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Yingying Meng
Anhui University

Dafeng Hui
Tennessee State University

Chaohe Huangfu
Anhui University

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Site conditions interact with litter quality to affect home-field advantage and rhizosphere effect of litter decomposition in a subtropical wetland ecosystem

Yingying Meng[a], Dafeng Hui[b], Chaohe Huangfu[a,*]

[a] Anhui Province Key Laboratory of Wetland Ecosystem Protection and Restoration, School of Resources and Environmental Engineering, Anhui University, Hefei 230601, China

[b] Department of Biological Sciences, Tennessee State University, Nashville, TN 37209, USA

*Corresponding author. E-mail: huangfuch@ahu.edu.cn; huangfu24@163.com, Tel: 865513861441 (C. Huangfu)

ABSTRACT

The home-field advantage (HFA) hypothesis predicts that plant litter would decompose more quickly beneath its own plant species in the soil than beneath other plant species. Theoretically, HFA can be induced by the rhizosphere of growing plants, due to so-called rhizosphere effect (RE). Despite growing evidence for the site condition-dependence of both effects, few work has be conducted to explore how site climate, vegetation type and soil properties interact to affect RE and HFA, and especially limited *in situ* representation from subtropical wetland systems. In a field experiment, we reciprocally incubated three root litter species (*Rumex dentatus* L.*,* *Carex thunbergii* Steud.*,* and *Polygonum cripolitanum* Hance) along a hydroperiod gradient in a subtropical wetland, which differed mainly with respect to vegetation and soil microclimate, with and without growing plants. The occurrence and magnitude of HFA and RE were mainly determined by litter quality and were stage-specific. Collectively, we detected significant HFA with chemically-recalcitrant litter from *C. thunbergii* and *P. cripolitanum*, but only at the first stage of decomposition. The presence of growing plants generally reduced litter decomposition, but the magnitude of the response was species-specific, with the positive effects detected only for root litters from *C. thunbergii* at the first stage of decomposition. In addition, we did not find a significant relationship between HFA and RE, indicating that plant species that produce litters exhibiting HFA may not accelerate litter decomposition via RE at same time. Structural equation models (SEM) revealed that site microclimate factors were conducive with soil properties in

regulating C dynamics. Overall, soil microclimate in this wetland ecosystem was likely important in driving C cycling, either directly by changing environmental conditions, litter quality, and plant trait spectra, or indirectly by interrupting the interactions between litter and decomposers.

Keywords: Home-field advantage; Rhizosphere effect; Root decomposition; Litter quality; Soil microclimate

1. Introduction

Litter decomposition serves as an important determinant in maintaining soil fertility, biogeochemical cycle, and nutrient balance in natural and semi-natural ecosystems (Berg and McClaugherty, 2014). Mounting evidence has found that when microclimatic variation is controlled among sites, many field studies found a home-field advantage (HFA), in which decomposition of litter is faster near the plant that produced the litter than at other places away from the plant (Gholz et al., 2000; Veen et al., 2015a). This enhanced decomposition occurs due to species sorting or selecting of particular genotypes of microorganisms (Barbe et al., 2019). Generally, the occurrence and strength of HFA are broadly controlled by the interactions of climate, vegetation, and soil properties (Veen et al., 2015a). Several authors have found that litter quality determines the functional abilities of the soil decomposers (Schimel and Schaeffer, 2012; Strickland et al., 2015) and thus the litter decomposition rate. In particular, for low-quality litter that contains highly recalcitrant

45 (such as lignin or tannins) or toxic and high C: N ratio compounds, HFA would be
46 quite strong because specialized decomposers are required to degrade such substrates
47 (Veen et al., 2015a). High-quality litters, by contrast, contain labile compounds that
48 can be exploited by most decomposers.

49 Belowground litters (i.e., roots) are increasingly regarded to dominate the carbon
50 cycling and carbon budget due to their close contact with soil and slow decomposition
51 in natural systems (Freschet et al., 2013). In contrast to above-ground parts,
52 decomposition of roots may strongly contribute to the formation of soil organic
53 carbon (SOC) as more recalcitrant component is often contained in roots (Xia et al.,
54 2015) which decay more slowly in soils (Crow et al., 2009; Kätterer et al., 2011). In a
55 wetland (e.g., a lake), environmental changes such as water table fluctuation are
56 expected to shift plant spatial distribution and separate plants from specialized local
57 decomposers, resulting in novel pairings of litter and decomposer species in the
58 littoral zone, and potentially decoupling the HFA (Bardgett et al., 2013). However,
59 most previous investigations of HFA have been conducted in forests (Chomel et al.,
60 2015; Asplund et al., 2018) and grassland (Rashid et al., 2013), we still have little
61 understanding of the important environmental drivers of litter decomposition and
62 whether HFA is also common in wetland ecosystems (Xie et al., 2019; but see
63 Franzitta et al., 2015; Leroy et al., 2017).

