the Bunaken National Park, at the north and west coast of North Sulawesi, Indonesia (Fig. 1), respectively. The mangrove forest at Tiwoho is situated on a relatively narrow elevated intertidal zone between the sea and mountainous hinterland and receives a smaller input of sediment and freshwater compared to Likupang. Seaward the Tiwoho forest is bordered by seagrass meadows and coral reefs. Both sites experience semidiurnal tides.

The two restoration sites have similar elevation (approximately 4.5 m above sea level) and experienced semidiurnal tides during the study period. Tidal inundation was monitored between July 18, 2019 and August 2, 2019 at Tiwoho and August 3, 2019 and August 21, 2019 at Likupang (Hobo Onset Water Level Loggers 0–4 m). At the estuarine Likupang site, the forest floor was inundated daily during the entire monitoring period. In contrast, at Tiwoho's fringing mangrove system, flooding only occurred at 8 out of the 15 monitored days (O'Connell et al. 2022). Maximum tidal ranges at Likupang were 140 and 60 cm at spring and neap tides, respectively, and 30 and 5 cm at Tiwoho.

Two wind systems affect local weather conditions at the two sites. The north-westerly winds from the South China Sea arrive in North Sulawesi in November, the onset of the rainy season. The dry season under the influence of south-easterly winds blowing from the wintery Australian land mass towards Eastern

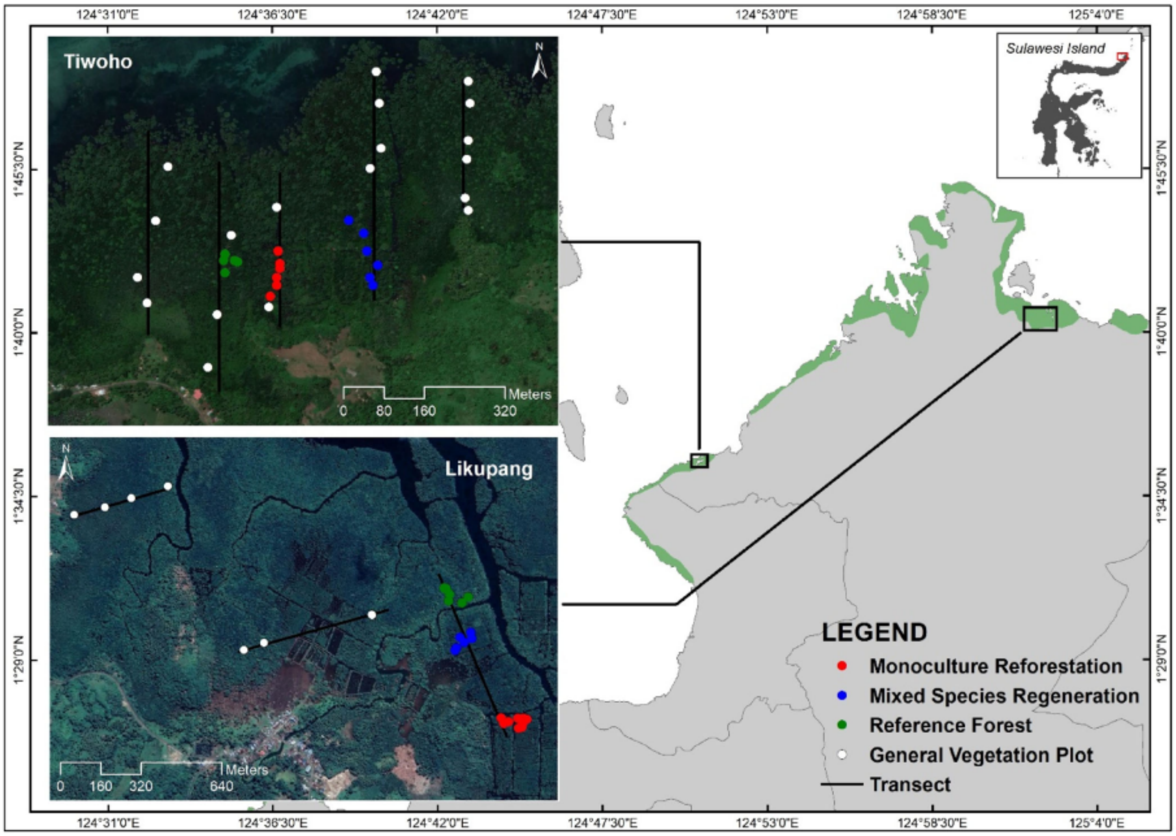

Figure 1. Location of the two focal study sites, the coastal fringing mangrove at Tiwoho and the estuarine mangrove system at Likupang, North Sulawesi, Indonesia. Inserts: Position of transects and plots (colored circles) at each site.

Sulawesi is usually short, extending from August to November or early of December. Total annual rainfall ranges from 2,501 to 3,000 mm, and air temperature varies little throughout the year, ranging between 25.[illegible] and 27.0°C (Djamaluddin 2019).

