

Article

Litterfall and Associated Macrozoobenthic of Restored Mangrove Forests in Abandoned Aquaculture Ponds

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Abstract: Mangrove restoration projects are now widely established, aiming to regain the carbon benefit of the mangrove ecosystem that is essential for climate change mitigation. This study aimed to investigate mangrove litter as the source of carbon in restored mangrove forests in Perancak Estuary, Bali, Indonesia, which previously experienced substantial mangrove loss due to shrimp aquaculture development. We assessed the production and decomposition of mangrove litter and associated macrozoobenthic biodiversity in restored forests with plantation age ≥ 14 years and intact mangrove forests as the reference. The monthly production of three groups of mangrove litter (leaf, reproductive, and wood) was assessed over 12 months. A leaf litter decomposition experiment was performed to inspect the interspecific and disturbance history variation in organic matter formation among four major mangrove species: *Rhizophora apiculata*, *Bruguiera gymnorhiza*, *Avicennia marina*, and *Sonneratia alba*. Our results showed that annual litterfall production from restored and intact mangroves in Perancak Estuary were 13.96 and 10.18 Mg ha⁻¹ year⁻¹, which is equivalent to approximately 6282 and 4581 kg C ha⁻¹ year⁻¹ of annual litterfall carbon sink, respectively. Although restored mangroves had significantly higher plant litterfall production than intact mangroves, no significant difference was detected in leaf litter decomposition and macrozoobenthic biodiversity between these forest types.

Keywords: litter production; leaf litter; decay and decomposition; organic matter; macrozoobenthos; mangrove restoration; blue carbon



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1. Introduction

Mangrove forests are halophytic ecosystems that can be found extensively in intertidal zones from temperate to tropical climates around the world [1]. The importance of mangrove forests to reduce the impact of climate change has been highlighted in many studies [2–4]. Although they inhabit only 0.5% of the global coastal area, the capacity of mangroves to store carbon is one of the highest among other vegetated ecosystems, which are termed “blue carbon” [3,5,6]. The largest carbon stock in mangroves lies in their soil pools, accounting for up to 75% of total mangrove carbon stock in the system [5].

The accumulation of organic matter on mangrove forest floors is affected by the magnitude and frequency of tides, micro and macro-organism activities, tree species and litter composition, moisture, and temperature [7]. Mangrove litterfall is an important part of the net primary production (NPP), being one of the major autochthonous sources for the carbon budget in tropical estuarine and coastal ecosystems [8–10]. Leaf litter is the major component of mangrove litterfall, while other sources of plant litter produced by mangrove plants are flowers, propagules, or fruits and twigs [11–13]. Litter decay and decomposition

preserve mangrove ecosystem productivity through the recycling of nutrients stored in senescent plant tissues and fueling both the forests and aquatic habitats, contributing to estuarine and coastal food webs [14,15].

Southeast Asia (SEA) is globally recognized as a region of significant organic carbon sequestration and production due to the extensive area of mangrove forests and seagrass meadows as the blue carbon ecosystems [16–18]. Mangrove forests in this region have suffered a widespread decline over the last decades due to aquaculture and agricultural land conversion [19]. Mangrove conversion to aquaculture ponds is reported to be a significant contributor to greenhouse gas (GHG) emissions [20,21], and the disturbance of stored carbon in biomass and sediment due to pond construction is comparable to CO₂ released from land conversion in peat swamp forests [22]. Indonesia, as the largest SEA country, has the largest global carbon stores in its estuarine mangrove forests and coastal peatlands with ~50% of global inventories of tropical peat swamp forests and ~25% of mangrove forests [23,24]. Therefore, the disturbance and conversion of mangrove forests in Indonesia would potentially contribute to global CO₂ emissions [17,21,25].

The reconversion of abandoned ponds to mangroves can be a potential tool for rebuilding carbon stocks of degraded mangroves [26]. In SEA countries, including Indonesia, huge efforts have been made by both governmental and non-governmental actors over the past two decades to conserve and restore mangroves, and most activities are mainly focused on the monoculture plantation of *Rhizophora* spp. seedlings [27,28]. In this context, we selected Perancak Estuary in Bali, Indonesia as the study site, where the mangrove restoration in abandoned ponds has occurred in the past 17 years [29]. The development of shrimp and milkfish aquaculture farms in Perancak Estuary started in the 1970s when 440 ha of the mangrove area had been converted into fragments of intensive brackishwater aquaculture ponds (>50% of the lower floodplain area) [20,30]. After 30 years of production, the aquaculture industry collapsed in the early 2000s, leaving about 70% of the ponds abandoned [30,31]. The abandoned ponds were then either planted by *Rhizophora* spp. seedlings or left bare [30–32] and naturally revegetated after pond walls were damaged [33]. As result, the mangrove area in Perancak Estuary was expanded from 55 ha to 125 ha between 2007 and 2015 [30].

Relatively high rates of mangrove growth and gains in sediment accretion can be gained when a restoration project takes place in suitable sites and with appropriate methods, which are favorable for ecosystem service provision and climate change mitigation [26,34,35]. Thus, the study of the dynamics of mangrove organic matter formation between intact and restored mangrove forests is relevant to understanding changes in forest productivity and evaluating the restoration process. In this study, litterfall as the source of organic carbon and macrozoobenthos composition in restored mangroves in abandoned ponds were investigated with intact mangrove forests as the reference. There were two major processes that were assessed: plant litter production and breakdown. We chose leaf litter for the decay and decomposition experiment, as the major plant litter produced in mangrove forests. We hypothesized that (1) the rates of plant litter production in restored and intact mangrove forests are significantly different; (2) the composition of macrozoobenthic in restored and intact mangroves are significantly different; (3) the breakdown of mangrove leaf litter is significantly affected by mangrove species and forest type variation; (4) environmental conditions significantly affect the shedding of plant litter.

2. Materials and Methods

2.1. Site Description

Perancak Estuary is located within the village of Perancak and Budeng in Jembrana Regency, Bali Province (8°23′40″ S, 114°37′29″ E; Figure 1). Perancak River is the main distributary channel in the estuary catchment, which receives sediment loads from the upstream and transports them to the coast. The catchment is a complex zone with rice fields, active and abandoned aquaculture ponds, and mangrove forests. Perancak Estuary has minerogenic settings with alluvial platforms and a well-mixed diurnal tidal range [33,36].

Despite monoculture plantation of *Rhizophora* spp., recent observation showed that there are at least 21 true mangrove species found in Perancak Estuary [29]. Based on the important value index (IVI), which represents the species dominance in a given ecosystem, mangrove species in this site are dominated by (from the highest to the lowest IVI) *Sonneratia alba*, *Rhizophora apiculata*, *Avicennia marina*, *Bruguiera gymnorhiza*, *Rhizophora stylosa*, *Rhizophora mucronata*, *Ceriops decandra*, *Ceriops tagal* and *Excoecaria agallocha* [37].

