Litter mixing effect on decomposition rate and nutrient release to water: low quality leaves of coastal species

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Abstract

Non-additive effect on litter decomposition often occurs in mixed terrestrial communities but little investigated on coastal ecosystems. We selected three common mangrove species and one alien saltmarsh species from a coastal wetland stand to test whether non-additive effect occurs when the litters of these coastal species mixed together. To avoid the heterogeneity of soil conditions and to detect nutrient release into water, we conducted an in vitro litter-bag experiment in a glasshouse. Among three litter mixtures, the non-additive effect was observed in the litter mixture composed of mangrove species *Aegiceras corniculatum* vs. *Kandelia obovata* (antagonistic) and *A. corniculatum* vs. *Avicennia marina* (synergistic), but not in the litter mixture of *A. corniculatum* vs. *Spartina alterniflora* (the alien saltmarsh species). The strength of non-additive effect was unrelated to litter initial trait dissimilarity. Instead, litter decomposition rate and mass remaining of litter mixtures were strongly related to the community-weighted mean of leaf carbon. The nutrients and carbon released into water were more likely controlled by litter decomposition rate rather than by litter initial nutrient concentrations. These findings would lead to the expectations on ecosystem scale that the mangrove stand mixed with *A. corniculatum* and *K. obovata* accumulates more organic carbon in the sediment and releases less nutrients into water column than the stand composed of *A. corniculatum* and *A. marina* . It is also implying that the alien species *S. alterniflora* invasion may not reduce soil carbon stock of mangrove forests. These hypotheses need to be further tested and which will be suggestive for the protection or reconstruction of coastal wetlands.

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Keywords

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1 Introduction

Leaf litters are often mixing together in nature, where the litter decomposition rate of single species may not represent the real decomposition rate (Handa et al., 2014), because litter mixing could cause litter decomposition rates to be different from the community-weighted mean rate of the component species, known as non-additive effect (Lecerf et al., 2011). In subtropical coastal area in China, *Kandelia obovata* , *Aegiceras* *corniculatum* (black mangrove) and *Avicennia marina* (white mangrove) are often dominant in mangroves. An alien salt marsh species *Spartina alterniflora* have found emerged in some of these communities (Zhang et al., 2012). Their litters must mix together, but it is unclear whether non-additive effect on litter decomposition occurs in these litter mixtures.

Litter decomposition rate has confirmed to be related to litter traits, including chemical traits, especially nitrogen (N) or C: N ratio and lignin concentrations, as well as some morphological traits such as leaf mass per area (LMA), specific leaf area (SLA) and leaf dry-matter content (LDMC) (Osono and Takeda, 2004; Cornwell et al., 2008; Fortunel et al., 2009; Wickings et al., 2012; Coleman et al., 2020). Mass-ratio hypothesis and niche complementarity hypothesis are the main trait-based theories to explain the non-additive effect on litter decomposition (Finerty et al., 2016; García-Palacios et al., 2017). The mass-ratio hypothesis states that the dominant trait values have the greatest impact on ecological processes including litter decomposition, which is indicated by the community-weighted mean of trait values (CWM) (Finerty et al., 2016; García-Palacios et al., 2017). The mass-ratio hypothesis pre-supposes that there is no interaction between litters, but this rarely occurs in nature. More likely is that the positive and negative interactions between litters cancel out each other, proposed as the "idiosyncratic annulment" hypothesis (Tardif and Shipley, 2013). In contrast, the niche complementarity hypothesis emphasizes the role of litter trait dissimilarity and the positive interaction between litters, such as N or C transfer between the litters with distinct concentrations of N (Schimel and Hättenschwiler, 2007; Handa et al., 2014) or C (Berglund et al., 2013). Although both mass-ratio and niche complementarity hypotheses could play critical role in litter decomposition and nutrient release (García-Palacios et al., 2017), their relative contributions varied with plant communities (Chapman and Koch, 2007).

Non-additive effect on litter decomposition and related mechanic theories were scarcely tested in coastal communities. However, coastal plants generally have low quality of litters due to their response to tidal stressful environments such as saline and nutrient-poor conditions (Feller et al., 2003). For example, mangrove plants generally have high C concentrations with particularly high recalcitrant compounds, such as phenolic compounds, condensed tannins, and lignin, which are highly resistant to decay (Kraus et al., 2003; Lin et al., 2006, 2007, 2010; Prescott, 2010).

The process of litter decomposition can impact many ecological functions of coastal wetlands such as C stock and water purification. Understanding the decomposition of litter mixture of coastal species will be benefit to coastal reconstruction with the aiming to recover the functions and services they provided. Thus, the aim of this study is to test: i) whether litter mixing affect litter decomposition rate and nutrient release; ii) if so, whether trait dissimilarity or CWM of litter mixture is related to the non-additive effect.

2 Materials and methods

To avoid the heterogeneity of soils and climates, we carried out a litter-bag experiment in the glasshouse in the Institute of Urban Environment, Chinese Academy of Science. The leaves were sampled from Quanzhou Bay Mangrove Reserve (24*57'24" N - 118*41'25" E), the south of Fujian, China (Hu et al., 2011). This site is characterized by an oceanic monsoon climate with a warm wet winter and hot rainy summer. The annual mean temperature is 20.4 *C and the average annual precipitation is 1095.4 mm (Lu et al., 2018). The dominant mangrove species encompassed*Kandelia obovata* , *Aegiceras corniculatum* , and*Avicennia marina* . Besides, an alien saltmarsh species*Spartina alterniflora* emerged, which has been invaded into many mangrove stands in China (Zhang et al., 2012). Three litter mixtures were set up based on species distributions in the field: *A. corniculatum* vs. *A. marina* , *A. corniculatum* vs. *K. obovata* , and *A. corniculatum* vs. *S. alterniflora* . The soil was collected from the mangroves in Xiamen city: electronic conductivity (EC 0.46 +- 0.05 ms cm^{-1}), organic matter (0.32 +- 0.04 mg g^{-1}), carbon (C 20.09 +- 0.67 mg g^{-1}), total nitrogen (TN 2.02 +- 0.08 mg g^{-1}), total phosphorus (TP 0.62 +- 0.03 mg g^{-1}), sulphate (S 0.72 +- 0.07 mg g^{-1}), potassium (K 13.73 +- 3.33 mg g^{-1}), calcium (Ca 8.47 +- 2.39 mg g^{-1}), magnesium (Mg 9.96 +- 0.22 mg g^{-1}) and pH (8.11 +- 0.06).