Likupang and Tiwoho have a similar history of deforestation for shrimp farming. In Likupang, approximately 500 ha of the approximately 900 ha of the estuarine riverine/system had been cut down in 1985 (personal communication of villagers). After shrimp farming had become unproductive due to disease and water fouling, most areas were left fallow for 8–10 years. In 2003, approximately 40 ha of this degraded area was restored by a community-based mangrove restoration initiative. Since regular tidal flooding still occurred, only the locks between ponds had to be opened, and in the following years dykes/dams broke down naturally. Most of the area (approximately 33 ha) was reforested with *Rhizophora mucronata* planted in narrow rows (i.e. Likupang "Monoculture Reforestation"). In the remaining approximately 7 ha of the area, an approach of facilitated regeneration was taken. Some few propagules and saplings of *R. apiculata* and *R. mucronata* were initially randomly planted (not in dense rows), followed by natural regeneration (i.e. Likupang "Mixed Species Regeneration"). Directly to the north of the former aquaculture area a large mature mangrove forest had remained that had never been logged for aquaculture. It served as the "Reference" stand for the Likupang site in this study (see below).

In Tiwoho, in 1991 approximately 15.2 ha of mangroves were cleared followed by construction of aquaculture ponds (Djamaluddin et al. 2019*b*). As in Likupang, the ponds quickly became unproductive and were abandoned in 1993. The area remained unused until a community-based restoration program was launched in 2004 (Brown & Djamaluddin 2017). The aim of this community-based project was to facilitate natural secondary succession of mangroves for most of the restoration area (approximately 13 ha). Man-made drainage channels were therefore filled in and dyke walls removed between November 2004 and February 2005 (Cameron et al. 2019; Djamaluddin et al. 2019*b*), which allowed the Tiwoho "Mixed Species Regeneration" forest to subsequently regenerate naturally (i.e. "Ecological Restoration," no facilitation planting involved). Nearby, monospecific planting with *Ceriops tagal* was undertaken in an area of approximately 2 ha, that is, the Tiwoho

"Monoculture Reforestation." The restored areas are surrounded by mature mangrove forest that has not been logged in the past (Cameron et al. 2019), which served as a "reference" area in this study (see below). In the following, when we speak of "14/16 years," we refer to the onset of restoration activities at Tiwoho and Likupang, respectively.

The two focal mangrove systems differ in their management status. The Likupang mangroves fall under the local coastal forest status, regulated by the local government at regional level, under the category of "protected forests" under North Minahasa Regency Regional Regulation No. 1 of 2013 (https://peraturan.bpk.go.id/Home/Details/22655). Only nondestructive activities and ecosystem service uses are permitted (e.g. permitting fisheries but not timber extraction), that do not change the functioning of the forest. Due to the lack of a dedicated authority, activities undertaken in the Likupang mangrove forests are not monitored and law enforcement is absent. In contrast, the mangroves at Tiwoho have been part of the Bunaken National Park since 1991 and managed under the scheme of national regulation for conservation areas since 1993, with stricter monitoring and control through the park's authority compared to Likupang.

The vegetation surveys for this study were conducted in August 2019 for Tiwoho Site, and in September 2019 for Likupang.

Assessment of Overall Number of Mangrove Species (Land-Seaward Transects)

At each focal site, the number of mangrove species was first assessed along land-seaward transects placed across the mangrove area. At Likupang, three line transects were selected to represent all dominant mangrove communities present. A total of 31 plots (10 m × 10 m each) were sampled along the transects to assess the vegetation. At Tiwoho, five line transects were put in place to cover all dominant association types across the mangrove belt. A total of 36 plots (10 m × 10 m each) were sampled along the line transects.

Within plots, all specimens of true mangrove species (Tomlinson 2016) were identified. Species identification was based on morphological characteristics and compared with reference literature (e.g. Ding-Hou 1958; Mabberley et al. 1995; Noor et al. 2006; Tomlinson 2016).

Comparative Assessment of Vegetation Structure, Diversity, Aboveground Biomass and Canopy Cover in Restored Plots Versus Reference Plots

Through comparison of vegetation structure and diversity of the mangroves inside the "Monoculture Reforestation," "Mixed Species Regeneration" and "Reference" stands, we assessed current status and similarities between the different methods of restoration and the reference forests 14- and 16-years post restoration.

For this comparison, a total of six 10 × 10 m "treatment comparison plots" from the total vegetation (transect) survey (see respective section above) were used per restoration area ("Monoculture Reforestation" and "Mixed Species Regeneration"), as well as the nearest forest stand that had not been deforested for aquaculture, serving as the "Reference" area. The total number of plots considered for the comparison was 18 in Likupang and 17 in Tiwoho, where only 5 plots were sampled at the reference area.

The vegetation structure inside the plots (as also true for all other data) was analyzed separately for Tiwoho and Likupang, given that the two focal sites have different geomorphological settings. Compositional analysis of the vegetation inside the plots was conducted to explore the difference in species composition among the three treatment areas (i.e. "Monoculture Reforestation" "Mixed Species Regeneration" and "Reference") using the R packages mvabund and ecocopula (Wang et al. 2012; Popovic et al. 2019; R Core Team 2020) that allow to perform Multivariate Generalize Linear Models using a negative binomial distribution. We tested for differences in the chosen uni- and multivariate response variables (number of mangrove species, Shannon diversity and compositional diversity, respectively) among the three treatments, with treatment being our categorical explanatory variable (three levels: "Monoculture Reforestation" "Mixed Species Regeneration" and "Reference"). To consider spatial pseudoreplication, "plot" was selected as a random factor within each treatment area. Prior to running the analysis of variance statistical tests, the underlying assumptions were checked, and DBH and Circumference response variable were log transformed from normality. To calculate species representativeness of the plots used for the comparison of the three treatments, the number of species contained in these plots was compared to the overall floral species surveyed in the forest running a Venn-diagram analysis using the R package ggVennDiagramm (Chen & Boutros 2011). Results are visualized by Chord diagrams using the package circlize (Gu et al. 2014).