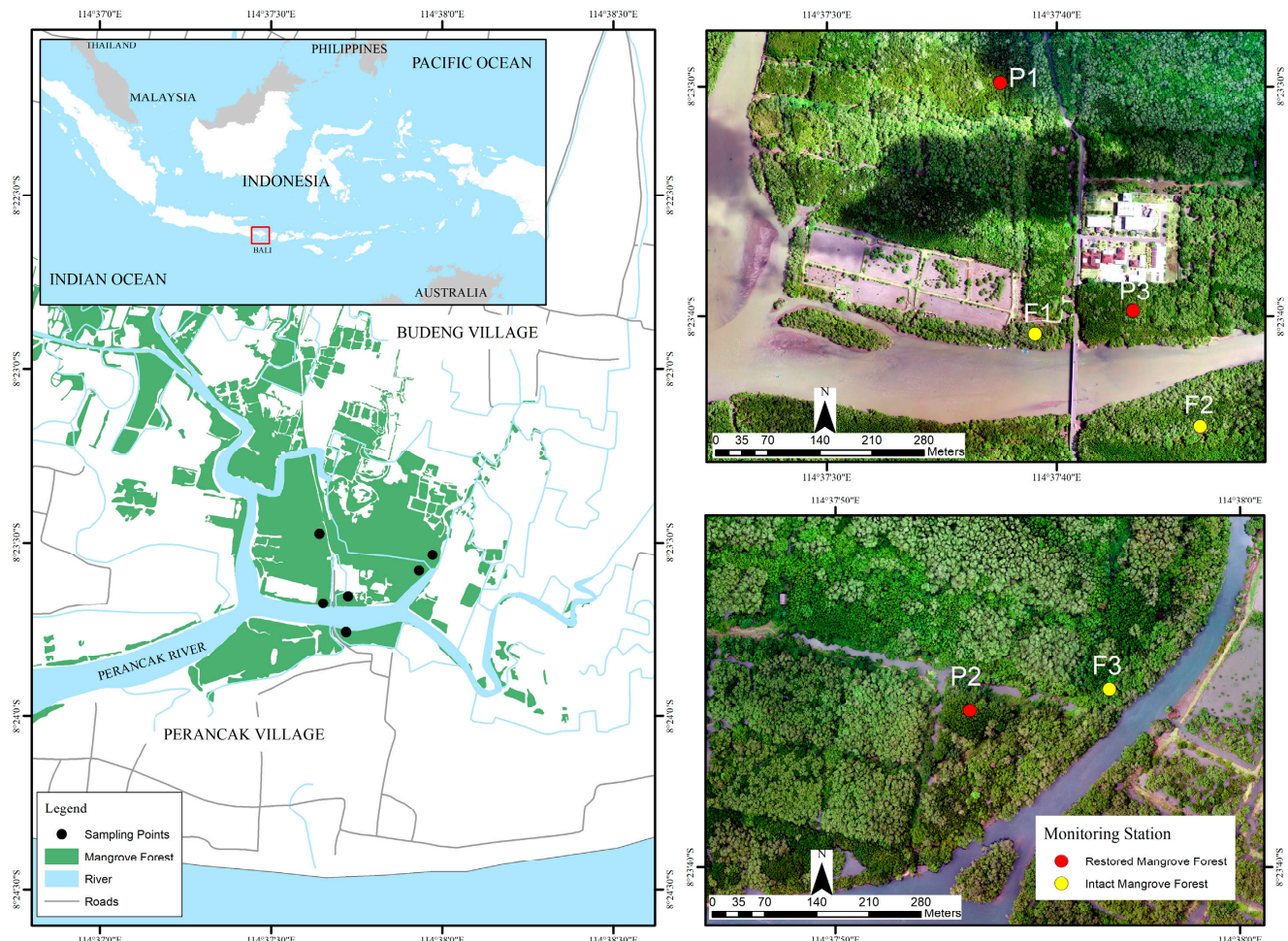


Figure 1. Location of study sites in Perancak Estuary. The monitoring station for litterfall production and leaf decomposition study comprises restored mangroves in abandoned ponds and intact mangroves, marked as P1–P3 (restored) and F1–F3 (intact).

The study sites were located on the land owned by the Institute of Marine Research and Observation (IMRO), where the abandoned ponds that were previously utilized for aquaculture research were partly planted with *Rhizophora* spp. or had undergone natural seedling recruitments. Then, these locations have become “open-air” monitoring stations and laboratories ever since. There are six permanent plots, consisting of three intact mangrove plots (Forest/F1–F3) and three restored mangrove plots in abandoned ponds (Pond/P1–P3) (Figure 1). The destruction of pond dykes has introduced tidal water exchange to the abandoned ponds, thus resulting in the dispersal and growth of unplanted mangrove species between planted species. Over the years, this natural recruitment allowed the planting site to resemble a similar forest structure to the intact mangrove forests (Table 1) [29,38]. In return, planting activity has caused the presence of *Rhizophora* stands in intact mangrove forests [30]. Forest age for restored mangroves in 2021 varies based on the time of the plantation, which is approximately 14 years for P1 and P3 and more than 15 years for P2 [30].

Table 1. Forest structure of Perancak mangroves based on a forest inventory survey in 2019 [38].

Plot	Forest Type	Abundance (ind/ha)	Basal Area (m ² /ha)	Species Richness (S)	Diversity (H')	Similarity (e)	Dominance (D)
F1	Intact forest	1233.77	22.61	19	1.51	1.09	0.34
F2		1753.25	16.62	27	1.53	0.95	0.27
F3		519.48	13.88	8	0.48	0.34	0.34
P1	Restored mangroves	1623.38	29.14	25	0.93	0.29	0.55
P2		909.09	18.85	14	1.53	0.95	0.27
P3		844.16	16.43	13	1.24	0.77	0.28

2.2. Plant Litterfall Production

Field campaigns consist of litterfall collection and porewater salinity measurement. Litterfall was collected using 1 mm mesh litter nets with a collection area of 0.25 m². Ten litter nets were set in each plot and placed at least 1 m above the ground surface to avoid tidal inundation. Damaged or lost litter nets were replaced at every sampling time. Litterfall was collected monthly between February 2020 and January 2021, placed in a plastic bag, marked, and then carried to IMRO Marine Research Laboratory where it was separated into three main categories: leaves (apical buds and stipules included), woods (i.e., branches and twigs), and reproductive parts (i.e., flower buds, flowers, fruits, and propagules). The assessment of genus-specific mangrove litterfall was also performed for three consecutive months from October to December 2020. Individual litterfall components were dried in a heating oven at 50 °C until reaching a constant mass value. The dry weight of each litterfall component was measured using a digital balance and the litterfall production was converted to carbon concentrations (kg C ha^{−1} year^{−1}) by multiplying by 0.45 [39]. We also separated the plant litterfall types from October to December 2020 based on their genera, to further understand the composition of the mangrove genus that contributes to litterfall production during the wet season. Porewater salinity was sampled at 30 cm sediment depth [40] in triplicate by a modified syringe on the same day as litterfall collection and then measured using a refractometer (Atago Master-S/Mill Alpha, Japan).

2.3. Leaf Litter Decay and Decomposition

To investigate the decay kinetics of leaf litter in intact and restored mangrove forests, the litterbag experiment was selected to study the breakdown of four major true mangrove species in the selected area, *Rhizophora apiculata*, *Bruguiera gymnorhiza*, *Avicennia marina*, and *Sonneratia alba*. Yellowish senescent leaves were randomly collected from the plants within the estuary. The leaf litter decay and decomposition of the above-mentioned species was performed following the litterbag experiment from [41], where the dry:fresh weight ratio was individually calculated for each litterbag. Litterbags were made of glass fiber mesh (200 mm × 200 mm, mesh size ~1 mm²). Three replicate bags for each species, sampling time, and site were randomly placed on the sediment surface, tied with cable ties to the roots, resulting in 288 data points in total. The experiment started in March 2020 and lasted for 42 days, with intermediate sampling at 14 and 21 days. The decay kinetics measured were the percentage of leaf mass remaining, decay rate, half-life (t_{0.50}), and 95% and 99% lifespans (t_{0.95} and t_{0.99}) [41,42].