2.1 Experimental design

Healthy green leaves were sampled from the trees of *K. obovata* ,*A. corniculatum* , *A. marina* and *S. alterniflora* in the same forest. Thus, all leaves exposed to similar climatic conditions, which facilitated interspecies comparison of litter mass loss. After being taken to the laboratory, the leaves were gently washed and all dirt particles were then removed by using a soft brush followed by rinsing in distilled water. Five replicates were set up for each litter or litter mixture.

All leaf litters were air dried to constant weight, 5 g of litter for each single species and 5 g of each litter mixture (2.5 g per species) was placed in each 75 x 75 mm nylon bag with 1 mm^2mesh size. There were 40 bags in total, including 15 bags of litter mixture (3 pairs) and 25 for single species (5 single species). All the litter bags were placed on the top of the soil in plastic containers (500 ml), all the containers consisted of 200 g soil and 200 ml water. Based on the previous observation that the decomposition of mangrove leaves generally become slow and steady after 7 weeks (Chanda et al., 2016), this experiment was then conducted for 90 days. The duration of 90 days is often representing short-term decomposition experiment (Keuskamp et al., 2013).

2.2 Element analysis

After 90 days of decomposition, litters and water were collected to the laboratory for mass and nutrient analyses. The water on the surface of soils was collected with a syringe and then stored in a polyethylene bottle. Litters were determined C and N concentrations with elemental analyser (Vario MAX, Vario MACRO, Germany Elementar) after grounded through 60 mesh sieves. Phosphorus (P) in litters was quantified with ICP-OES (Inductively Coupled Plasma Optical Emission Spectrometer, Optimal 7000DV, PerkinElmer USA) after digested with nitric and perchloric acid. The ammonium–nitrogen (NH_4-N), nitrate-nitrogen (NO_3-N) and nitrite-nitrogen (NO_2-N) were quantified by ultraviolet spectrophotometer (UV6100, mapada instrument, China) following the standard methods of water and waste monitoring and analysis method (Wei et al., 2002). Digestion of the water by alkaline potassium persulfate and potassium persulfate were carried out after filtration of water sample, and then the total N and total P were determined respectively according to the standard methods (Wei et al., 2002), NH_4-N, NO_3-N and NO_2-N then analysed by ultraviolet spectrophotometer (UV6100, mapada instruments, China). Due to the specific characters of mangrove leaves (Lin et al., 2007), the condensed tannin of the leaves of the four species were also determined before decomposition experiment conducted. The total condensed tannin was the sum of the extractable, protein-bound and fibre-bound concentrations. The extraction process was followed by the method of Lin et al. (2007).

2.3 Calculation

The litter mass loss was calculated by comparing the initial mass and the mass after decomposition. The initial mass remaining after decomposition was calculated based on the following formula (Wu et al., 2013):

$$X_r = \frac{X_i}{X_t} \times 100$$

Where X_r is the percentage (%) of mass remaining after decomposition, X_i is the initial litter mass, X_t is the mass of the remained litter in the litter bags after a given time period (t) of decomposition.

The decomposition rate (k) was calculated by exponential decay model, the litter mass remaining after decomposition and initial litter mass:

$$\frac{X_t}{X_i} = ^{-kt}$$

Where, k is the decomposition rate coefficient; t is the time duration of decomposition.

The percentage of the initial litter nutrient remaining (N_r) during decomposition was calculated by the following equation (Zhang et al., 2014):

$$N_r = (X_t \times [N_t] + X_i \times [X_i]) \times 100$$

We also calculated the expected rate of the litter mixture after decomposition using the following formula:

$$X_{\text{exp}} = \left(\frac{X_{i1}}{X_{i1} + X_{i2}} \times X_{r_1} + \frac{X_{i2}}{X_{i1} + X_{i2}} \times X_{r_2} \right) \times 100$$

Where X_{exp} is the percentage of the expected mass remaining (MR) after decomposition, X_1 and X_2 are the initial dry masses in single species which was 2.5 g, and X_{r1} and X_{r2} are the mass remaining from the single decomposition species. The effect strength was calculated by the difference between the observed mass remaining (%) and the expected mass remaining (%) (O-E): additive (no significant difference between observed and expected values), synergistic non-additive (negative value, meaning an acceleration of litter decomposition), antagonistic non-additive (positive value, meaning a deceleration of litter decomposition) (Lecerf et al., 2011).

The community-weighted mean value of traits (CWM) was calculated as the mean value of each species in the mixture, because the two litters mixed as 1: 1 of mass in this study (Roscher et al., 2018).