Inside each plot, tree diameter and height (the latter not presented here) were measured to estimate aboveground biomass. Diameter measurements using a measuring tape were made at breast height (about 1.3 m) for trees with a single stem. For multi-stemmed trees, all stems were measured at about breast height. For mangrove shrubs, diameter measurements were made at the base (i.e. the lower part of the stem approximately 10 cm above the aboveground root system).

Aboveground biomass (AGB) is presented for the treatment plots. It was calculated using the equation proposed by Komiyama et al. (2005):

$$W_{top} = 0.251 \rho D^{2.46}$$

where W_{top} (aboveground biomass, kg), ρ (wood density, g/cm^3), D (diameter breast height, cm). In this study values of wood density followed Komiyama et al. (2005) that were 0.475 for *Sonneratia alba*, 0.770 for *Rhizophora apiculata*, 0.746 for *Ceriops tagal*, 0.701 for *R. mucronata*, 0.699 for *Bruguiera gymnorrhiza*, and 0.7316 for *Avicennia marina* (World Agroforestry Centre 2021).

Canopy closure inside the plots was also assessed, using an across wire on a free-swinging vertical tube with a 45° mirror, developed by Winkword and Goodall (1962) and adapted for mangroves by Djamaluddin (2004). Measurements were made when the movement of foliage was minimal as recommended by Specht and Morgan (1981).

Results

Assessment of Overall Number of Mangrove Species (Land-Seaward Transects)

A total of 24 true mangrove species were identified across both sites, belonging to 11 families and 15 genera (Table 1). At Tiwoho, 22 species, from 11 families and 14 genera were recorded (Table 1), three were widely distributed across the forest, including *R. apiculata*, *Sonneratia alba*, and *Bruguiera gymnorrhiza*. In the landward zone, *Acanthus ilicifolius* was common. 11 of the 22 species were categorized as uncommon and seven as rare. The latter were found at higher elevations further inland, including one *S. ovata* specimen.

At Likupang, 21 species, from 10 families and 14 genera, were observed (Table 1). Nine were common throughout, including two species of *Rhizophora* (*R. mucronata* and *R. apiculata*), *S. alba*, *B. gymnorrhiza*, and in the landward margin *B. sexangula*, *Avicennia marina*, *Acanthus ilicifolius*, *Nypa fruticans*, and *Xylocarpus granatum* were common. Eight species were uncommon and four rare, including *Avicennia alba*, *Pemphis acidula*, *Bruguiera parviflora*, and *Excoecaria agallocha*. In the restored areas *R. mucronata* was the dominant species.

Comparative Assessment of Vegetation Structure, Diversity, Aboveground Biomass, and Canopy Cover in Restored Versus Reference Plots

Number of Species in Treatment Plots Compared to Transect Surveys. At both Likupang and Tiwoho, the "treatment comparison plots" contained fewer species than encountered across the entire land-seaward transect sampling. The Likupang treatment plots contained 68% (see Fig. 2. for absolute species numbers) of the species in total, with 17 and 42% each for the "Monoculture Reforestation," "Mixed Species Regeneration" and 58% for the "Reference" treatment areas, respectively (Fig. 2A). In Tiwoho, the "treatment comparison plots" contained 75% of the species found along the total length of the land-seaward transects, with 38, 50, and 63% for the "Monoculture Reforestation," "Mixed Species Regeneration" and "Reference" treatment areas, respectively (Fig. 2B).

Community Structure

Alpha Diversity and Aboveground Biomass. Overall, species number (Fig. 2A,B) and likewise Shannon alpha diversity (Fig. 3A,B) differed significantly between treatments in both Likupang (Shannon diversity: analysis of variance [ANOVA], $F_{[2,15]} = 6.81$, $p < 0.001$) and Tiwoho (Shannon diversity: ANOVA, $F_{[2,15]} = 4.33$, $p < 0.05$). However, pairwise comparison revealed that at both sites only the difference between "Monoculture Reforestation" and "Reference" was significant.

Relative species abundance (i.e. individuals per species in [illegible]) shows a clear trend at both sites, with a dominance of *R. mucronata* and *C. tagal* in Likupang's and Tiwoho's "Monoculture Reforestation" treatment area, respectively (Fig. 3C,D). Aboveground biomass revealed a clear pattern with lowest values for "Monoculture Reforestation," intermediate values for "Mixed Species Regeneration" and highest values for "Reference" (Fig. 3E,F).