64 In addition to this resource-consumer interaction, growing plants can also influence
65 the degradation of organic materials by the activity of their living roots (Saar et al.,
66 2016; Huo et al., 2017). Rhizosphere effect (RE) often refers to a change of SOC

decomposition rate due to the presence of living roots and aboveground vegetation (Dijkstra et al., 2013). Many studies have examined RE on SOC (old organic materials) (Huo et al., 2017), and several theoretical mechanisms have been formulated that could be used to predict this effect, including microbial N mining (Fontaine et al., 2011), microbial competition (Fontaine et al., 2003), and preferential substrate utilization (Cheng, 1999; Lyu et al., 2018). Relatively, few studies have focused on RE in plant litter decomposition, even this fresh organic materials-based effect has been invoked for its relevance for our understanding of C cycling (Saar et al., 2016; Rosenzweig et al., 2017; Huangfu et al., 2019), with especially little know about how litter quality and site conditions affect RE on root litter *in situ* (Eisenhauer et al., 2013). HFA and RE, both occurs in the rhizosphere of plants, are functions of decomposition processes driven by composition and functioning of soil decomposers, if RE can affect litter decomposition, then logically, it should also influence the magnitude and direction of HFA. However, less studied is the hypothesized contribution of RE to HFA (Saar et al., 2016), and therefore it remains unclear how HFA and RE for litter decomposition are related. Site conditions, including microclimate, vegetation type, soil properties, are foundational drivers in influencing these below-ground litter-site interaction processes (e.g., Lyu et al., 2019; Veen et al., 2015b). The hydroperiod formed within a wetland, for example, can directly influence edaphic conditions and environmental factors (e.g., temperature, moisture) and indirectly influence vegetation composition, in turn controlling the spatial variation of HFA effects on litter decomposition. Despite the importance of this system, study

89 investigating how these plot-scale variables as drivers of RE, and so possible HFA in
90 a wetland ecosystem remains scarce.

91 Additionally, the direction of HFA may be determined by the interactions between
92 initial substrate quality, decomposition stage, and the decomposer composition and
93 functions (Wickings et al., 2012; Wallenstein et al., 2013; Chávez-Vergara et al.,
94 2018). Initial differences in litter chemistry and HFA were both assumed to decrease
95 as decomposition processes (the chemical convergence hypothesis, Wickings et al.,
96 2012; Yuan et al., 2019). Although the initial differing in chemical compositions (e.g.,
97 C: N ratio) between substrates would converge over time (Rashid et al., 2017), the
98 kinetics of litter-decomposer interactions and the way by which growing plants
99 regulate over time are poorly understood (but see Ayres et al., 2009; Fanin et al.,
100 2016).

101 Lakeshore wetlands are one of the hot spots for biogeochemical processes. The
102 major goal of this study was to determine how soil microclimate (mainly temperature
103 and moisture), and litter quality and soil properties interacted to affect HFA and RE.
104 To this end, we established a reciprocal litter transplanting experiment at three sites
105 along a hydroperiod gradient, using the dominant plant species in the Shengjin Lake,
106 Anhui, China where three species *Rumex dentatus*, *Carex thunbergii* and *Polygonum*
107 *cripolitanum* co-occurred but dominated different site conditions with respect to soil
108 properties and microclimate. In addition to measuring HFA, we examined the effects
109 of the growing plants on litter decomposition and associated C mineralization at their
110 'home' habitat with or without vegetation. This design allowed us to determine the

111 relative importance of vegetation, soil conditions and the quality of litter in
112 determining RE on litter decomposition and possible HFA. We hypothesized that 1)
113 low-quality litters with recalcitrant compounds would enhance HFA; 2) According to
114 the “microbial N mining” hypothesis, the growing plants would stimulate
115 decomposition as the soils in such lake-wetland are often characteristic of N-limited
116 (Wang et al., 2014), but the size of this effect would differ by plant species and litter
117 quality; 3) that the occurrence and strength of HFA and RE would be stage-dependent
118 as litter chemical components change when decomposition proceeds; 4) The variation
119 of HFA is correlated with RE, i.e., root litter decomposition is accelerated in its home
120 soil, RE will also be accelerated in the presence of conspecific species and *vice versa*.
121

122 # 2. Materials and methods

123 *2.1 Experimental site and species selection*

124 We conducted a field experiment in the Shengjin Lake National Nature Reserve (30°
125 15 'N-30°30' N, 116°55 'E-117°15' E) in the southern Anhui Province, China (Fig. 1).
126 The climate of this site belongs to subtropical monsoon, with a mean annual rainfall
127 of ca.1600 mm, most falling between May and August, and a mean annual
128 temperature of 16.4°C (Li et al., 2014). Soils belong to yellow red soil subtypes of red
129 soil based on the Chinese soil classification system (Pan et al., 2008). Multiple
130 shallow ephemeral wetlands were formed due to summer monsoonal flooding and
131 drawdown in water levels during the autumn and winter (Zhang et al., 2018). Mean
132 water level was 10.88 m (Zhang et al., 2018). This ecosystem was a mixture/mosaic

of different plant communities with large contrasts in both plant species and chemistry (Fig. 1). This allowed us to study variation in litter decomposition processes among vegetation types with different plant species and litter traits. In this area, the littoral zone plant community mainly consists of *Carex thunbergii* Steud. (Cyperaceae), *Polygonum cripolitanum* Hance (Polygonaceae), *Echinochloa caudate* Roshev. (Poaceae), *Miscanthus floridulus* (Lab.) Warb. ex Schum et Laut. (Poaceae), *Paspalum distichum* Linnaeus (Poaceae), *Artemisia annua* L. (Asteraceae), *Alternanthera philoxeroides* (Mart.) Griseb. (Amaranthaceae), and *Rumex dentatus* L. (Polygonaceae) (Liu et al., 2017). Furthermore, across this gradient, soil microclimate factors such as moisture declines with increasing elevation during the growing season. The variations of plant traits and microclimate factors along this gradient enabled us to examine the role of different extrinsic drivers underling HFA and its context dependency over a small geographic area (Sundqvist et al., 2013).