2.4 Statistical analysis

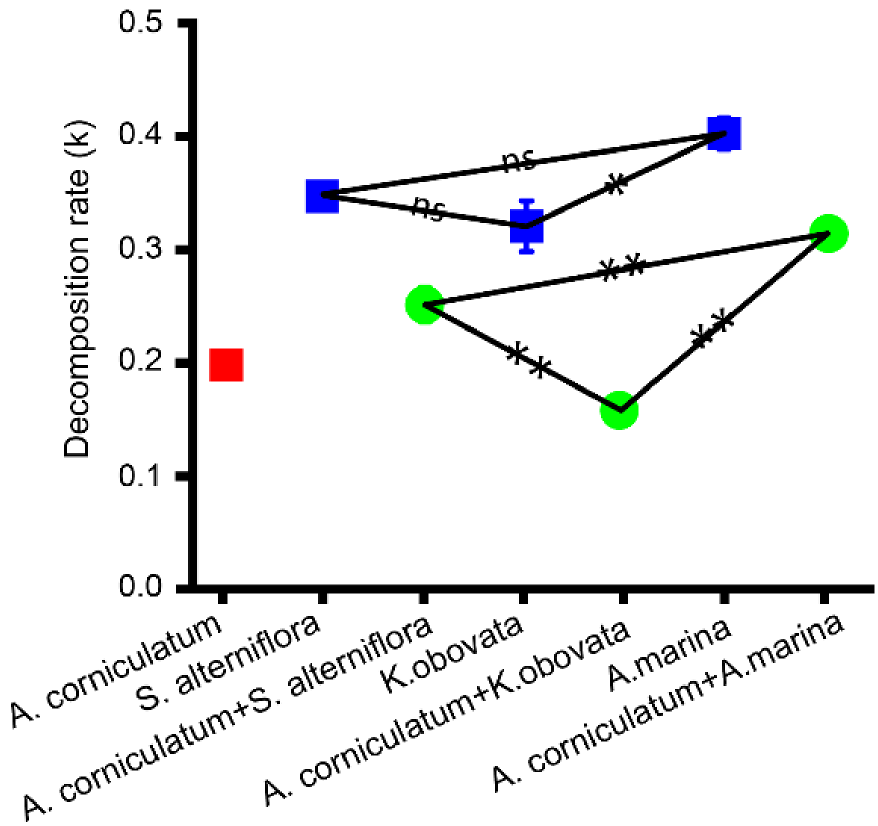
Statistical analysis was performed with IBM SPSS Statistics 23. All data were removed outlier and checked for the normal distribution and homogeneity of variances before the statistical analysis was carried out. One-way ANOVA was used to detect the differences in decomposition rate and nutrients in water among litters, as well as in trait dissimilarity and CWM among each trait. The differences in mass remaining and nutrients in water between observed and expected values were analysed by independent t-test. The variation of the difference in mass remaining between observed and expected values from zero (i.e the observed equals to expected value) was detected by one-sample t-test analysis. The linear correlations of decomposition rate or mass remaining with leaf trait dissimilarity or CWM were assessed through the correlation process. This process was also used to identify the correlation between nutrients in water and in leaves.

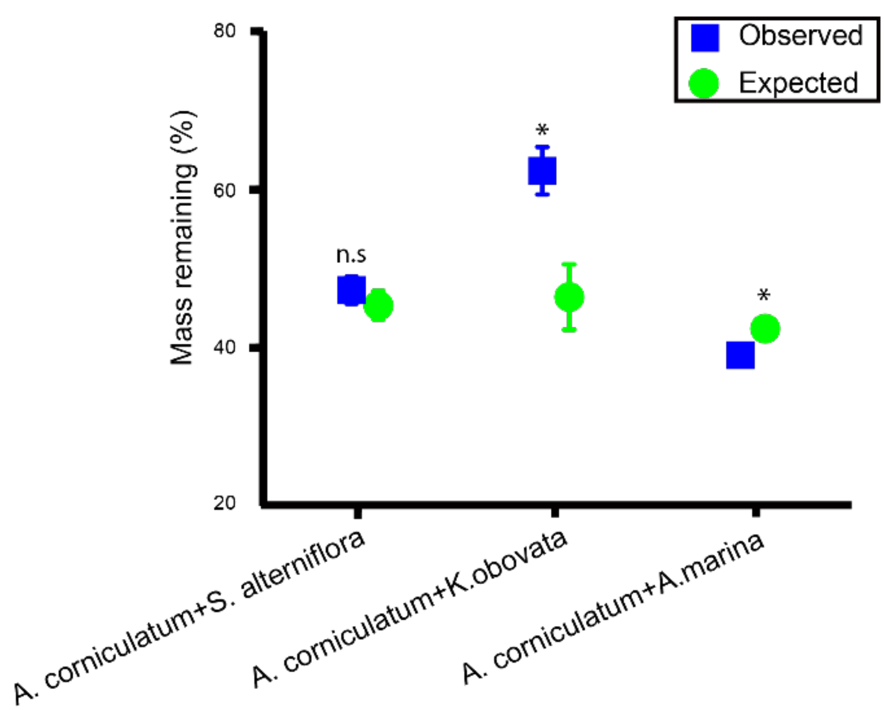
3 Result

Non-additive effect on litter decomposition were found in the litter mixtures from three mangrove species. Nutrients in water, the initial trait dissimilarity and CWM of litter mixtures varied with species composition.

3.1 Decomposition rate (k) and mass remaining

Non-additive effect on litter decomposition was detected in the litter mixtures from mangrove species, but not in the mixture of *A. corniculatum* vs. *S. alterniflora* (Fig. 1a, b). The observed mass remaining of the mixture of *A. corniculatum* vs. *K obovata*was substantially higher than the expected value, whereas the observed mass remaining of the mixture of *A. corniculatum* vs. *A. marina* was lower than the expected one ($p < 0.05$), only the mixture of *A. corniculatum* vs. *S. alterniflora*did not show significant difference between the observed and the expected values ($p > 0.05$; Fig. 1b).


Decomposition rate (k)
0.5
0.4
0.3
0.2
0.1
0.0
ns
ns
*
**
**
**
A. corniculatum
S. alterniflora
A. corniculatum+S. alterniflora
K.obovata
A. corniculatum+K.obovata
A.marina
A. corniculatum+A.marina


Observed
Expected
Mass remaining (%)
80
60
40
20
n.s
*
*
A. corniculatum+S. alterniflora
A. corniculatum+K.obovata
A. corniculatum+A.marina

(a) (b)

Figure 1 The decomposition rate (a) and the mass remaining (b) of litter mixtures. The square and circle symboles are presenting single litter and mixed litter, respectively. The asterisks denote significant difference (**p* [?] 0.05, and ***p* [?] 0.01), while n.s denotes no significant difference.

The strength and the direction of non-additive effect were indicated by the deviation of non-additive effect from zero (Fig. 2). The mixture of*A. corniculatum* vs. *K. obovata* performed a positive and strongest non-additive effect than the other mixtures. Whereas, *A. corniculatum* vs. *A. marina* showed a negative non-additive effect. The mixture of *A. corniculatum* vs. *S. alterniflora*did not show non-additive effect.