Table 1. Presence of true mangrove species at Tiwoho and Likupang. *** (common species—widely distributed or consistently found in low, middle, or high intertidal zones of the transects), ** (uncommon species—found only at specific localities), * (rare species—very occasionally found only), X (absent)

Family	*Species*	*Tiwoho*	*Likupang*
Acanthaceae:	*Acanthus ilicifolius* L.	***	***
	Avicennia marina (Forssk.) Vierh.	**	***
	Avicennia alba Blume	X	*
Arecaceae:	*Nypa fruticans* Wurmb.	**	***
Combretaceae:	*Lumnitzera littorea* (Jack) Voigt	**	X
Euphorbiaceae:	*Excoecaria agallocha* L.	*	*
Meliaceae:	*Xylocarpus granatum* J.Koenig	*	***
	Xylocarpus moluccensis (Lam.) M.Roem.	*	**
Primulaceae:	*Aegiceras corniculatum* (L.) Blanco	**	**
Pteridaceae:	*Acrostichum aureum* L.	**	**
	Acrostichum speciosum Willd.	**	**
Rhizophoraceae:	*Bruguiera gymnorrhiza* (L.) Lam.	***	***
	Bruguiera parviflora (Roxb.) Wight & Arn. ex Griff.	*	*
	Bruguiera sexangula (Lour.) Poir.	**	***
	Ceriops tagal (Perr.) C.B. Robinson	**	**
	Ceriops zippeliana Blume	*	X
	Rhizophora apiculata Blume	***	***
	Rhizophora mucronata Poir.	**	***
	Rhizophora stylosa Griff.	*	**
Rubiaceae:	*Scyphiphora hydrophyllacea* C.F.Gaertn.	**	**
Lythraceae:	*Pemphis acidula* J.R.Forst. & G.Forst.	X	*
	Sonneratia alba Sm.	***	***
	Sonneratia ovata Backer	*	X
Sterculiaceae:	*Heritiera littoralis* Aiton	**	**
Number of species		22	21

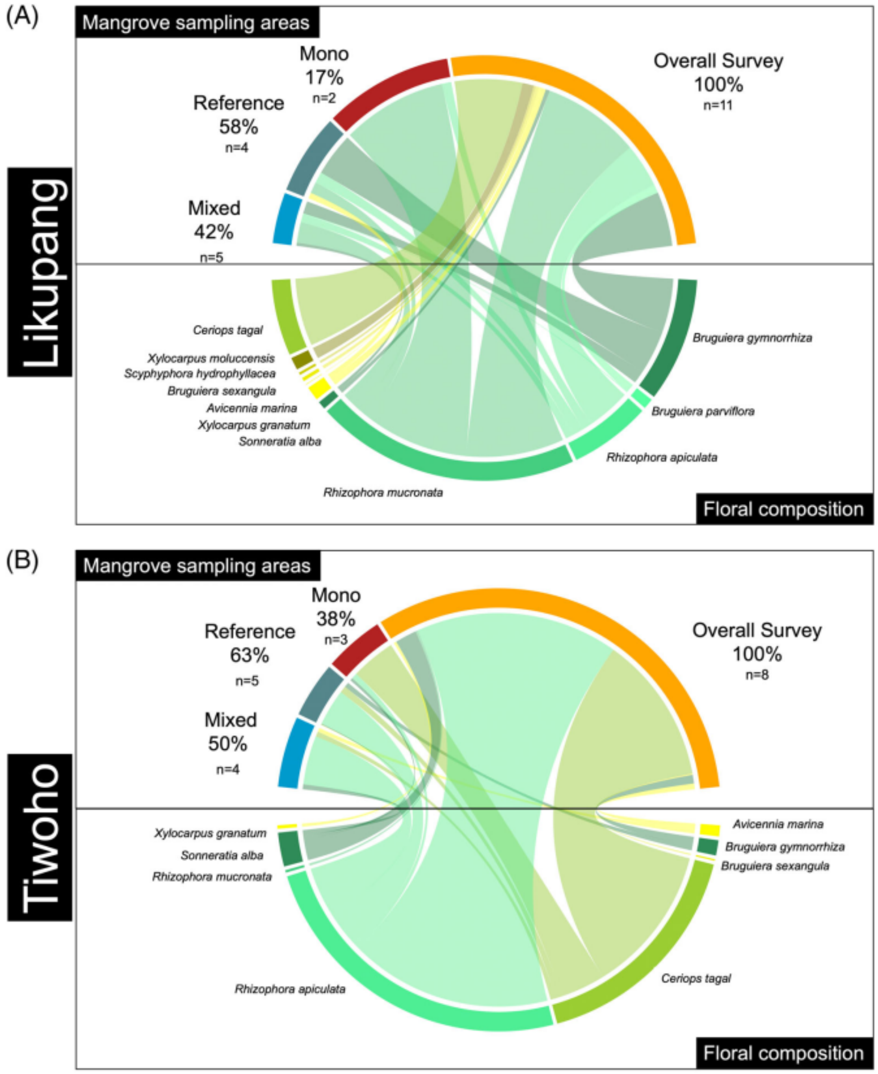

Figure 2. Chord diagrams showing the proportion of mangrove species present in the treatment areas "Monoculture Reforestation," "Mixed Species Regeneration" and "Reference," compared to the species encountered in plots over the entire length of the land-seaward transect survey sampling, at Likupang and Tiwoho, respectively. Numbers underneath % values indicate the number of species encountered.