We identified three sites along the hydroperiod gradient in which we transplanted litters of three vegetation types. The three sites had similar slope but presented different microclimatic conditions, especially for soil moisture and elevation (Table S1). The distances between two sites ranged from 50 to 200 m. At each site, near-pure stands of plant species were selected from one of the three species: *R. dentatus*, *C. thunbergii*, and *P. cripolitanum*. Plants from different functional group occupy different hydrological niches (Yuan et al., 2017). Thus, the hydroperiod gradient plays an important role in forming plant communities and determines other abiotic factors for litter decomposition such as temperature and moisture. *R. dentatus* occupied the

lower elevation with longer hydroperiod, *C. thunbergii* the mediate elevation and hydroperiod, and *P. cripolitanum* the higher elevation with shorter hydroperiod.

Litters were collected from the three dominant species, with the sampling areas were generally located within the nearly pure stands to prevent litter mixing and avoid any difficulty in interpretation of the results. The litters of the three study species varied in quality, therefore we expect they could different in decomposability, from easily degraded (*R. dentatus*) to difficultly decompose (*P. cripolitanum*). All selected sites were expected to have built up specialized decomposer communities due to a long, stable history of exposure to the focal litter input.

At the end of November 2018, roots were excavated as root-soil mixture in the field to a maximum depth of 20 cm. Then, soil surrounding roots was gently shaken loose by hand until roots could be removed intact. In the lab, root samples were cleaned on a 0.2 mm sieve with distilled water. Only fine roots (< 2 mm) were used, while care was used to exclude all the rhizomes and senescence/broken root segments. Sampled root litters were fully air-dried to fill the litterbags mentioned below. We used fresh materials of roots in this study as it was not possible to accurately determine the timing of the death of fine roots in soil although nutrient resorption could occur during root senescence (Freschet et al., 2010). Subsamples of the air-dried root litter from focal species were oven-dried at 60°C to determine the change in mass between air temperature and 60°C. One gram (air-dried) of either *C. thunbergii or R. dentatus* litter, or 0.5 g of *P. cripolitanum* root litter (because of limited litter availability) were placed in 96 μm mesh litterbags (8 cm × 8 cm in size) to allow soil microbes

colonization, while excluding larger organisms (Swift et al., 1979).

2.2 Field deployment and collection of root litterbags

We used a fully factorial design with three litter species, two retrieval dates, and three incubation sites, resulting in 18 treatment combinations with six replicates per treatment (N = 108). In January 2019, before the regrowth of the vegetation we established six replicates/blocks of litter incubation plots at each site, for a total of 54 plots. Litterbag deployment coincided with the period of natural senescent during winter (late December to early February of next year). Each block consisting of nine plots contains all the possible combinations of litter species and vegetation type. The distance between plots within the same site was 10 - 20 m. A fully reciprocal transplant decomposition experiment was implemented using the litterbag approach at each site, with two litterbags deployed in each plot (for two retrieval dates). At each site, we also created control plots by selecting bare land adjacent to corresponding vegetation plots (thereby allowing the possible rhizosphere effect to be tested), with the distance between two types of plot varying between 0.5 m to 1.0 m, and in the control plot, only litter of the species that dominated the stand of the site was incubated. It was generally easy to choose these control plots since focal species grow in patch. This resulted in additional 3 (litter species) × 2 (retrieval dates) × 6 replication litterbags = 36 litterbags. We did not reciprocally transplant litter between bare land plots across sites to preclude the possibility that differences in RE effects across litter species were confounded by intrinsic site differences in soil moisture (or other relevant parameters such as nutrient availability) other than living root effects.

In mid-January 2019, 48 litterbags were prepared for each site, 12 of which were placed under the original growing plant ("home" decomposition) and 24 of which were randomly assigned to the other two vegetation types ("away" decomposition, 12 litterbags each) to measure HFA. The remaining 12 litterbags were deposited in control plots to test rhizosphere effect. Litterbags were buried in the plots (to simulate root decomposition in soil) based on the reciprocal transplant method described above, while the control plots only contained litterbags with original root litter to test a possible rhizosphere effect from the home soil. Each litterbag was inserted 10 cm diagonally into the soil and the space between litterbags was 5 cm. Six blocks were established at each site. Each block was comprised of multiple rows, with each row randomly assigned to a particular litter species. Litterbags were sampled after 60 or 90 days of decomposition had occurred (mid-March and mid-April, respectively). The two retrieval dates allowed us to test the decomposition effect at early decomposition stage, where the ratio between labile and recalcitrant components changes over time (Chávez-Vergara et al., 2018). After litterbags were brought back to the laboratory, foreign impurities and soil particles on the surface were carefully removed with tweezers, rinsed with distilled water in a 0.5 mm sieve, litter remaining in the litterbag was put into a paper envelope, dried in an oven-dried and weighed. We focused our study on the water-level drawdown phase because plant litter decomposition (especially belowground parts) in seasonally flooded wetland system primarily occurs during this relative *dry* season while flooding often slow decomposition of root litter by creating anoxic conditions (Neckles and Neill 1994; von Haden and Dornbush

2014).