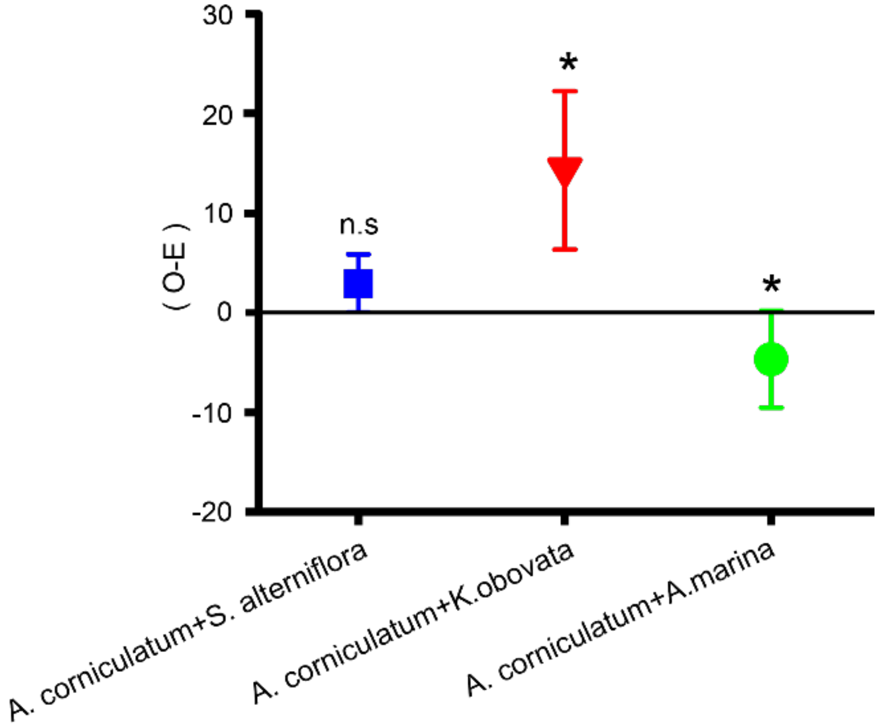


Figure 2 The direction and strength of non-additive effect indicated by O-E (Observed – Expected mass remaining). The asterisk is presenting significant deviation from zero ($p < 0.05$), while n.s means no significant deviation.

3.2 Nutrient content in water after decomposition

There was no difference in total N in water between observed and expected value of all litter mixtures (Fig. 3b), but for total P, the observed content lower than the expected value was found in the mangrove litter mixtures (Fig. 3c). Among litter mixtures of the observed values,*A. corniculatum* vs. *K. obovata* were lower in all nutrients than *A. corniculatum* vs. *A. marina* (significantly) and*A. corniculatum* vs. *S . alterniflora* (slightly) (Fig. 3).

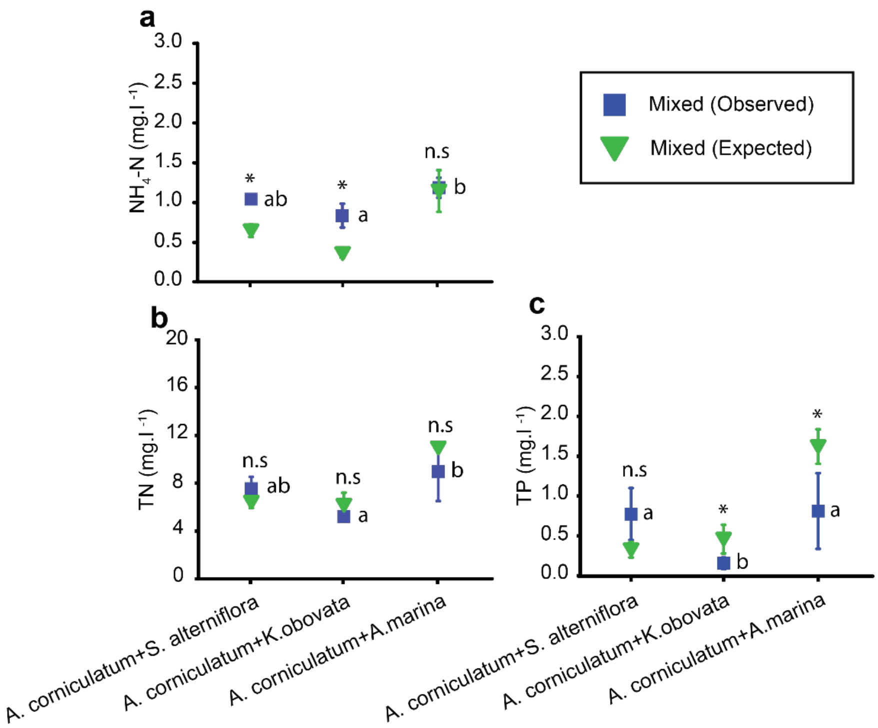


Figure 3 The nutrient content in water after litter decomposition. The symbols of square and circle are presenting observed and expected values. The asterisk and n.s are representing significant difference (*, *p* [?] 0.05) and no significant difference between the observed and the expected content ($p > 0.05$), while the different lowercase letters and the same letters are denoting the significant difference (*p* [?] 0.05) and no significant difference ($p > 0.05$) among litter mixtures.

3.3 The initial trait dissimilarity and CWM of litter mixtures

The litter mixture of *A. corniculatum* vs. *K. obovata* had lower dissimilarity in leaf N and P, and greater in LDMC than the other litter mixtures (Fig. 4b, c, e). *A. corniculatum* vs. *A. marina* showed greater dissimilarity in leaf C and P or LDMC (Fig. 4a, c), while *A. corniculatum* vs. *S. alterniflora* had lower dissimilarity in leaf C and LDMC but greater in leaf N and SLA than the others (Fig. 4a, b, d, e).