Beta Diversity

Compositional analysis revealed a significant difference of the floral community among the three treatments (Fig. 4A,E, Table S1; Manyglm for Likupang $\text{Deviance}_{2,15} = 80.91$, $p < 0.001$; Manyglm for Tiwoho $\text{Deviance}_{2,15} = 61.67$, $p < 0.001$) and clearly separated communities (Fig. 4) at both focal sites: in Likupang the main discriminatory species was *B. gymnhorrhiza* (Fig. 4B), with highest abundance in the "Reference" area, while *R. mucronata* (Fig. 4C) was significantly more abundant in the planted "Monoculture Reforestation" area compared to "Mixed Species Regeneration" and "Reference." *S. alba* (Fig. 4D) was only present in the "Mixed Species Regeneration" plots (albeit in low numbers). In Tiwoho, *R. apiculata* abundance was higher in the "Mixed Species Regeneration" and "Reference" areas than in the "Monoculture Reforestation" (Fig. 4F), where *C. tagal* was significantly more abundant (Fig. 4G). Although not frequent, *B. gymnorrhiza* was significantly more abundant in the "Reference" plots than in the other two treatment areas.

Structural Parameter (DBH and Canopy Cover)

The difference in floral composition is mirrored by different structural parameters inside the areas investigated, that is,

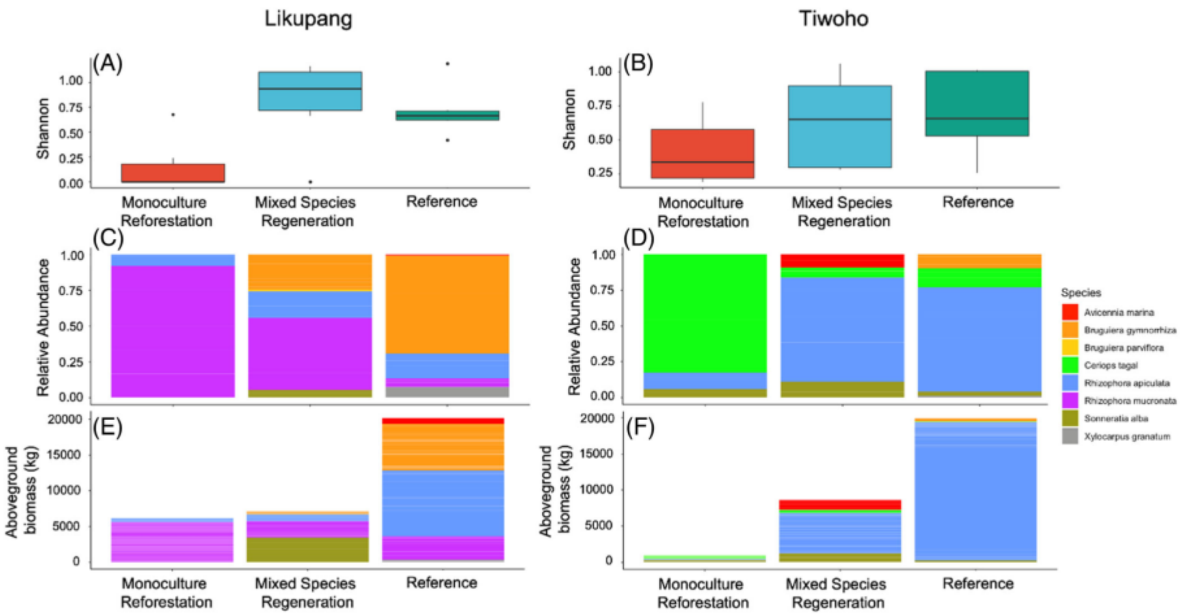

Figure 3. Alpha diversity (calculated as Shannon index) (A,B); relative abundance (C, D); total standing stock aboveground biomass (E, F) at the two focal sites Likupang and Tiwoho, respectively.