Prior to the start of the experiment, we collected six random soil cores (10 cm depth, 9 cm dia.) in each site for physicochemical analysis. Since there was no significant difference between planted plots and paired control ones within each site in term of soil properties (Table S1), these results were reported at site level. At each retrieval event, soil cores were also taken from all plots, and cores were put in a chest with ice and transported to the laboratory.

2.3 Litter chemical analysis and soil properties

Oven-dried litter subsamples from treatments on each sampling date were ground into powder with a ball mill (Retsch MM 400, Retsch, Haan, Germany). The carbon (C) and nitrogen (N) contents were analyzed using an elemental analyzer (EA, Flash 2000 HT, Thermo Scientific). The initial levels of lignin, acid detergent fiber (ADF - cellulose, lignin, insoluble ash), and neutral detergent fiber (NDF - total fiber) were sequentially obtained according to Van Soest (1963) using an Ankom 2000i Fiber Analyzer (Ankom, Macedon, NJ, USA). Air-dried subsamples were treated with a series of aggressive extractants to determine NDF, ADF and lignin. All these carbon fractions were expressed as a percentage of total mass. A soil subsample was sieved through 2 mm mesh, oven-dried and ground to determine total C and N contents with the Element Analyzer. Soil pH was measured for a 1:5 (soil: water) solution (w/v) using a pH meter, and total phosphorus content was measured using molybdenum antimony blue calorimetry (Murphy and Riley, 1962).

243

244 *2.4 Soil moisture and temperature measurement*

245 At each retrieval event, soil moisture and temperature at 10 cm below the soil surface
246 were measured for six replicates at random points within each incubation site with a
247 multi-parameter soil moisture recorder (TZS-2X-G, Zhejiang Top Instrument Co., Ltd.
248 Hangzhou, China).

249

250 *2.5. Estimations of litter decomposition rate and rhizosphere effect*

251 For all litterbags, we calculated mass loss as shown in equation (1):

252 $$\text{Mass loss}\ (\%) = ((M_0\text{-}M_1) / M_0) \times 100 \qquad (1)$$

253 where M_0 and M_1 refer to the dry mass of the initial litters and the dry mass of the
254 remaining litters, respectively. Net C (or N) loss of litters (C_{loss}) was calculated using
255 the mass of litters before and after the experiment (M_i and M_P) and their C (or N)
256 concentrations (C_i and C_p) using equation (2) (Kai et al., 2019):

257 $$C_{loss}\ (\%) = [(M_i \times C_i)\text{-}(M_p \times C_p)]/(M_i \times C_i) \times 100 \qquad (2)$$

258 Most studies of HFA have examined the effect of HFA on litter mass loss rates,
259 recent works have suggested that HFA might also apply to the change in chemical
260 constituents of plant litter (Ayres et al., 2009; Yu et al., 2015). In this study, we used C
261 loss in litter rather than mass loss to preclude possible inorganic contamination in fine
262 roots retrieved from soils when they were directly in contact with soil. Actually, the
263 relationship between the two metrics (litter C loss and litter mass loss) could be used
264 interchangeably (Keiser and Bradford, 2017; Yuan et al., 2019). The decomposition

constant of litters (k) was calculated after Olson (1963) as shown in equation (3):

$$\ln (C_t / C_0) = -kt \quad (3)$$

where C_t is the litter C (%) at time t, C_0 is the initial litter C (%) at the beginning of the study, and t is the duration of litter incubation in years. We estimated the values of k with ordinary least square regression. In addition, we calculated the time required for litter decomposition of 50% ($T_{0.5}$ = 0.693/k) and 95% ($T_{0.95}$ = 3/k) (Singh and Singh 1999).

Rhizosphere effect (RE) was estimated as the difference of the litter C loss between the unplanted treatment and the planted treatment using equation (4) (Huo et al., 2017):

$$\text{RE}\ (\%) = (C_{loss\ \text{planted}} - C_{loss\ \text{unplanted}}) / C_{loss\ \text{unplanted}} \times 100 \quad (4)$$

where $C_{loss\ \text{planted}}$ is the C loss of litter in the presence of growing plants, and $C_{loss\ \text{unplanted}}$ represents the C loss of same litter species in corresponding bare land. A positive value represents the positive influence of plant presence on the C loss of litters, and *vice versa*.

2.6. Decomposer Ability Regression Test (DART) model

We used the Decomposer Ability Regression Test (DART) to calculate litter quality, soil ability (i.e., abiotic conditions and decomposer efficiency), and the real HFA for each species (Keiser et al., 2014), as shown in a least squares regression model (5):

$$Y_i = \alpha + \sum_{l=1}^{N} \beta_l \text{Litter}_{li} + \sum_{s=1}^{M} \gamma_s \text{Soil}_{si} + \sum_{h=1}^{K} \eta_h \text{Home}_{hi} + \varepsilon_i \quad (5)$$

where Y_i is the degree of C loss in litters for the ith observation and α is the intercept, which represents the average C loss across all observed values in the data set after