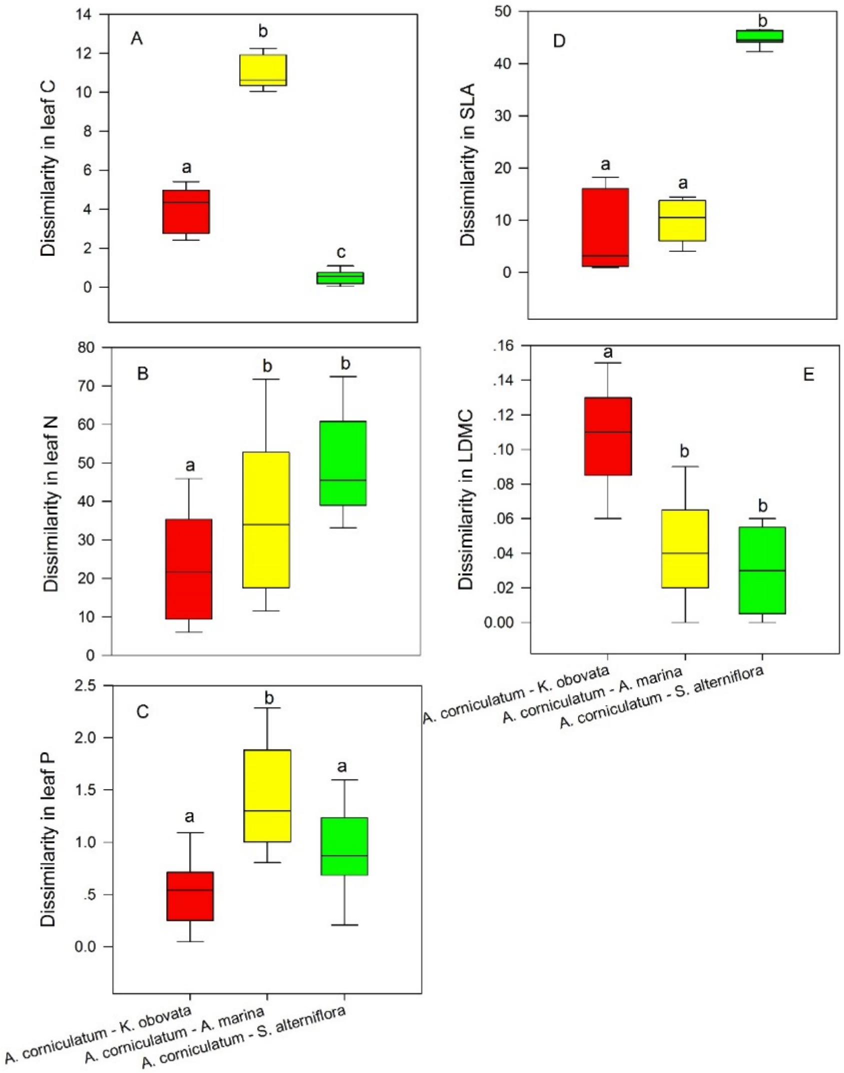


Figure 4 Trait dissimilarity of litter mixtures. The lowercase letters indicate the difference in trait dissimilarity among litter mixtures.

The mixture of *A. corniculatum* vs. *K. obovata* had higher leaf C but lower leaf nutrients (N and P) than the others, while*A. corniculatum* vs. *A. marina* had higher leaf nutrients and SLA but lower leaf C: N than the others (Fig. 5). In contrast, the mixture of *A. corniculatum* vs. *S. alterniflora* had lower leaf nutrients and SLA but higher LDMC than the others (Fig. 5).

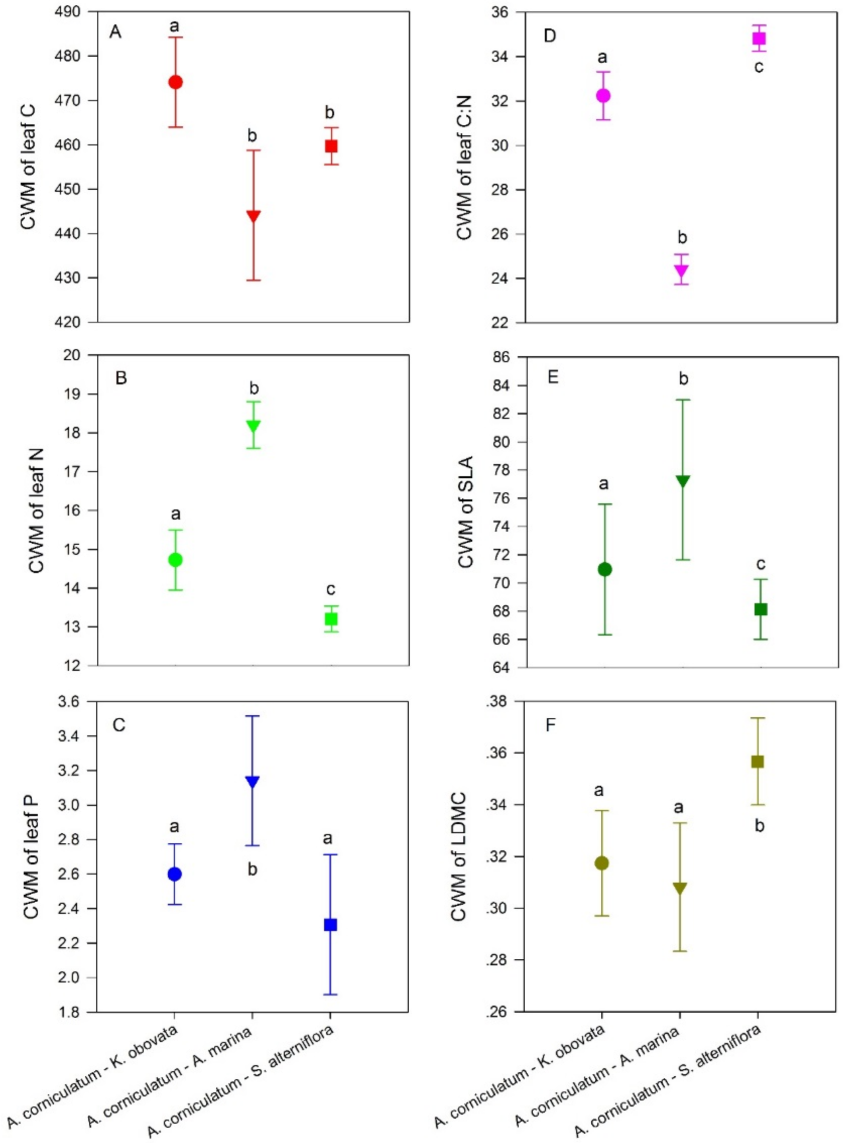


Figure 5 Trait CWM of litter mixture. The lowercase letters indicate the difference in trait CWM among litter mixtures.