2.4. Macrozoobenthos Sampling and Biodiversity Indices Assessment

Samples of macrozoobenthos were collected within three 1 m × 1 m subplots randomly selected from a 10 m × 10 m transect on the same day (9 March 2022). Sample collection was manually carried out during low tide using a portable shovel. The sediment samples were then sieved to separate macrozoobenthos from sediment using a sieve net filter (1.0 mm × 1.0 mm mesh size) [43]. Macrozoobenthos were placed inside a labeled sample bag and subsequently identified using a dichotomous key as previously reported [43,44]. After identification, the samples were rinsed with distilled water and placed inside a sterile

plastic bag containing 70% alcohol for preservation [45]. The validity of the scientific names was further confirmed by consulting the World Register of Marine Species database (<http://www.marinespecies.org>, accessed on 25 March 2022).

Sediment overlying water, termed as the water environmental parameter, was also measured during the macrobenthos sampling campaign, which includes water temperature, dissolved oxygen (DO), and pH. A water temperature (WT) measurement was taken using a portable thermometer. DO was measured by titrimetric Winkler procedure [45], while pH was measured using a pH meter (HM 30R, TOA DKK, Tokyo, Japan). Salinity (Sal) was measured using a refractometer (Atago Master S28 M, Tokyo, Japan).

The diversity index, similarity index, and dominance index were calculated according to [46]:

- (a) The diversity index (H') for each site was calculated using the following formula:

$$H' = - \sum_{i=1}^s P_i \ln P_i \quad (1)$$

where H' is the Shannon–Wiener diversity index, P_i is the proportion (n_i/N) of individuals of one particular species found (n_i) divided by the total number of individuals found (N), and S is the number of species.

- (b) The similarity index was calculated as follows:

$$E = \frac{H'}{H_{\max}} \quad (2)$$

where E is the similarity index (evenness), and $H_{\max} = \log S$.

- (c) The dominance index reflects the central level of dominance (mastery) in a community. The dominance index was calculated using the following formula:

$$D = \sum_{i=1}^s \left(\frac{n_i}{N} \right)^2 \quad (3)$$

where D is Simpson's dominance index.

2.5. Data Analysis

Prior to statistical comparison, data normality was tested using the Shapiro–Wilk test. Square root transformation was applied when necessary to meet statistical assumptions of normality. Data uncertainty was expressed in a $\pm 95\%$ confidence interval (95% CI) or $\pm$ standard deviation (SD). Two-way ANOVA was utilized to study forest type and monthly differences in plant litter production. For leaf litter decomposition data, the effects of interspecific and disturbance history differences on leaf decomposition over time were analyzed through repeated measures ANOVA. Student t -tests were performed to assess the significance of biodiversity indices of macrozoobenthos in intact and restored mangroves. Post hoc analyses of litter production and decomposition and macrozoobenthos datasets were performed using Bonferroni multiple comparison tests ($\alpha = 0.05$). The relationship between the leaf litter production and environmental and climatic data (porewater salinity, rainfall, wind speed, daylight hours, and air temperature) was determined using correlation coefficient matrices ($\alpha = 0.05$), and multicollinearity between environmental parameters was checked prior to matrix production, with Variance Inflation Factor (VIF) threshold of 5. Data analysis and visualization were performed using R ver. 4.0.3 and RStudio ver. 1.4.1103.

3. Results

3.1. Plant Litter Production

3.1.1. Monthly Mangrove Litterfall Production

During 12 months of observation, total litterfall production in restored mangrove forests was significantly higher than intact mangroves (two-way ANOVA $p < 0.0001$;

Bonferroni post hoc test $p < 0.0001$; Figure 2). Total litterfall was found to be the highest in May 2020 ($6.02 \pm 1.81 \text{ g m}^{-2} \text{ day}^{-1}$) and in October 2020 ($5.86 \pm 1.72 \text{ g m}^{-2} \text{ day}^{-1}$) in restored mangroves. The proportion of leaf litterfall dry weight may reach up to 97.8% of total litterfall, while for reproductive parts and wood litterfalls, the highest percentages were 32.5% and 36.9%, respectively.

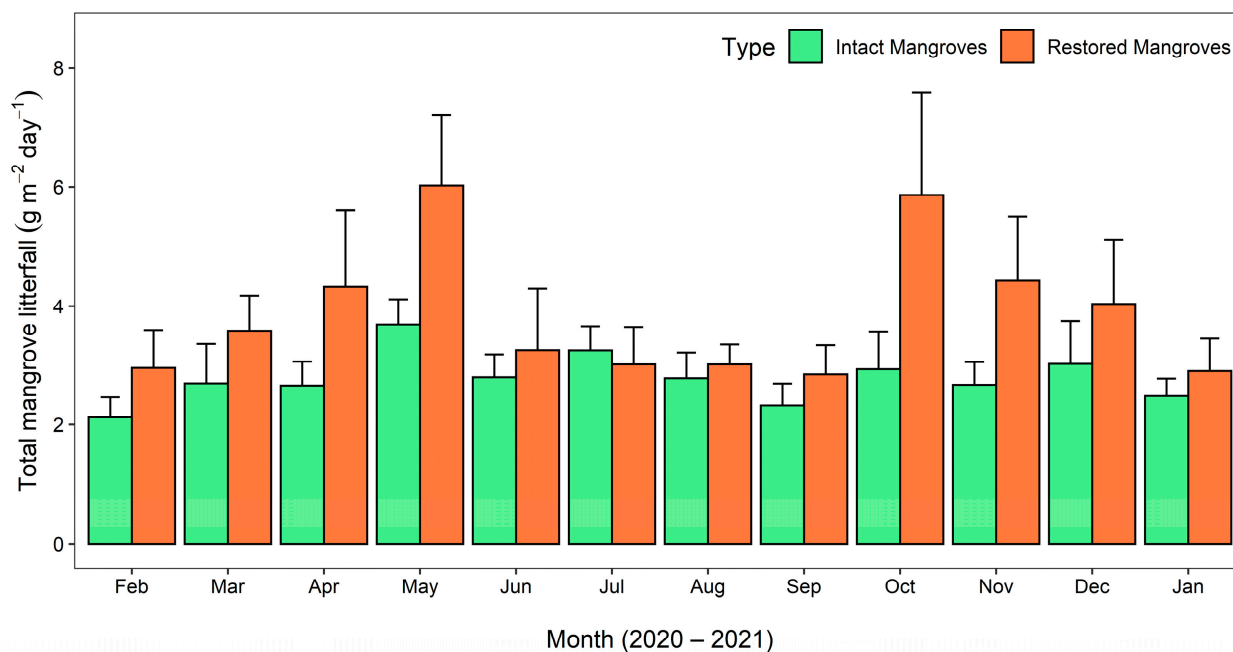


Figure 2. Total mangrove litterfall at Perancak Estuary in February 2020–January 2021. Error bars represent the 95% confidence interval of the mean ($n = 678$).

Leaf litterfall of both mangrove types was the highest in May 2020, which was $4.37 \pm 1.01 \text{ g m}^{-2} \text{ day}^{-1}$ in restored forests and $3.45 \pm 0.41 \text{ g m}^{-2} \text{ day}^{-1}$ in intact forests (Figure 3A). In contrast, the highest litterfall of reproductive parts was found in October 2020 in restored forests ($2.21 \pm 1.14 \text{ g m}^{-2} \text{ day}^{-1}$) and for wood litterfall in November 2020 in restored forests ($0.60 \pm 0.31 \text{ g m}^{-2} \text{ day}^{-1}$) (Figure 3B,C). Significant forest type and month differences were detected for all litter types, and the significance was $p < 0.0001$ for total, leaf, and reproductive parts litterfall. Significance in wood litterfall was detected only for month variance ($p < 0.0001$). A substantial difference in wood litterfall production was only observed between intact and restored forests in November 2020.