287 controlling for home-field parings, litter species, and soil community. This model
288 proposes that decomposition (Yi) for ith observation is equal to β_l plus γ_s plus η_h, with
289 which we estimated. Parameter β_l, litter quality index, is the ability of litter species l
290 (or a ranking of the chemical quality of litters in this study, from species 1 to N), and
291 γ_s, soil ability, represents inherent functional capability of the soil decomposer
292 community s (from soil type 1 to M) to decompose all litter species, η_h estimates the
293 strength/ advantage of a decomposer community decomposing its home litter species
294 in combination of h (HFA, from home combination 1 to K). That is to say,
295 $\text{Home}_h = \text{Litter}_l * \text{Soil}_s$ when l and s are home-field pairings. Each parameter (litter
296 quality index, soil ability, and HFA) produces unitless estimates by which the soil
297 communities or litter types can be compared. Both $\sum_{l=1}^{N} \beta_l$ and $\sum_{s=1}^{M} \gamma_s$ are limited to 0
298 to avoid perfect collinearity (i.e., the non-independence of predictor variables). Litter l,
299 Soil s and Home h are dummy variables that equal 1 or 0 depending on the presence
300 or absence of the litter species, soil community or home combination, respectively.
301 Also, ε is the error term. The model parameters were estimated using SAS 9.4 (SAS
302 Institute, Cary, NC) using the code suggested by Keiser et al. (2014). The effects of
303 functional ability index of soil decomposer communities (γ_s), litter quality index (β_l),
304 and HFA index (η_h) on the C loss were estimated.

305 *2.7. Statistical analysis*

306 Prior to data analysis, we tested the variables for normality and homogeneity of
307 variance. Data met the assumptions of ANOVAs. One-way ANOVA was used to test
308 for differences among plant species in litter chemical traits and we used Tukey's HSD

for post hoc comparisons among litter species. We conducted three-way ANOVAs to test litter species, incubation site, incubation time, and their interactive effects on litter mass loss, C loss, N loss and C: N, and decomposition constant. Post-hoc tests were performed to determine differences between treatment levels for variables that were significant and had more than two levels. To evaluate the differences between treatments of litters, one-way analysis of variance (ANOVA) and the Least Significant Difference (LSD) test was used to analyze the *k* value. All litter quality, soil ability and HFA index and RE values were then tested for deviation from 0 using a *t*-test. Structural equation modelling (SEM) was used to understand the causes of the direct and indirect effects of soil microclimate factors, soil properties and litter traits, and their combined influence on litter C loss. In our model, independent exogenous variables that influenced all the response variables were considered. Before the SEM procedure, Principal Component Analysis (PCA) was conducted to reduce the number of variables for soil properties, litter traits, and microclimate factors (Veen et al., 2010). Litter traits (variables in Table 1), soil properties (variables in Table S1), and microclimate factors (soil temperature and moisture at each retrieval time) were used for the PCAs (Table S2; Fig. S1). The first principal components (PC1) were used in the subsequent SEM analysis (Wei et al., 2013). In this analysis, we used all treatments with growing plants but did not include effects associated with control plots. Maximum likelihood estimation was used to fit data to the models. Both analyses were carried out separately for each retrieval time. A combination of χ^2 tests and root mean square error of approximation (RMSEA) tests were used to assess the

goodness of the models. A non-significant χ^2 test ($P > 0.05$) and a low RMSEA value ($P < 0.05$) was taken as evidence of an adequate model fit (Grace, 2006). We removed or added relationships between variables in the prior models according to Modification Indices to improve the adequacy of the model (Veen et al., 2010). We also used simple regression analyses, with RE values as response variables, while soil properties, litter traits and site variables were used as predictor variables, with each plot serving as an independent data point. Finally, regression analyses were used to test for the relationships between HFA and RE. The significance threshold for all statistical analyses was $P < 0.05$.

3. Results

3.1 Biotic properties and initial litter chemical composition

Generally, soils from *R. dentatus* had higher total N, C, and P contents, while soil C: N ratios and pH increased over those from *C. thunbergii* and *P. cripolitanum* ($P < 0.05$, Table S1). The differences between latter two species were not significant for these variables.

All three species were significantly different in initial root litter chemical composition (Table 1). Differences in litter chemistry between species were particularly apparent for lignin, N content, C: N ratio, and lignin: N ratios. Overall, *C. thunbergii* had lower N and higher C concentrations in litter than other two species, thus leading to the highest C: N ratio among the three species ($P < 0.05$), while *P. cripolitanum* had the highest lignin concentration and lignin: N ratios, indicating that

353 the litters of both species were more chemically recalcitrant. In contrast, these
354 variables of *R. dentatus* litter were generally moderate, indicating a more
355 chemically-labile litter. The content of acid detergent fiber and acid detergent lignin in
356 *P. cripolitanum* litter was significantly higher than that in *C. thunbergi* litter and *R.*
357 *dentatus* litter, but neutral detergent fiber content in *R. dentatus* litter was significantly
358 lower than that in *C. thunbergii* and *P. cripolitanum* litters (Table 1).
359
360 *3.2 Litter N and C loss and decomposition constant*
361 The litter mass loss, N and C loss, C: N ratio and decomposition constant (*k*) were
362 affected by the two-way and three-way interaction among the litter species, incubation
363 site, and retrieval time (Table 2; Fig. S2). Among the main factors, litter species
364 dominated the variation (more than 10% as shown by variation partitioning analysis,
365 Table 2). Litter C loss and therefore *k* values of *R. dentatus* were higher than that of *C.*
366 *thunbergii* litter and *P. cripolitanum* litter regardless of incubation site and time (Table
367 2 and 3; Fig. 2), while *P. cripolitanum* often had the smallest C loss and *k* values for
368 the same incubation site and time combination (Table 3). We also found a significant
369 retrieval time effect, especially on litter C loss and decomposition constants ($P < 0.05$,
370 Table. 2). Although incubation site had no significant main factor effect ($P > 0.05$), the
371 interaction between litter species and incubation site served as an important driver
372 which explaining 17.2% of the variation in litter C loss (Table 2), indicating the
373 existence of the HFA effect (Table 2; all $P < 0.001$). For example, the highest C loss
374 was most often observed with *P. cripolitanum* soils across all focal litter species (Fig.