Additionally, the condensed tannin was higher in *A. corniculatum*(100.59 ± 25.47 mg g^{-1}) and *K. obovata* (162.78 ± 8.00 mg g^{-1}) than in *A. marina* (1.93 ± 0.33) and *S. alterniflora* (3.21 ± 0.68 mg g^{-1}).

4 Discussion

This study revealed that litter mixing affected litter decomposition rate and nutrient release. Non-additive effect on decomposition was observed in the litter mixtures composed of mangrove species. The CWM of leaf C was likely the key factor controlling the litter decomposition of these litter mixtures. Nutrient release was more likely controlled by litter decomposition rate rather than by litter nutrient concentrations.

4.1 Mixing effect differing among litter mixtures

These three mangrove species are among the widest spread species in China (Yang et al., 2014). Particularly, they are often living together and form a two-species-dominated forest in subtropical coast. How their mixed litters performed must impact the C storage and nutrient cycling of these stands. Surprisingly, we did not find related study examined the non-additive effect on litter decomposition of mangroves. We found that the non-additive effect occured in the litter mixtures composed of mangrove species but the directions were different with an antagonistic effect on the litter mixture of *A. corniculatum* vs. *K. obovata* while a synergistic effect on *A. corniculatum* vs.*A. marina* . If these results are extended to community scale, it is implying that the stand composed of *A. corniculatum* and*K. obovata* would have slower leaf litter decomposition rate than the stand dominated with *A. corniculatum* and *A. marina* .

The litters mixed with *A. corniculatum* and *S. alterniflora*showed a weak non-additive effect. This is consistent with the result from a study in Georgia, USA, where the litters of *S. alterniflora* mixed with the other two saltmarsh species *Juncus roemerianus* and *Quercus virginiana* did not show impact on decomposition rates (Treplin et al., 2013). This indicated that the invasion of *S. alterniflora* would not reduce the soil C stock of mangrove forests.

4.2 Relationships of trait dissimilarity and CWM to the decomposition rate

In general, strong non-additive effect occurs in litter mixture with divergent traits (Kuebbing and Bradford, 2019). For example, deciduous subordinates significantly impacted litter decomposition in an evergreen-dominated forest due to the contrasting traits between deciduous and evergreen species (Guo et al., 2020). In contrast to the general idea, we found no relations of trait dissimilarity with litter decomposition and the strength of non-additive effect. Instead, we found that the CWM of some traits was related to the decomposition rate of litter mixtures (Fig. 7). These findings agreed with the results from European tree species. Even there were 28 litter mixtures (two-species combinations), no significant relationships were found between decomposition rate and litter trait dissimilarity (Frainer et al., 2015). However, in another study on five groups of litter mixtures composed of 14 European tree species revealed that CWM exerted the strongest effect on mass loss (Finerty et al., 2016).

Trait CWM is related to the mass-ratio hypothesis and trait dissimilarity related to niche complementarity hypothesis (Handa et al., 2014; Finerty et al., 2016; García-Palacios et al., 2017). The core point of these two mechanistic hypotheses is the interaction between litters (Tardif and Shipley, 2013; Handa et al., 2014; Finerty et al., 2016; García-Palacios et al., 2017). Although we did not directly examine the interactions between litters, the strong correlation of trait CWM and decomposition rate indicated that there was no interaction between litters of litter mixtures based on the mass-ratio theory. This is consistent with the weak interaction between these alive species in our previous field study (Ndayambaje et al., 2021).

Among litter mixtures, *A. corniculatum* vs. *K. obovata* had the highest CWM of leaf C, also the lowest rate of litter decomposition and the strongest non-additive effect (Fig. 6). The CWM of leaf C of*A. corniculatum* vs. *A. marina* and *A. corniculatum*vs. *S. alterniflora* were similar, but *A. corniculatum* vs.*A. marina* had higher CWM of leaf N and P concurrently with a faster decomposition rate than *A. corniculatum* vs. *S. alterniflora* (Fig. 6). These results indicate that C concentration in the litter mixtures is a key trait strongly controlling litter decomposition, and leaf nutrients can adjust the effect.