Genus-specific litterfall was assessed in the wet season to investigate the effect of rainfall on the production of fallen litter from different mangrove genera (*Avicennia* spp., *Bruguiera* spp., *Rhizophora* spp. *Sonneratia alba*, and *Xylocarpus* spp.) (Figure 4). *Xylocarpus* litter was detected in restored forests, with a high mass of reproductive parts litter, but not in intact mangroves. In November 2020 which had the heaviest rainfall, the high dry weight of fallen litter ($>10 \text{ g m}^{-2} \text{ day}^{-1}$) was sourced from *Xylocarpus*, *Sonneratia*, *Bruguiera*, and *Rhizophora*, respectively, while in December 2020, the fallen litter from genera other than *Rhizophora* dropped substantially. *Avicennia* and *Ceriops* had less than $3 \text{ g m}^{-2} \text{ day}^{-1}$ of fallen litter during our three-month observation. Peak reproductive parts litter was different between months, showing different phenology of these six mangrove genera.

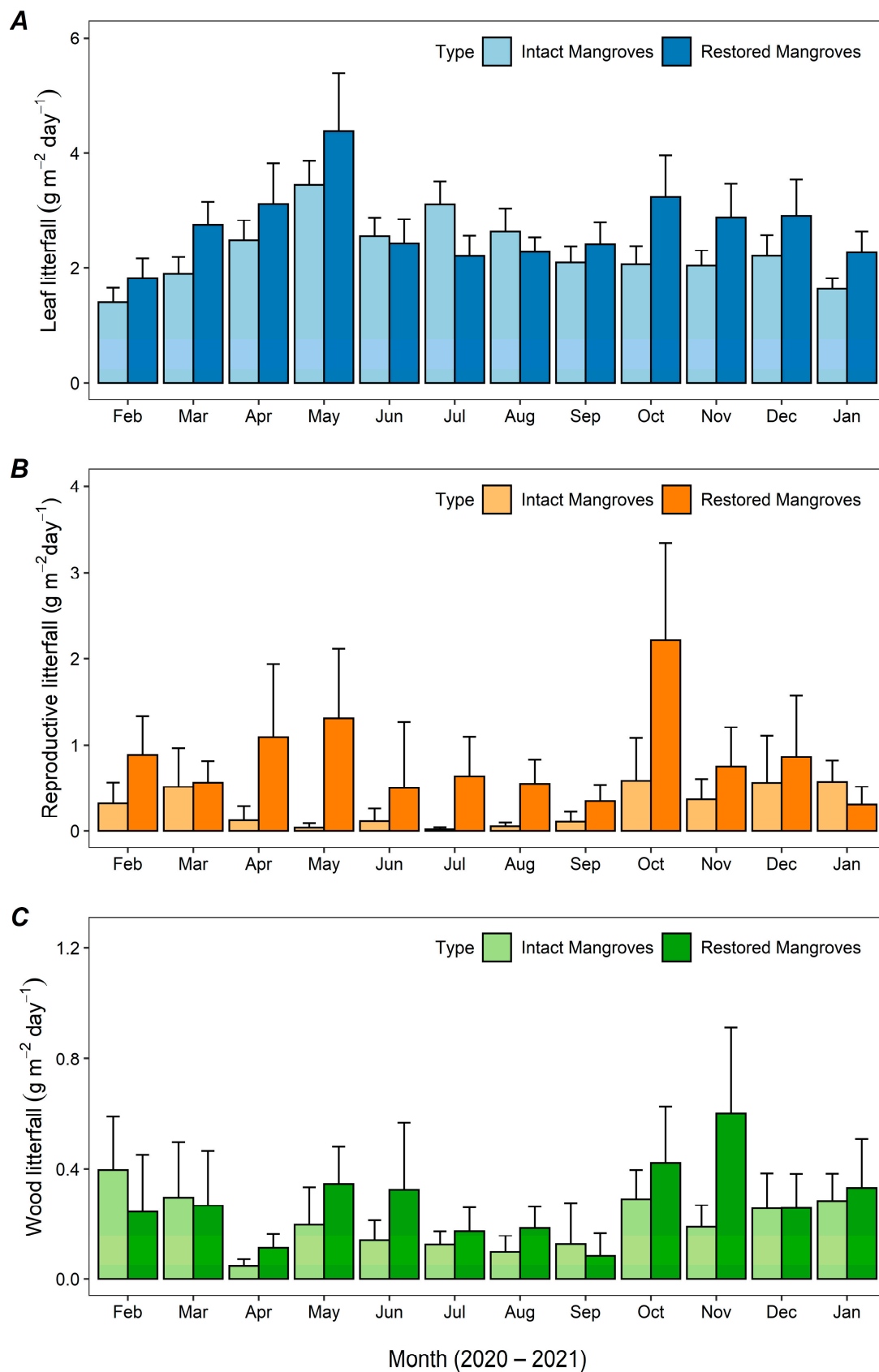


Figure 3. Dynamics of (A) leaf litterfall, (B) reproductive parts litterfall, and (C) wood litterfall at Perancak Estuary in February 2020–January 2021. Error bars represent the 95% confidence interval of the mean ($n = 678$).

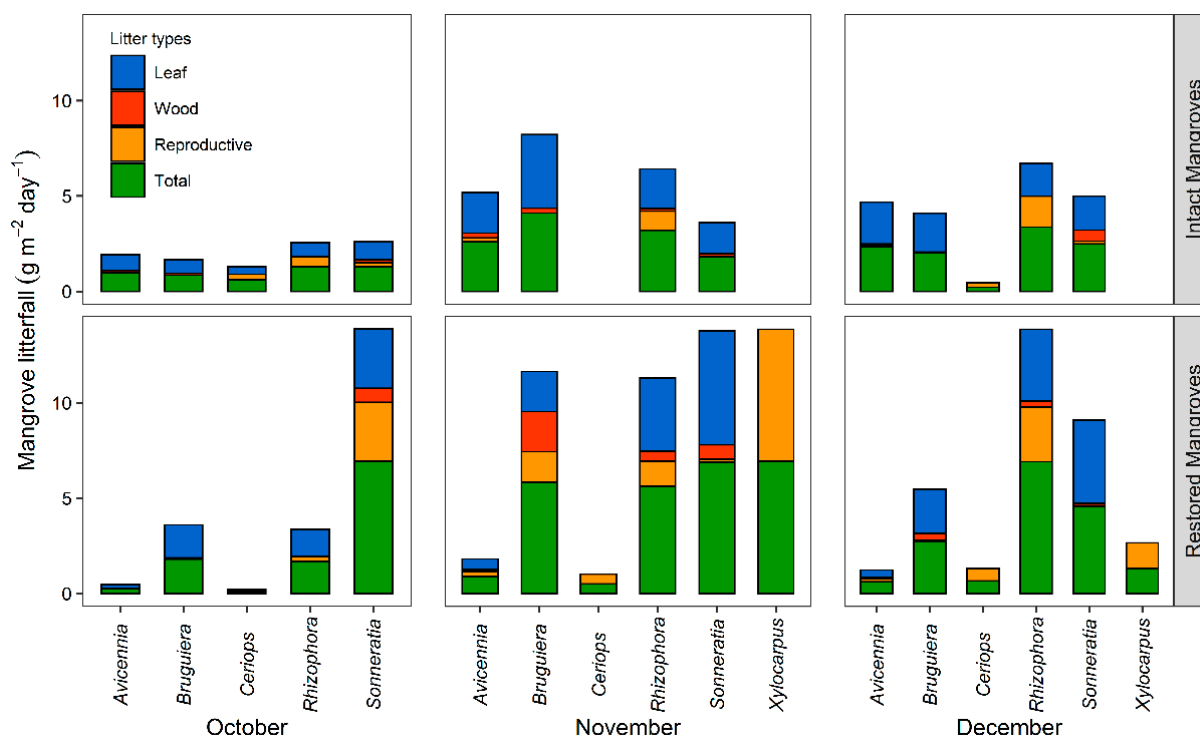


Figure 4. Detailed litterfall dynamics of different litter types and genera between October to December 2020 ($n = 358$). Possible species for each genus according to [29,47]: *Avicennia*: *A. alba*, *A. marina* and *A. officinalis*; *Bruguiera*: *B. gymnorrhiza*; *Rhizophora*: *R. apiculata*, *R. stylosa* and *R. mucronata*; *Sonneratia*: *S. alba*; *Xylocarpus*: *X. granatum* and *X. moluccensis*.