2). This effect was also highly dependent on retrieval time (Table 2; all $P < 0.001$), with the interaction between litter species × incubation site × time explaining the highest proportion of all variance (18.7%). The *k* values of the same litter in the same soil type after 90 days was often lower than that after 60 days, with the exception of *P. cripolitanum* root litters decomposing in its home soil or *C. thunbergii*'s soil (Table 3). When comparing the differences between incubation times (i.e., 60 days vs. 90 days), we found that the average contribution of the incubation site increased over the course of decomposition, ranging from 2.1% at 60 days to 5.4% by the end of the experiment (90 days). By contrast, the mean variance explained by litter species decreased from 47.2% to 46% over the same time scale (Table S3).

3.3 HFA, soil ability and litter quality

The DART model indicates that the litter quality index of *R. dentatus* was the highest and *P. cripolitanum* litter the lowest at 60 days, showing that in all soil communities, *R. dentatus* litter decomposed fastest and *P. cripolitanum* litter the slowest, while *C. thunbergii* litter had an intermediate value (Fig. 3a). But at 90 days, the litter quality index of *C. thunbergii* litter was the lowest, and *P. cripolitanum* litter had an intermediate value (Fig. 3a). As for the ability of soil organisms to degrade all litter species (γ_s), it was significant at two retrieval times, with all abilities associated with *R. dentatus* being significantly positive across the incubation period (Fig. 3b), indicating that *R. dentatus* soil community had a higher functional ability to decompose all litter compared to the soil community in *P. cripolitanum* and *C.*

thunbergii soils at 60 and 90 days. The ability of *C. thunbergii* soil community to decompose all litters species was lower than that in *P. cripolitanum* soil community at 60 days, while the opposite was true at 90 days (Fig. 3b). Overall, the decomposer community functional ability and site soil moisture roughly overlapped in this field study (Table S4). That is, the site having most favorable microclimate for decomposition co-occurred with the decomposers having rapid litter-processing capacity. The HFA index (η_h) estimated from DART model consistently positive for *P. cripolitanum*, followed by the *C. thunbergii* litter at 60 days (Fig. 3c, $P < 0.05$), confirming that these litters decomposed more rapid in soil where the litter originates from; however, this effect was transient and decreased at 90 days ($P < 0.05$). Meanwhile, *R. dentatus* litter showed neutral HFA at both retrieval times ($P > 0.05$ over the whole decomposition period, Fig. 3c), showing that this litter species degraded at a comparable rate across all soil environments.

3.4 Rhizosphere effect (RE)

Positive RE values were only associated with *C. thunbergii* litter at 60 days ($P < 0.05$), but negative effects found with *P. cripolitanum* and *R. dentatus* litter ($P < 0.05$, Fig. 4a). On the other hand, RE values at 90 days changed from neutral to negative (Fig. 4b).

3.5 An integrated analysis of the plant-soil-litter system

SEM was carried out based on the known relationships between litter C loss and their

419 main drivers. At the first stage of litter decomposition (60 days), SEM revealed that
420 soil properties, along with soil microclimate factors, had the greatest predictive power
421 for explaining the variation in root C loss, while litter quality had little effect in this
422 process (Fig. 5a). However, at the later incubation stage (90 days), litter species
423 dominated the decomposition process as shown by the causal relationship between
424 litter species and litter C loss (0.49, $P < 0.01$). At the same time, soil type had only a
425 marginally significant direct effect on C loss, whereas the direct effect of soil
426 microclimate factors was negligible ($P > 0.05$, Fig. 5b). In addition, soil microclimate
427 had an indirect but significant contribution to C loss by modifying soil properties at
428 this time.
429
430 *3.6 Relationship between REs and litter traits, soil properties, micro-climate factors*
431 *and HFA*
432 RE was significantly related to the majority of litter traits, soil properties, and
433 micro-climate factors. Across the whole incubation time, RE increased with litter C
434 content and litter C: N ratios, while it decreased with litter cellulose, N, lignin content
435 and lignin: N ratios (Fig. S3). In addition, the RE was related to many of the measured
436 environmental factors, but only to a significant level at the later stage of the
437 incubation ($P < 0.05$). To be specific, the RE decreased with soil temperature, soil
438 moisture content, soil N content, and soil C: N ratio at 90 days of decomposition (Fig.
439 S3). These results indicated that these environmental factors, relative to litter quality,
440 tended to be more important in determining the RE. However, there was no linear

441 relationship between litter HFA and RE effects at either retrieval time ($P > 0.05$).