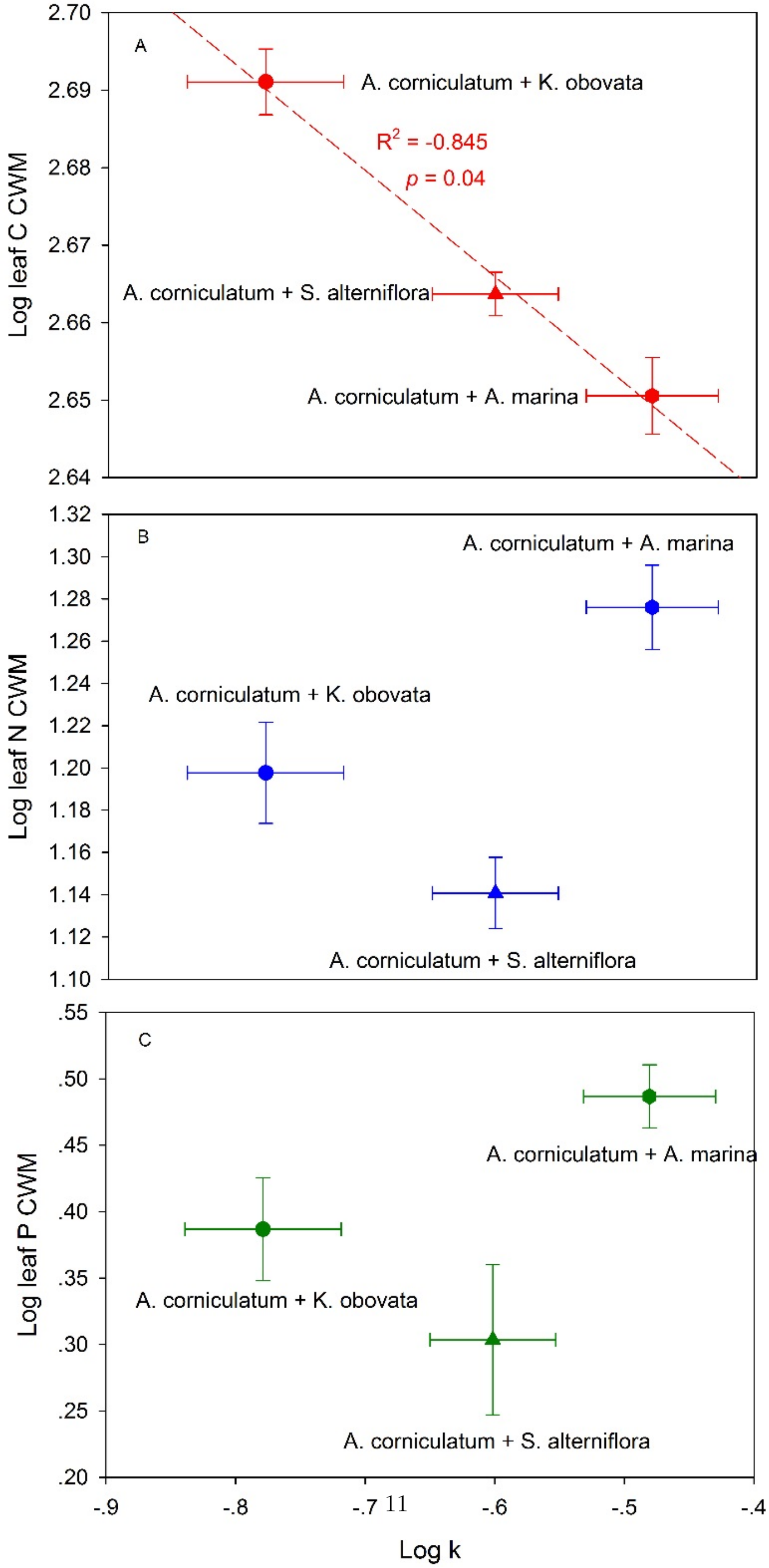

A
A. corniculatum + K. obovata
R2 = -0.845
p = 0.04
A. corniculatum + S. alterniflora
A. corniculatum + A. marina
Log leaf C CWM
2.70
2.69
2.68
2.67
2.66
2.65
2.64
B
A. corniculatum + A. marina
A. corniculatum + K. obovata
A. corniculatum + S. alterniflora
Log leaf N CWM
1.32
1.30
1.28
1.26
1.24
1.22
1.20
1.18
1.16
1.14
1.12
1.10
C
A. corniculatum + A. marina
A. corniculatum + K. obovata
A. corniculatum + S. alterniflora
Log leaf P CWM
.55
.50
.45
.40
.35
.30
.25
.20
-.9
-.8
-.7
-.6
-.5
-.4
Log k

Figure 6 The correlation of decomposition rate (k) to the CWM of C, N and P in litter mixtures. Only the CWM of C was strongly correlated with decomposition rate k.

Mangrove species litters are generally characterized by low-quality (Kraus et al., 2003; Lin et al., 2006, 2007, 2010; Prescott, 2010). Lignin-derived phenols can be lost at a lower rate during decomposition than total neutral sugars and bulk organic C (Marchand et al., 2005). Condensed tannins tend to bind more strongly to protein than to fibre, which enable to sequester nitrogenous materials and conserved N in leaf litter rather than providing to soil microbe, such mechanism could retard litter decomposition rate (Lin et al., 2006; Zhou et al., 2012). Among the four mangrove species, *A. corniculatum* and *K. obovata* had profoundly greater concentrations in leaf condensed tannin than *A. marina* and *S. alterniflora* in our study. Some other studies also found that *A. corniculatum* had highest total polyphenols, and *A. marina* had very low or even undetectable levels (Zhou et al., 2010; Wang et al., 2014). These observations provide additional support to explain why the litter mixture of *A. corniculatum* vs. *K. obovata* showed lower decomposition rate than*A. corniculatum* vs. *S. alterniflora* and *A. corniculatum* vs. *A. marina* .

4.2 Potential factors control nutrient release

Nutrient release during litter decomposition could be the nutrient source for water column. Despite accumulated studies have explored the effect of litter decomposition on water quality (McClaugherty et al., 1985; Zhai et al., 2019), little is known about the effect of litter mixing on the nutrient release in water due to decomposition. Our results indicated that nutrient release was mainly controlled by litter decomposition rate but not the initial leaf nutrient concentrations.

The effect of litter on nutrient release during decomposition can be related directly or indirectly with the initial litter quality and the decomposition rate, even though most studies paid attention to the effect of litter quality (Liu et al., 2010). But we did not find the relationship between the nutrient content in water and the nutrient concentration in leaves, only found a close correlation between N and P in water (Fig. 7).