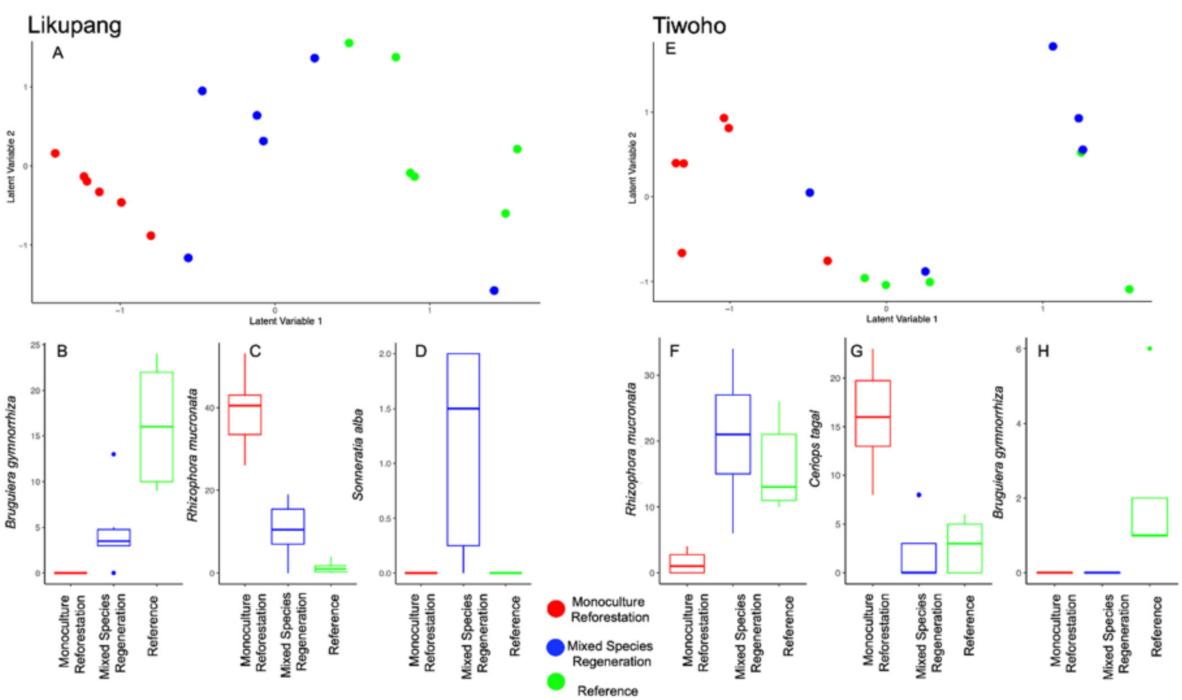

Figure 4. (A,E) Ordination analysis using latent variable methods to explore the floral composition in the treatment areas ("Monoculture Reforestation," "Mixed Species Regeneration" and "Reference") at Likupang (B-D) and Tiwoho (F-H). For each of the discriminant mangrove species identified, the y-axis reports the abundance as the number of individuals per 100 m^2.

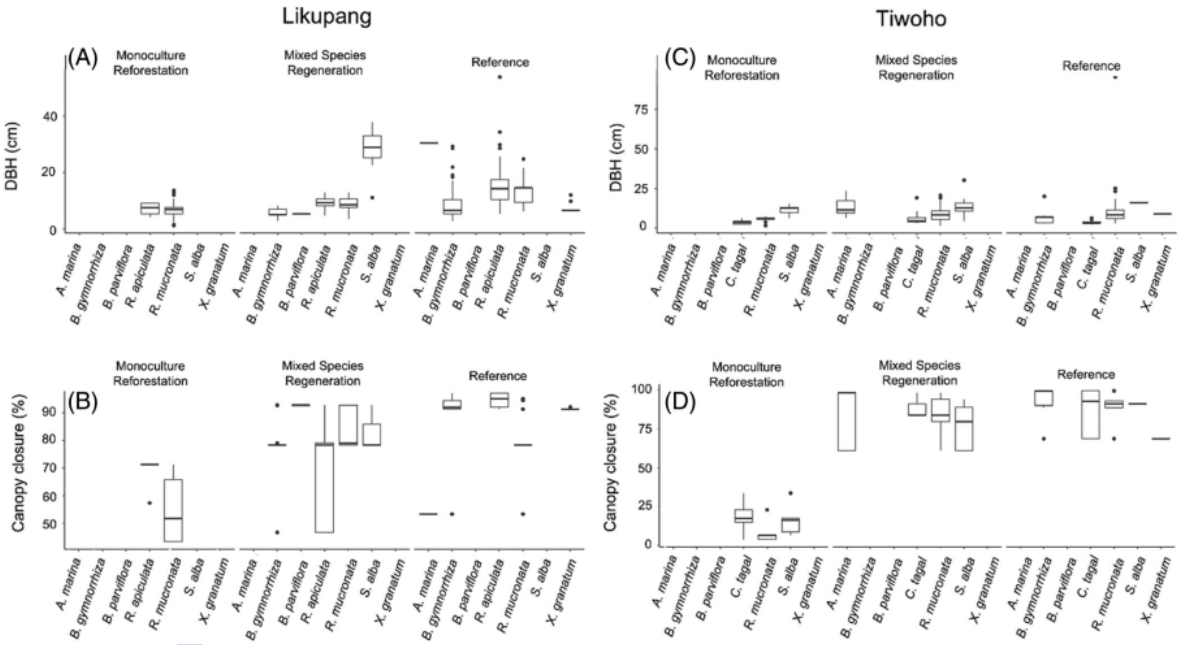

Figure 5. (A,C) DBH (Diameter at Breast Height) for each mangrove tree species at the two study sites, Likupang and Tiwoho, respectively. (B,D) canopy coverage of the mangrove tree species across the three treatment areas studied for Likupang and Tiwoho, respectively.

canopy cover (Likupang $F_{[3,505]} = 30.6259$, $p < 0.001$; Tiwoho $F_{[4,342]} = 4.0711$, $p < 0.001$) and diameter (Likupang $F_{[3,505]} = 0.7096$, $p < 0.05$; Tiwoho $F_{[4,342]} = 2.3234$, $p < 0.05$) of the mangrove trees inside the treatment plots (Table S2; Fig. 5). The trees inside the "Monoculture Reforestation" area in Likupang had a similar canopy cover ranging from 50 to 70%. In Tiwoho, despite (again) similar tree diameter, canopy coverage in the "Monoculture Reforestation" area was around 25%, hence leaving most of the area uncovered by the vegetation. In the "Mixed Species Regeneration" areas at both focal sites, tree diameter was significantly larger than in the "Monoculture Reforestation" area. In both treatments, *S. alba* had the largest diameter. The "Reference" area in Likupang had the highest tree diameter across all species, while at Tiwoho, tree diameter in the "Reference" area was similar to the "Mixed Species Regeneration" area. At both focal sites, "Reference" and "Mixed Species Regeneration" areas had almost full canopy cover, with 85 and 75%, respectively.

Discussion

We evaluated mangrove restoration success using several biodiversity and forest structure indices, going beyond the minimally adequate metrics of survival rate and area restored.