As the highest rainfall was observed in November 2020, the porewater salinity between November and other months was significantly different, except for October 2020 (Bonferroni post hoc test $p = 0.072$). Porewater salinity of intact and restored mangrove forests was the lowest in November 2020 compared to the other months (24.9 ± 2.88 and 20.3 ± 6.91 , respectively; Supplementary Material S1, Figure S1.2). Intact mangrove forests had relatively lower porewater salinity than restored mangroves in high rainfall months (e.g., May, October, and November). Porewater salinity of different forest types and months was significant (two-way ANOVA $p < 0.0001$; Table S1.1).

3.1.2. Annual Mangrove Litterfall Production

As corresponds to monthly litterfall production in Perancak Estuary, annual mangrove litterfall production in restored mangrove forests was higher than intact forests, which is equivalent to 4581 and 6282 kg C ha⁻¹ year⁻¹ of annual carbon storage supplied by intact and restored mangrove forests originated from litterfall (Table 2). The proportion of leaf, reproductive, and wood litterfall in intact mangroves was 82.6%, 10%, and 7.4% of the total litterfall. A higher proportion of reproductive parts litter was observed in restored mangroves, which was 21.5% of the total litterfall.

Table 2. Annual mangrove litterfall production in Perancak Estuary.

Litterfall Types	Annual Litterfall Production (Mg ha ⁻¹ year ⁻¹)	
	Intact Mangroves	Restored Mangroves
Leaf	8.38 ± 0.39	9.90 ± 0.60
Reproductive	1.01 ± 0.29	2.98 ± 0.62
Wood	0.75 ± 0.13	1.01 ± 0.18
Total	10.18 ± 0.48	13.96 ± 1.02

Data: Mean ± CI 95%. Leaf litter: leaf, apical bud, and stipule; reproductive litter: flower, fruit, and propagule; wood litterfall: twig and branch.

3.2. Leaf Litter Decay and Decomposition

Initial leaf litter mass loss was observed for all species during the first 14 days, followed by a slower mass loss after 21 and 42 days, in which the decay and decomposition pattern resembled a single negative exponential model (Figure 5). The goodness of fit (R^2) of all exponential equations was above 0.80, which confirms the fitness of the selected model and therefore the calculation of 95% and 99% lifespan is applicable (Table 3) [42]. The remaining mass proportion of *Avicennia alba* litter was relatively higher than the other species, with slower decay observed in restored mangroves. However, interspecific and forest-type differences in leaf litter decay were not significant (RM ANOVA $p = 0.127$ and $p = 0.107$). Mass loss between different time intervals was significant ($p < 0.001$), with significant differences found between Day 0 and 14, 21, and 42 and also between Day 14 and 42.

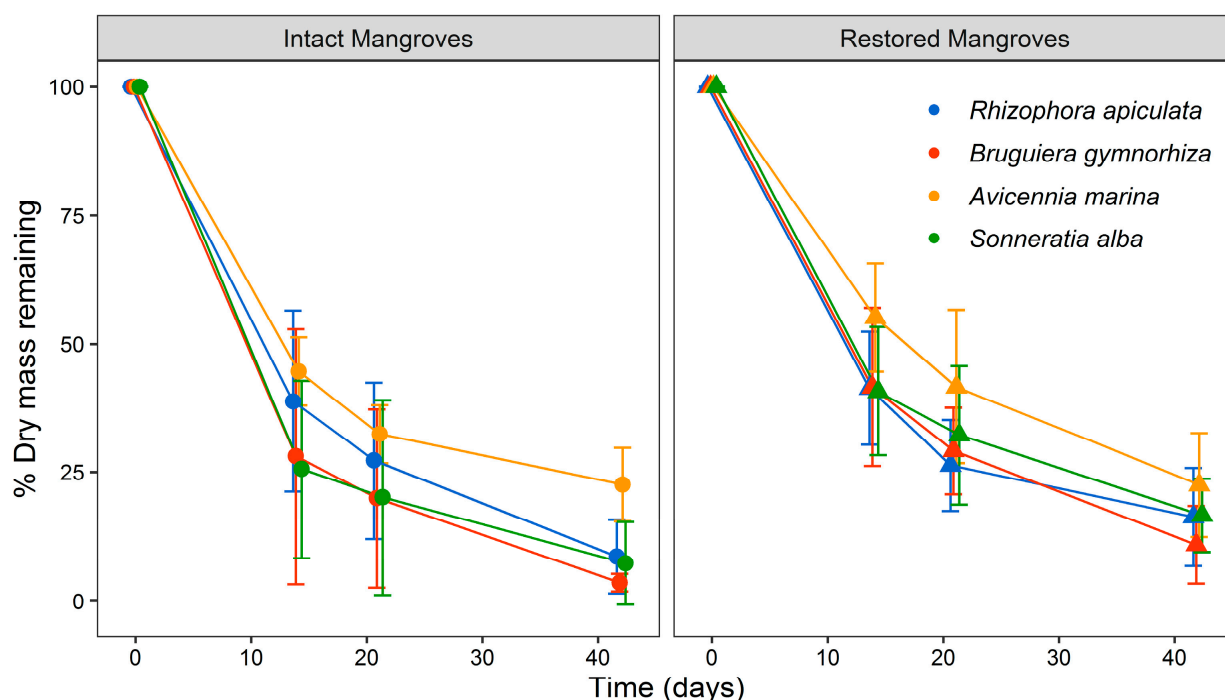


Figure 5. Leaf litter decay of *Rhizophora apiculata*, *Bruguiera gymnorhiza*, *Avicennia marina*, and *Sonneratia alba* in intact and restored mangrove forests of Perancak Estuary. Error bars represent the 95% confidence interval of the mean ($n = 288$).

Table 3. Leaf litter decay constant (k), half-life ($t_{0.50}$), 95% and 99% lifespan ($t_{0.95}$ and $t_{0.99}$) of different mangrove species and forest types obtained from negative single exponential equations.