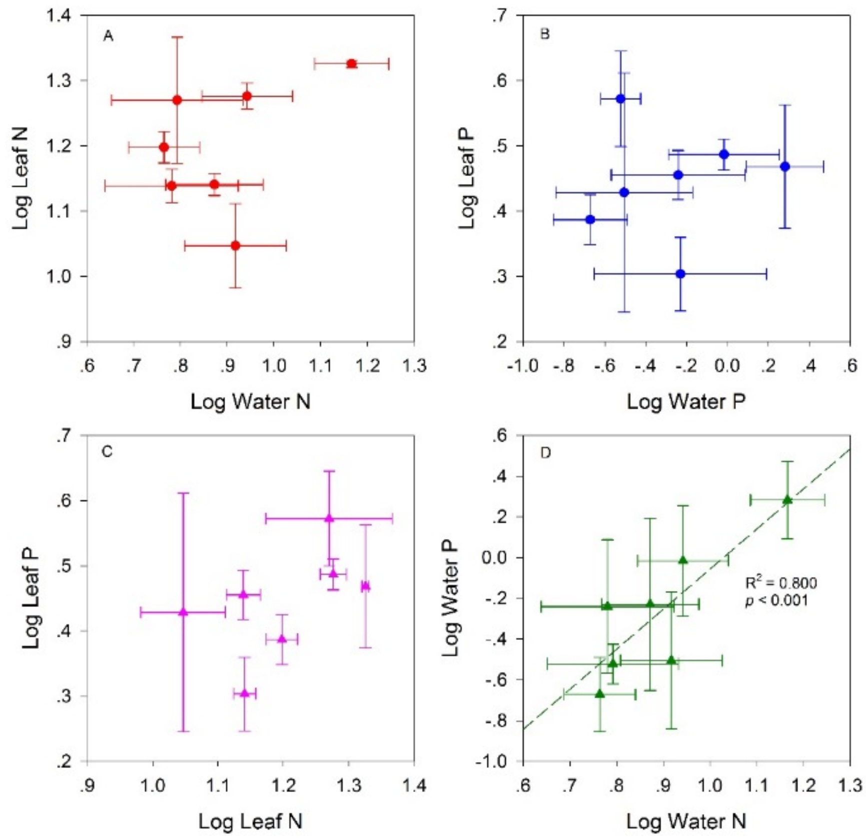


Figure 7 The correlations between N and P in water and in leaves. The significant correlation was only found between the N and P in water.

We further confirmed that the nutrients released into water were controlled by the decomposition rate of litter mixtures indicated by the positive correlations between water nutrient contents and the decomposition rate of litter mixtures (Fig. 8). Despite such relation has been confirmed in some aquatic plants (Wu et al., 2017) and algae (Cao et al., 2015), all of these studies focused on single species litter.

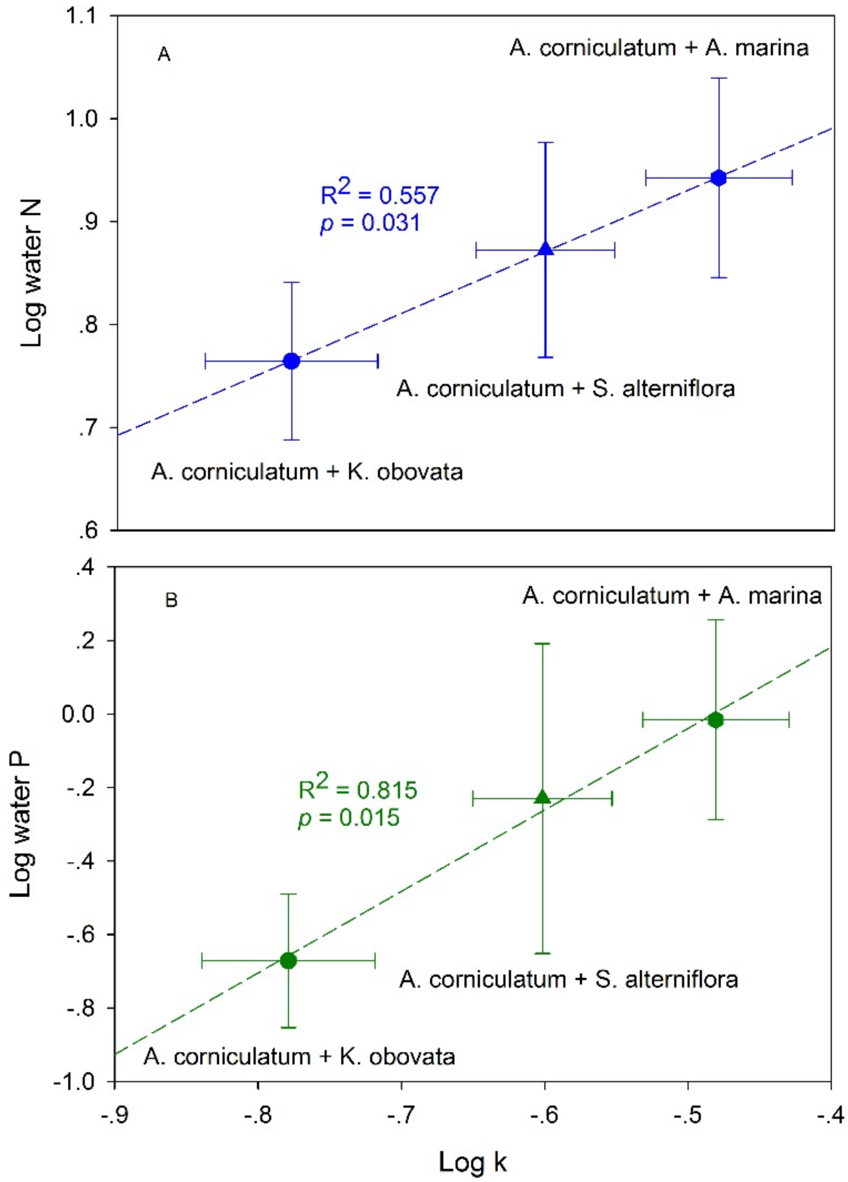


Figure 8 The correlations between the nutrient contents in waters and the decomposition rate (k) of litter mixtures.

5 Conclusion

This study revealed that litter mixing affected litter decomposition rate and litter nutrient release in both synergistic and antagonistic patterns. The decomposition rate of litter mixture was strongly related to CWM of leaf C, and leaf nutrients could adjust the effect. However, the nutrient contents in water were more likely controlled by litter decomposition rate but not the leaf nutrient concentrations.

Even this study included only four species and three litter mixtures, our findings are interesting and meaningful. The two common mangrove species *A. corniculatum* and *K. obovata* living together would be benefit to soil organic C stock. And, the invasive species*S. alterniflora* mixed with *A. corniculatum* did not alter litter decomposition rate significantly, implying that the invasion of*S. alterniflora* may not reduce organic C storage in mangrove forest at least at the high tidal zone where the leaves sampled from. Our findings may be helpful in understanding the effect of plant composition on C stock in mangroves and the effectiveness in maintaining water quality by coastal wetlands.

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Author Contribution

LW conceived the ideas. LW and PN wrote this manuscript. All authors contributed to the improvement of this manuscript and gave final approval for publication.

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