442

443 # 4. Discussion

444 Through a field reciprocal transplant decomposition experiment, we examined the
445 relative importance of microclimate, soil properties, and litter traits on litter C
446 mineralization over time. In accordance with our hypotheses, results revealed that root
447 litter decomposition of three wetland species depended on the interaction between
448 microclimate, soil properties, and litter quality. Furthermore, these interactions varied
449 with decomposition stages. Considering the differences between terrestrial and
450 wetland ecosystems in key ecological processes and functions and their sensitivity to
451 climate change (Xie et al., 2019), our results highlighted the role of plot-scale
452 differences in vegetation type and site conditions in determining C cycling in a
453 wetland ecosystem.

454

455 *4.1 Litter quality as a major controller of decomposition and HFA*

456 In agreement with previous studies (e.g., Huangfu et al., 2019), we found the greatest
457 proportion of the variation in litter C loss was explained by litter species among all
458 main factors (Table 2). Litter quality is often suggested as a primary factor explaining
459 variation in soil ability between sites and HFA (Fanin et al., 2016; Keiser et al., 2014;
460 Veen et al., 2015a; Huangfu et al., 2019). In particular, strong HFA is often detected
461 when home litter is difficult to decompose or very different from other litters
462 (Hoyos-Santillan et al., 2018; Palozzi and Lindo, 2018). In this study, positive HFAs

were observed with litter having high litter C: N ratios, low litter N content and/ or high lignin and thereby high lignin: N ratios (Table 1), and were often observed at sites with a low litter quality index (Fig. 3c). Therefore, these findings support our first hypothesis and the idea that plant litters which are difficult to break down require specialized decomposers for decomposition (Milcu and Manning, 2011). Indeed, the concept of higher HFA values for low versus high-quality litters suggests that the decomposition of *P. cripolitanum* and *C. thunbergii* litter requires microbial specialists, which might have lower resource-use plasticity and be less abundant in the *R. dentatus* soil community (Yeung et al., 2019).

4.2 Edaphic factors interacted with litter quality to affect HFA effect

Functional dissimilarity among microbial communities can be measured with the functional breadth hypothesis, which suggests that soil microbial communities from sites with chemically-recalcitrant litter may have better processing capacity to decompose a broader range of substrates (van der Heijden et al., 2008) and consequently a superior *ability* (Keiser et al., 2014; Fanin et al., 2016; Keiser and Bradford, 2017). However, there was no consistent either low or high ability at sites with a low or high litter quality index (Fig. 3), which suggests that the capacity of soils to degrade litter is not directly linked to the litter quality. Instead, we found that *R. dentatus* soil community had higher functional ability to decompose all litters than the soil community in *P. cripolitanum* and *C. thunbergii* over time (Fig. 3b), indicating that the decomposers in this soil has a broad functional ability to degrade

485 different substrates. In comparison, HFA found for *P. cripolitanum* and *C. thunbergii*
486 litter in their home soil was due to an adaptation of soil decomposers, rather than an
487 overall ability of their soil communities to decompose all litter types (Keiser et al.,
488 2014).

489 This inconsistence may be due to the fact that abiotic factors interacted with (or
490 even overrode) litter quality to affect decomposer communities in determining the
491 breakdown of substrates. In the present study, the large differences in abiotic
492 environment (moisture and temperature) contribute to the decomposition rate between
493 sites, thus indirectly stimulating decomposer communities to decompose a wide range
494 of substrates. In particular, soil microclimate and soil ability estimates appeared to be
495 perfectly overlapped, especially at the first stage of decomposition, as indicated by
496 SEM analysis (Fig. 5a). Since decomposer (Evans and Wallenstein, 2014) and enzyme
497 activity (Averill et al., 2016) are influenced by moisture availability and temperature,
498 warmer and moister soils promote the decomposer activity, resulting in faster litter
499 degradation on litters of all quality (Aerts, 1997). The ability estimates here were
500 likely to reflect the microclimate and decomposers' overall functional capacity to
501 degrade all litter types (Keiser and Bradford, 2017). In such conditions, unlike many
502 studies conducted in terrestrial ecosystems (e.g., Adair et al., 2008), soil microclimate
503 in our system significantly affected, either directly or indirectly, the litter C loss at the
504 very beginning of decomposition as shown in Fig. 5a, where soil moisture and
505 temperature explained the greatest variation in C loss at 60 days. Thereafter, the
506 relationship between soil microclimate indices and C decomposition dynamics

becomes weaker (r^2 < 0.15, P > 0.05) than litter traits (r^2 = 0.49, P < 0.05, Fig. 5b), suggesting that environmental drivers at the later stage when the recalcitrant components of litter were dominating the decomposition are not as critical as at the first stage. Consequently, a high litter quality index and soil functional ability did not lead to greater HFA for *R. dentatus*. Therefore, it is plausible that moisture-mediated soil ability advantage was strong enough to override HFA for high-quality litters, while the soil communities in *P. cripolitanum* and *C. thunbergii* preferred their own litter than communities from *R. dentatus* soil. This idea can be further tested to isolate the community effect independent of other factors, including soil abiotic variables, using an inoculum approach (e.g., Keiser and Bradford, 2017).