Species	Forest Type	R^2	Intercept	Decay Rate (day^{-1})	$t_{0.50}$ (days)	$t_{0.95}$ (days)	$t_{0.99}$ (days)
<i>Rhizophora apiculata</i>	Intact	0.96	0.0594	0.059	12	51	84
	Restored	0.96	0.0509	0.051	14	59	98
<i>Bruguiera gymnorhiza</i>	Intact	0.87	0.0789	0.079	9	38	63
	Restored	1.00	0.0589	0.059	12	51	85
<i>Avicennia marina</i>	Intact	0.91	0.0362	0.036	19	83	138
	Restored	0.99	0.0391	0.039	18	77	128
<i>Sonneratia alba</i>	Intact	0.94	0.0808	0.081	9	37	62
	Restored	0.93	0.0443	0.044	16	68	113

3.3. Climate Data

Meteorological data (rainfall, wind speed, daylight hours, and air temperature) were collected from the Indonesian Meteorological, Climatological, and Geophysical Agency (BMKG), from January 2020 to February 2021, over the time frame during which the fieldwork was conducted. The Jembrana climate observatory station was located in the city of Negara, ~8 km from the Perancak Estuary. The average air temperature fluctuated approximately 25.6 °C from the coldest month to 28.27 °C on the hottest month, and the mean annual air temperature ($\pm$ SD) during the study period was 27.24 ± 0.92 °C. The mean of monthly daylight hours was 176.2 ± 37.16 h month⁻¹. The monthly rainfall during the study period ranged from 48 mm month⁻¹ in June 2020 to 454.2 mm month⁻¹ in November 2020, and the annual rainfall was 2691.5 ± 139 mm yr⁻¹. The monthly maximum wind speed varied from the lowest 4.76 m s⁻¹ in December 2020 to the highest 6.74 m s⁻¹ in August 2020 (Supplementary Material S1, Figure S1.1).

3.4. Macrozoobenthic Community Structure

3.4.1. Environmental Conditions during Macrozoobenthos Sampling

The environmental conditions of two mangrove forest types during macrozoobenthos sampling were recorded. Water temperature ranged from 28.57 °C in intact forests to 28.87 °C in restored forests; oxygen levels were 5.99 and 5.84 mg/L, respectively. Water pH ranged from 8.03 to 8.09, while salinity ranged between 25.67–30.00‰ (Table S1.2).

3.4.2. Macrozoobenthos Abundance, Diversity, Similarity, and Dominance Indices

A total of 372 and 263 invertebrate individuals composed of 18 species were recorded from intact and restored mangroves (Table 4). The macrozoobenthos consisted of crabs and snails. The total abundance of macrozoobenthos at both sites ranged from 11 to 106 and 11 to 82 individuals (ind.) per square meter of intact and restored forest, respectively. The macrozoobenthos were most abundant in F1 (intact forest) with a total abundance of 106 ind/m²; the lowest abundance was observed in P2 (restored mangroves) with a total abundance of 11 ind/m² (Table 4). *Cassidula nucleus* was the most abundant macrozoobenthos at both sites.

Table 4. Macrozoobenthos species observed in this study.

Family	Genus	Species	Habitat	Number of Species (Individual)	
				Intact	Restored
Crabs					
Ocypodidae	<i>Tubuca</i>	<i>T. flammula</i>	Epifauna, infauna	12	1
Sesarmidae	<i>Parasesarma</i>	<i>P. eumolpe</i>	Epifauna, infauna	7	5
Snails					
Assimineidae	<i>Optediceros</i>	<i>O. breviculum</i>	Brackish water, epifauna	9	nf
Cerithidae	<i>Cerithidea</i>	<i>C. quoyii</i>	Brackish water, epifauna	14	21
Ellobidae	<i>Cassidula</i>	<i>C. angulifera</i>	Epifauna	89	16
	<i>Cassidula</i>	<i>C. aurisfelis</i>	Brackish water, epifauna	55	28
	<i>Cassidula</i>	<i>C. nucleus</i>	Brackish water, epifauna	138	129
	<i>Cassidula</i>	<i>C. sowerbyana</i>	Brackish water, epifauna	4	2
	<i>Cassidula</i>	<i>C. sulculosa</i>	Brackish water, epifauna	11	23
	<i>Cassidula</i>	<i>C. vespertiolinis</i>	Brackish water	nf	22

Table 4. Cont.

Family	Genus	Species	Habitat	Number of Species (Individual)	
				Intact	Restored
Littorinidae	<i>Littoraria</i>	<i>L. articulata</i>	Epifauna	3	1
	<i>Littoraria</i>	<i>L. carinifera</i>	Epifauna	1	3
	<i>Littoraria</i>	<i>L. melanostoma</i>	Epifauna	1	nf
	<i>Littoraria</i>	<i>L. intermedia</i>	Epifauna	1	nf
	<i>Littoraria</i>	<i>L. scabra</i>	Brackish water, epifauna	12	3
Muricidae	<i>Chicoreus</i>	<i>C. capucinus</i>	Arboreal, Epifauna	1	nf
Neritidae	<i>Nerita</i>	<i>N. baltata</i>	Epifauna	1	2
Placunidae	<i>Placuna</i>	<i>P. ephippium</i>	Arboreal	1	nf
Potamididae	<i>Terebralia</i>	<i>T. sulcata</i>	Epifauna	12	6
Total				372	263

nf = not found.

Macrozoobenthos diversity, as measured by the Shannon–Wiener diversity index, ranged from 0.74 in restored mangroves to 1.77 in intact forests, which is considered a low-medium diversity range (Table 5). The similarity index (e) ranged from 0.24–0.84, and the dominance index (D) ranged from 0.24 to 0.68. The differences between the above indices were not significant according to Student's *t*-test (Bonferroni post hoc test $p > 0.3$), similar to the findings of leaf litter decay.

Table 5. Abundance (K), diversity index (H'), similarity index (E), and dominance index (D) of macrozoobenthos.

Index	Intact Mangroves	Restored Mangroves
Abundance (K)	44.53 $\pm$ 30.9	45.17 $\pm$ 20.54
Diversity (H')	1.48 $\pm$ 0.15	1.36 $\pm$ 0.31
Similarity (E)	0.71 $\pm$ 0.08	0.62 $\pm$ 0.19
Dominance (D)	0.27 $\pm$ 0.03	0.48 $\pm$ 0.10

Data are means of triplicate analyses (Mean $\pm$ SD).

4. Discussion

4.1. Mangrove Litterfall and Its Affecting Factors

Our analysis showed that the amount and composition of litterfall varied between the forest types, which may correspond to the differences in maturity stages of mangrove stands, forest structure (i.e., canopy and understory arrangements), soil properties, and tidal elevation [48]. The forest structure of restored mangroves in Perancak Estuary has changed gradually over the years, visually observed by increasing tree diameter and height to fluctuating density (i.e., increasing density during the growth of young stands followed by natural thinning after the stand's maturation). In early forest stand development, the aboveground net primary production (ANPP) of mangrove stands is gradually increasing and then declines as stands age [49]. It is also known that a high proportion of mangrove ANPP is shed as litter [50]. Young stands of planted mangroves are found to have an increasing trend of litterfall production following their stand's age, as observed in Gazi Bay, Kenya, and Tam Giang Lagoon, Vietnam [11,51].

Litterfall input of our study location (3.96 Mg ha^{−1} year^{−1} (restored) and 10.18 Mg ha^{−1} year^{−1} (intact)) lies within the range of tropical mangrove litter production (3–18 Mg ha^{−1} year^{−1} globally, 5–18 Mg ha^{−1} year^{−1} SEA) [52]. Besides forest succession stages (i.e., pioneer plants–young forests–mature forests), forest management (e.g., selective pruning or harvesting) and anthropogenic disturbance (e.g., coastal development) can influence litterfall production (Table 6). In Florida, USA, selective pruning of

R. mangle-dominated forest results in decreased litterfall production [53]. Moderate litterfall input in Perancak mangroves may correspond to minimum pruning and harvesting activities by the local communities. The litterfall production of intact mangrove forests without significant anthropogenic disturbance from previous studies in the tropical region of both Indo-West Pacific (IWP) and Atlantic-East Pacific (AEP) ranges from 16 to more than 20 Mg ha^{−1} yr^{−1} (i.e., Apar-Adang Nature Reserve, Indonesia [52], Sibuti Mangrove Forest Reserve, Malaysia [54] and Atrato River Delta, Colombia [9]).