With a total of 24 mangrove species from 11 families and 15 genera (sea-landward transects), species richness at our two study sites in North Sulawesi is high, in line with what can be expected for this Indo-pacific biodiversity hotspot (Struebig et al. 2022). Similar species numbers are known from Tomini Bay, North Sulawesi (Utina et al. 2019; Djamaluddin et al. 2019*a*), central Sulawesi (Wahyuningsih et al. 2012), Papua (Prawiroatmodjo & Kartawinata 2014; Dharmawan & Widyastuti 2017; Wanma et al. 2019), eastern Kalimantan (Ardiansyah et al. 2012; Warsidi & Endayani 2017) and northern Philippines (Primavera 2000). The absence of *L. racemosa* and *B. cylindrica* at our Tiwoho study site is noteworthy since both species are present in several locations nearby (Djamaluddin 2018), pointing to differences in microhabitat conditions. Mangrove species vary in their tolerance to, for example, duration of tidal flooding, degree of shading, elevation of the land, among other environmental variables (Kairo et al. 2001; Duke 2011). Accordingly, species composition varied in sub-habitats across Bunaken Island National Park in Northern Sulawesi, characterized by different tidal inundation, freshwater influence, nature of soil, and topography.

The three treatment areas at the two focal sites contained 68 to 75% of the total number of mangrove species recorded in the transect vegetation surveys (see above). 14 or 16 years after the restoration activities, species number (and also Shannon diversity) still clearly mirrored site history, with highest numbers in the "Reference" area (relative to transect survey: Likupang 58%; Tiwoho 63%; absolute species number: Likupang: 5, Tiwoho: 6), followed by the "Mixed Species Regeneration" (relative to transect survey: Likupang 42%, Tiwoho 50%; absolute species number: Likupang: 5, Tiwoho: 4) and "Monoculture Reforestation" areas (relative to transect survey: Likupang 17%; Tiwoho 38%; absolute species number: Likupang: 2, Tiwoho: 3). Relative species abundance similarly reflects past restoration regimes, with highest values for the "foundation" species planted in narrow rows in the "Monoculture Reforestation" stands at both sites.

14 or 16 years on, only one nonplanted species was found at the "Monoculture Reforestation" plots at Likupang (*R. apiculata*) and two in Tiwoho (*R. apiculata and S. alba*), demonstrating the low success of "newcomers" in getting established in the narrow rows of densely planted mangroves. Shading through dense canopy and roots have likely reduced the chance for establishment of naturally arriving propagules, rather than a shortage of propagules of other species being flushed into the monoculture stands (since these were found on the ground). The more natural/stochastic restoration that was applied to the "Mixed Species Regeneration" treatments gave more opportunities for "new" species (i.e. Likupang—*S. alba*, *B. gymnorrhiza*, and *B. parviflora*; Tiwoho: all four species observed since none was planted) to establish, evidenced by the higher overall species number. While in the fringing mangroves of Tiwoho natural regeneration had to be facilitated by digging tidal trenches, in the estuarine forest of Likupang no other hydrological intervention than opening the locks of the shrimp ponds was necessary, but natural regeneration was initially facilitated by randomly planting saplings of *R. mucronata* and *R. apiculata* in low density.

Compared to more natural diverse forests with heterogeneous tree ages, monoculture mangrove plantations are more vulnerable to stand diebacks and windfall, due to their homogenous cohort structure and regular spacing constellation (Kautz et al. 2011). A study from the Can Gio Biosphere Reserve, Viet Nam suggested the importance of small natural disturbances, such as lightning strikes, to mitigate against windfall in planted homogenous forests. In the absence of natural small-scale disturbances of sufficiently high-enough frequency, manually creating small gaps may be an appropriate management strategy to help drive such mangrove plantations towards more natural, resilient forests (Kautz et al. 2011; Vogt et al. 2013).

Similar to diversity and relative species abundance, mangrove aboveground biomass also reflected the history of the three treatment areas. At both sites it was highest in the old "Reference" stands. When comparing the two restoration treatments, aboveground biomass was lowest in the densely planted "Monoculture Reforestation" stands, due to lower tree-height and stem diameter. In the similar aged, more heterogeneous "Mixed Species Regeneration" stands, trees were higher and stems thicker. Mangrove "blue carbon" is stored above and belowground, with belowground carbon far exceeding aboveground stocks (Donato et al. 2011; Alongi et al. 2015; Malik et al. 2020). While it is vital to restore mangrove forests for climate change mitigation (to name just one of many more good reasons), it is of utmost importance to conserve the remaining valuable old natural mangrove forests, since carbon stores in these are often essentially irrecoverable on human timescales (Noon et al. 2022).