Table 6. Comparison of annual total litterfall production (Mg ha^{−1} y^{−1}) in global mangrove forests.

Sites and Countries	Mangrove Species	Forest Type	Total Litterfall Production (Mg ha ^{−1} y ^{−1})	References
Southwest Florida, USA	<i>Rhizophora mangle</i> dominated	Intact	3.73	[53]
		Selective pruning	3.05	
Atrato River Delta, Southern Caribbean, Colombia	<i>Rhizophora mangle</i> dominated	Intact	20	[9]
Gazi Bay, Kenya	<i>Rhizophora mucronata</i> and <i>Sonneratia alba</i>	Planted (5–13 years)	5.22–10.15	[51]
	<i>Rhizophora mucronata</i> and <i>Sonneratia alba</i>	Intact	8.36–10.15	
Tam Giang Lagoon, Vietnam	<i>Rhizophora apiculata</i>	Planted (7–24 years)	8.86–14.16	[11]
Sibuti mangrove forest, Sarawak, Malaysia	Mixed species	Intact	16.41	[54]
Tritih, Central Java, Indonesia	<i>Rhizophora mucronata</i>	Planted (7 years)	7.06–10.40	[55]
Kema-Bitung, North Sulawesi, Indonesia	Mixed species	Disturbed	6.66–8.93	[56]
Apar-Adang Nature Reserve, East Kalimantan, Indonesia	Mixed species	Intact	23.7	[52]
Perancak Estuary, Bali, Indonesia	Mixed species	Intact	10.18	This study
	<i>Rhizophora</i> spp. dominated	Planted (≥14 years in 2021)	13.96	

Annual total litterfall is selected based on studies that consist of at least 12 months.

The effect of environmental and climatic variables (porewater salinity, rainfall, wind speed, daylight hours, and air temperature) on litter production varied between intact and restored mangroves (Figure 6). Our data showed that total litterfall production in intact mangroves was not correlated with environmental variables, but significant correlations (Pearson correlation coefficient $r > 0.50$) were detected in individual litter components, for instance, a positive correlation of rainfall with reproductive parts litter ($r = 0.64$) and wood litter ($r = 0.56$) or negative association between reproductive parts litter with a monthly mean of maximum wind speed ($r = -0.55$) and porewater salinity ($r = -0.63$). In relation to porewater salinity, our observation was similar to a previous study that assessed the litterfall of *Rhizophora mangle* [57], while for wind speed our finding was opposite to previous studies that evaluate the litter discharge of *Kandelia obovata* [58] and *Xylocarpus mekongensis* [59].

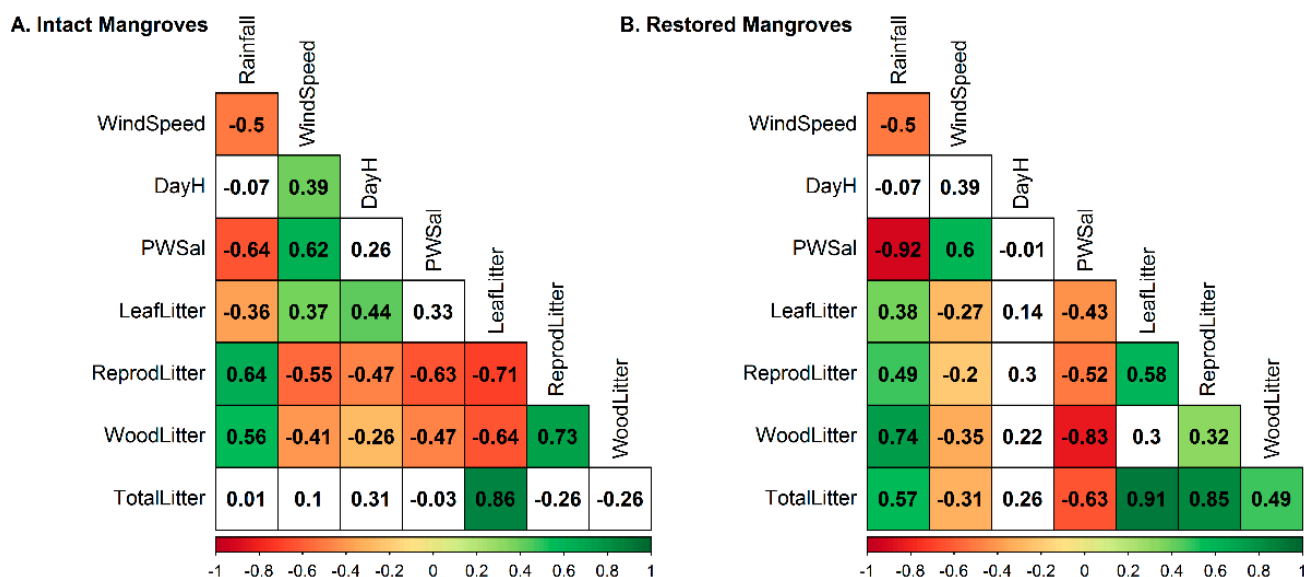


Figure 6. Heat maps of correlation coefficients between environmental variables and plant litterfall in (A) intact mangroves and (B) restored mangroves. Significant negative correlation visualized in red color and significant positive correlation in green color ($\alpha = 0.05$; n for each forest = 12). *WindSpeed*: maximum wind speed (m s^{-1}), *DayH*: daylight hours (h), *PWSal*: porewater salinity, *LeafLitter*: leaf litterfall, *ReprodLitter*: reproductive parts litterfall, *WoodLitter*: wood litterfall, *TotalLitter*: total litterfall. Monthly litter production in $\text{g DW m}^{-2} \text{ days}^{-1}$. The average air temperature was excluded in correlation matrices due to its high correlation to the maximum wind speed variable.

In restored mangroves, rainfall showed a positive correlation with total litterfall production ($r = 0.57$) and a negative correlation with porewater salinity ($r = -0.92$). Total litter was negatively correlated with porewater salinity ($r = -0.63$), in which wood litter had the highest association compared to other litter components ($r = -0.83$). Along with increasing litter production, previous studies stated that higher salinities also cause a decrease in microbial respiration, thus suppressing decay rates and resulting in increased soil C stocks [35,60]. Association of wind speed with litterfall was generally lower than intact forests, but all litter types along with total litter had a weak negative correlation. Compared to other climatic variables, monthly daylight hours had the weakest association with litter production in restored forests.

In alignment with our findings, rainfall is suggested to be the best climatic predictor of mangrove ecosystem carbon stocks [61]. Other abiotic variables that affect the regulation of organic matter diagenesis are nutrient availability and porewater salinity [62]. Porewater salinity is a major driver of mangrove productivity and spatial distribution due to the species-specific salinity tolerance of mangrove species [40]. Seasonal variability of porewater salinity is influenced by the infiltration of inundated fresh water, water residence time, and water replacement dynamics, with porewater salinity levels similar to that of seawater during the dry season and to that of fresh water during the rainy season [33,36,63]. As the pond walls in restored mangroves were damaged, we found that the water inundation level during high tide or high rainfall events was higher than intact forests, which may explain the higher variability of porewater salinity in restored forests. Water availability has an effect on litterfall production, which triggers higher litterfall in the wet season due to rainfall, as well as in the dry season as a response to reduce evapotranspiration [64,65].

Mangrove species distributions, including their seedling dispersal and establishment, are influenced by abiotic conditions and the net effect of biotic interactions, such as competition, facilitation, and consumer pressure [66,67]. Early successional vegetation, e.g., shrubs, herbs, and grasses, may facilitate mangrove recruitment through multiple mechanisms, from amelioration of environmental conditions to propagule trapping and structural sup-

port [68–70]. Apart from their hydrochory and viviparous properties, mangrove dispersal dynamics are defined by their propagule characteristics, for instance, buoyancy, longevity, and morphology (esp. shape and density) [71–73]. A flume laboratory experiment discovered that mimic *Rhizophora* roots trapped fresh fragmented and decayed mangrove leaves, while mimic *Avicennia* roots only trapped decayed leaves [74], thus the leaf-trapping capacity of mangrove roots may differ interspecifically and affect the dynamics of carbon burial and exports in coastal ecosystems. From our study, plantation of *Rhizophora* spp. in abandoned ponds may contribute to the settlement of native mangrove seedlings by the above mechanisms, in which young *Rhizophora* stands act as the early successional vegetation in planted abandoned ponds and resulting in heterogeneous mangrove stands coexistence after >10 years of restoration program as displayed by their litterfall species composition in Figure 4. On the other hand, the structure of damaged pond walls in restored mangroves, which has a similar function to permeable breakwaters, may assist sediment accumulation and establishment of mangrove seedlings in restoration sites [33,75].

4.2. Leaf Decomposition and Associated Macrozoobenthos

In contrast to litterfall observation, there was no significant difference in leaf litter decay and decomposition between the two forest types; therefore it is suggested that these processes become more similar between restored and intact mangroves in the recent years. Abiotic factors such as wind, temperature, moisture, rainfall, salinity, pH, and tidal and current dynamics play a significant role in litter decomposition by stimulating the degradation processes [76]. Frequent tidal flushing at the selected study sites is predicted to contribute to optimal physico-chemical conditions for decomposition, resulting in an increased decay rate [77].

The decay and decomposition of plant litter principally goes through three major stages: (1) leaching of soluble components (e.g., K^+ , Mg^{2+} , and Ca^{2+} ions, amino acids, monosaccharides, and phenolics) (2) microbial oxidation of refractory components such as cellulose and lignin, and (3) physical and biological fragmentation [78,79]. Mangrove litter in Perancak Estuary has been observed to decompose quickly in the first 10 days of exposure in the field, presumably due to leaching, which contributes the greatest mass loss compared to other processes [80]. The loss of phenolics upon leaching accelerates litter degradation by promoting microbial activity and increasing litter palatability to detritivores [41,81].

Benthic detritivores process up to 50% of the total litterfall produced in mangrove forests, while the remaining material is either swept away by the tides or further decomposed by various microorganisms [82]. Macrofauna, specifically burrowing crabs, have been shown to influence the microbial abundance and extracellular enzymatic activity in mangrove sediments [83]. Fast fragmentation of decayed leaf litter in Perancak Estuary compared to another study with a similar experiment setup in Matang, Malaysia [41] is probably due to the high abundance of small gastropods, crustaceans, and other benthic species that consume the leaf litter on the surface or inside the litterbag. Similar findings were found in a previous study from East Kalimantan, Indonesia, which showed that macrozoobenthic plays a role in mangrove litter consumption [52].

The similarity in macrozoobenthic biodiversity indices between the two forest types was also observed, which rejects our hypothesis. Macrozoobenthos epifauna and species composition in our study location were possibly connected with environmental condition parameters, similar to other findings from the Philippines [84] and Sumatera Island, Indonesia [43]. The indicator species for restored mangroves found in this study have epifaunal or infaunal behaviors (linked to young plantations on [84] and planted mangroves on [43]). Other arboreal invertebrates, such as *N. balteata* (Neritidae), were less important in characterizing communities in relation to sediment environmental attributes and, contrary to previous findings, were strongly associated with intact and reforested mangrove forests [43]. However, this species was observed in low abundance in both intact and restored mangroves. It is interesting to note that the abundance of gastropods, *C. nucleus* (both sites), and

C. angulifera (only intact forest) supported the previous study on indicators of mangrove and environmental stability [85]. These gastropods were mainly distributed at *Rhizophora* stands, using the mangrove habitat for survival, food acquisition, protection, and breeding. Macrobenthos diversity is influenced by the level of contamination in the substrate, the abundance of food sources, competition between and among taxa, the level of disturbance, and the condition of the surrounding environment [86–88]. Although macrozoobenthic biodiversity has been assessed in this study, further identification of the contribution of macrozoobenthic to the breakdown is needed.

4.3. Implications for Mangrove Conservation and Restoration

Large-scale monogeneric planting of *Rhizophora* spp. has been the dominant strategy for mangrove restoration in Southeast Asia, including Indonesia [27,89]. Instead of recovering the environmental condition of the damaged habitat, planting seedlings in dense formation is more favored, leading to the lack of habitat complexity and species diversity [27]. Our study has important implications for mangrove restoration action, showing the evidence of the recovery of mangrove forest productivity after restoration took place in abandoned aquaculture ponds. The restored mangroves with dense mangrove seedlings plantations are currently appeared to have a distinct young forest structure with high canopy cover and lower diversity of mangrove species compared to intact mangroves, which may explain the higher rate of litterfall production. Over the years, the monoculture mangrove plantation site resembled a mixed mangrove forest, which can be identified with moderate to high canopy cover [90]. However, interestingly, the decomposition rates and macrozoobenthic biodiversity indices between restored and intact mangrove forests are alike. Mangrove litter production and decomposition has a substantial role in carbon sequestration, hence understanding its changes and differences is essential for predicting mangrove ecosystem services of global climate regulation from restoration programs [54,91,92].

The hydrology restoration in abandoned ponds by partial removal of pond walls in Perancak Estuary contributes to the establishment of mixed-species mangrove forests after ≥ 14 years of *Rhizophora* plantation by allowing the seedling transportation from existing mangrove stands as the seedling source to the ponds [33]. The natural recruitment of pioneer species of *Avicennia* and *Sonneratia* occurred in planting sites, suggesting a suitable biophysical condition for mangroves to colonize is already met [93]. When mangrove planting in abandoned aquaculture ponds is performed in an area with no surrounding mangrove vegetation, we suggest that species diversity should be taken into account to enhance the succession of mangrove ecosystems in the destined area.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/su14138082/s1>, Supplementary Material S1. Temporal variability of environmental parameters in Perancak Estuary and results of two-way Analysis of Variance (ANOVA) of porewater salinity (Figure S1.1 Monthly (A) rainfall, (B) average air temperature, (C) maximum wind speed and (D) daylight hours from February 2020 to January 2021; Figure S1.2 Monthly porewater salinity of intact and restored mangrove forests during sampling periods; Table S1.1 Two-way ANOVA of time and forest type differences on porewater salinity; Table S1.2 Environmental characteristics of each forest type during macrozoobenthos sampling), Supplementary Material S2. Results of Repeated Measures Analysis of Variance (RM-ANOVA) of interspecific and forest type differences on mangrove leaf litter decay (Table S2. RM-ANOVA of the effects of species and forest type differences on leaf litter percent leaf mass remaining upon decay (species x forest type x time)) and Supplementary Material S3. Results of Two-Way ANOVA of time and forest type differences on mangrove litterfall production (Table S3.1–4 Two-way ANOVA of the effects of forest type and time differences on the production of total, leaf, reproductive parts and wood litterfall, respectively).

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