Mangrove compositional analysis of the three treatment areas revealed different floral communities, again mirroring the original restoration actions at each focal site. In Likupang, *B. gymnorrhiza* showing low abundance in the "Mixed Species Regeneration" area compared to the "Reference" area, where this species dominated, was likely suppressed by the success of *R. mucronata*, and, to a lesser extent, of *Rhizophora apiculata*, as well as *S. alba*. The presence of *S. alba* in the "Mixed Species Regeneration" area at this focal site illustrates how this pioneer species succeeded in self-colonizing the new habitat created after logging and the destruction of pond infrastructure. In the "Monoculture Reforestation" area this species was unable to establish within the narrow rows of planted *R. mucronata*. Considered a pioneer species, it is no surprise that *S. alba* did not occur in the plots of the older, more mature "Reference" area. In Tiwoho, the dominance of *R. apiculata* in the "Mixed Species Regeneration" area compared to the other two treatment areas likely resulted from the changes in habitat conditions following the hydrological restoration conducted. The hydrological restoration increased the level and duration of tidal immersion, and altered sediment texture, bringing back habitat conditions suitable for *R. apiculata* (Djamaluddin et al. 2019*b*). The improved hydrology also facilitated development and growth of the planted *C. tagal* seedlings in the "Monoculture Reforestation" area. Seedlings of *S. alba and A. marina* naturally established already within 3 years after the restoration activities had taken place (Djamaluddin et al. 2019*b*). *B. gymnorrhiza* was only found in the "Reference" plots. This particular species might have failed to establish in the ex-shrimp pond areas, as these areas were still waterlogged in the early stages of the hydrological restoration, hampering seedling growth. A previous study indicated that waterlogging is the most likely factor influencing the success of early establishment of *B. gymnorrhiza* seedlings (Ye et al. 2003). Why the species has not established in later years is not clear. Today, tidal inundation did not differ significantly between the three areas (O'Connell et al. 2022).

The differences in floral composition were also reflected by DBH. At Likupang, the higher variation in DBH in the "Reference" area compared to the other two areas was likely linked to the overall higher age of the trees, the lower density (*R. mucronata* compared to the planted trees in the "Monoculture Reforestation" plots) and higher species diversity. The highest DBH was recorded for the fast-growing *S. alba* in the "Mixed Species Regeneration" area, typical for pioneer species (Oliver & Larson 1996). Young trees of this species grow particularly fast compared to other species (Djamaluddin 2019). In Tiwoho, tree DBH in the "Mixed Species Regeneration" area was similar to the "Reference" area, where DBH was much lower than in the Likupang "Reference" area. The difference in DBH between the reference forests of the focal sites was likely related to their different geomorphology—Tiwoho being a drier fringing mangrove forest compared to the estuarine Likupang site.

The difference in floral composition was also reflected by canopy cover. Higher values in the "Reference" and "Mixed Species Regeneration" areas at both sites indicate more natural growth conditions compared to the densely planted trees in the "Monoculture reforestation" areas that likely experience much higher intraspecific competition and growth inhibition.

The key aim of the communities in Likupang and Tiwoho when deciding to restore their local mangroves was to bring back diversity, ecosystem functioning and provisioning services. Whilst the restored mangroves, particularly the "Mixed Species Regeneration" area, have begun to resemble the nearby reference sites, after only 14 or 16 years they still remain significantly different when compared with the chosen baseline. Mangroves vary largely in their recovery time following major disturbances, such as through deforestation or tsunami/earthquakes, from 10 to over 100 years, both within and between different mangrove areas (e.g. González et al. 2010). Furthermore, there is no standard as to what constitutes "recovery" since, in the case of restoration/rehabilitation (R/R) projects, this will depend upon the original goals of such projects. For example, if timber production for construction was the goal, R/R success would likely be reached faster than if bringing back biodiversity and complex ecological networks (O'Connell et al. 2022) was the goal.

Assessing R/R successes through comparison with present-day diversity and forest structure of nearby reference stands could benefit from complementary analysis of past variability of mangrove forests (Jeffers et al. 2015; Sheaves et al. 2021; Yando et al. 2021). For most mangroves, long-term monitoring of vegetation to track recovery time following disturbance is not available or only covers a short period of time at annual and occasionally at decadal resolution. Palaeoecological data generated by analyzing sediment cores for vegetation "proxies" (i.e. pollen) could provide pre-human impact vegetation baselines. However, even more important is their ability to identify long-term processes and cycles that allow natural resource managers to set targets bearing in mind a dynamic landscape (Willis et al. 2010; Wingard et al. 2017). Ecological baselines are arbitrary and refer to the state of a spatially delimited environment at a specific point in time. The decision of where to set the baseline is driven by the aims of the restoration project. Here we have followed the conventional method of comparing restored sites with a nearby reference site that had not been subjected to deforestation and establishment of shrimp aquaculture ponds. While the reference mangroves at both sites were more diverse and less degraded than the restored mangroves, little else is known about their own levels of environmental degradation. Archeological evidence attests to the common exploitation of mangroves throughout prehistory across Southeast Asia (e.g. Rabett 2005; Boulanger et al. 2019; O'Donnell et al. 2020) and the impact of natural events can result in adjacent mangroves stands representing communities at different stages along the disturbance/recovery continuum. Incorporating archeological, historical and palaeoecological data in the future could therefore provide useful insight into the site-specific history of reference and restored mangrove areas alike to establish their natural ranges of variability and ensuring that sites are not restored or compared with a system in a different but already degraded state (Soga & Gaston 2018; Manzano et al. 2020).

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Supporting Information

The following information may be found in the online version of this article:

Table S1. ANOVA table (main test and pairwise comparison) of the multivariate generalized linear model analysis for the composition of the floral species among the three treatment areas for each study site (Likupang and Tiwoho).

Table S2. ANOVA table of the canopy closure and DBH among the species in the three treatment areas for each study site (Likupang and Tiwoho).

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