4.3 Plant presence attenuated root litter decomposition rate

Recently, several researchers suggested that the magnitude and direction of RE might be largely dependent on growing plant identity and the litter quality involved (Chen et al., 2014; Saar et al., 2016; Barel et al., 2019), with most negative REs detected for litters having low P- and N-contents (Saar et al., 2016), but that was not the case in this study where RE was negative to litter N contents. Moreover, unlike Barel et al. (2019), we found that the decomposition reduction in the presence of plants could not be the result of competition between saprotrophic microbes and the plant for mineral N since REs on litter decomposition tended to relate negatively with decreasing litter decomposability to a varying extent (Fig. S3). Also, the negative relationship between soil mineral N and RE after 60 days further precluded the possibility that saprotrophic

529 microbes experienced N competition with the plant. In this study, soil N status was the
530 lowest in *P. cripolitanum* soil compared with the other two sites, but the prominent
531 negative REs were most often observed in *R. dentatus* soil. At the same time, a slight
532 positive RE was detected in *C. thunbergii* soil, while both other sites had relatively
533 high soil N (Table 1). Alternatively, we could not preclude the possibility of the
534 microbial substrate preference utilization due to the lack of correspondence between
535 litter HFA and RE, whereby micro-organisms switch to rhizodeposits as a labile
536 source of energy and nutrients compared to decomposing litter (Chen et al.,
537 2014). While other abiotic parameters like soil moisture can also affect litter quality,
538 decomposer composition, and consequently litter decomposition (Coûteaux et al.,
539 1995), this effect was significant at the later stage of decomposition. Altogether, our
540 results did not support our second hypothesis, and REs were generally affected by
541 substrate quality, while microclimate and edaphic factors could modify these
542 relationships.
543
544 *4.4 Both HFA and RE changed over time but not correlated*
545 Support for HFA variation during the decomposition process (i.e., by stage) is often
546 anecdotal (Ayres et al., 2009; Gergócs and Hufnagel, 2016), our third hypothesis was
547 partly supported by the results. This was often resulted from the decoupling of
548 specific interactions between plant and associated microbe when the focal litter
549 species was degraded in a foreign site, resulting in the local accumulation of
550 recalcitrant compounds and the emergence of similarities in nutrient concentrations

between litters with time (Wallenstein et al., 2013). Stoichiometry of substrate is also an important factor in driving local litter degradation such as the HFA because of changes in its chemical composition during decomposition (Moore et al., 2004). Litter chemical composition convergence often occurs when about 75%-80% of the initial litter mass lost (Preston et al., 2009; Moore et al., 2011; Wickings et al., 2012) and when slow-growing, k-strategist decomposers colonize and decompose the more recalcitrant compounds (Fontaine et al., 2003). HFA was found to be the strongest at 90 days across all litter species but then converged after one year (Gergócs and Hufnagel, 2016). Ayres et al. (2009) also found that the HFA increased during the initial phases of decomposition, but decreased later, suggesting that the importance of the coupling of litter quality and soil decomposers depended on decomposition stage (Chávez-Vergara et al., 2018). Most litters progress towards relative enrichment in recalcitrant compounds over labile ones which have been decomposed with time. Obviously, this stage-specific decomposition should also be considered in testing the existence of HFA for litters. Overall, significant HFA effects can occur even after several weeks (Fanin et al., 2016), although this effect does not necessarily become stronger over time (Veen et al., 2018). Alternatively, the overall ability of decomposers might be underestimated mainly due to the exclusion of soil animals' contribution to decomposition (e.g., mesofauna, St. John et al., 2011) using litterbags with restrictive mesh sizes (Milcu and Manning 2011) where we only measured a subset of decomposition processes, whereas certain microbial decomposers, especially fungi, participated in driving HFA regardless of mesh size or other habitat restrictions

573 (Chomel et al. 2015; Lin et al. 2019). To mechanistically reveal the way by which
574 HFA may be changed over time, longer scales of explicit field testing would be
575 required.

576 The lack of correspondence between HFA and RE may indicate that both effects
577 may be determined by indigenous environmental factors in addition to litter quality.
578 This finding contrasts our fourth hypothesis and previous work by Di Lonardo et al.
579 (2018) which showed a positive relationship between HFA on litter and rhizosphere
580 effect on SOM decomposition at home locations. Although mounting works have
581 suggested that compatibility of a litter type and the soil matrix or resource-consumer
582 interactions (Veen et al., 2015b) could be crucial in determining the magnitude and
583 direction of HFA, this effect might be overridden by fine scale differences in microsite
584 attributes of the wetland ecosystem as we mentioned above.

585

586 ## 5. Conclusion

587 This study represents a first step in addressing the role of site conditions and litter
588 quality in regulating HFA and RE of litter decomposition in a short time scale in a
589 subtropical wetland ecosystem. Our results highlighted that the effect of a specialized
590 decomposer community driving HFA might be mediated by the microclimate of litter
591 incubation in this system. Even both effects were highly dynamic through time, the
592 plant community dominated by *C. thunbergii* was expected to experience fast C
593 turnover in the home soil, at least at the early of decomposition. Furthermore, the lack
594 of correspondence between HFA and RE indicated that plant species that produce

litters exhibiting HFA may not accelerate litter decomposition via RE at same time. Overall, this study provides insights into how environmental change (e.g., due to water table fluctuation) induced decoupling of plant and soil communities impact soil C dynamics. Additional work on the activity and community composition of decomposers is expected to provide mechanism regulating these resource-consumer interactions.

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Conflict of interest statement

Authors declared that they have no conflicts of interest to this work.

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866 *Figures*

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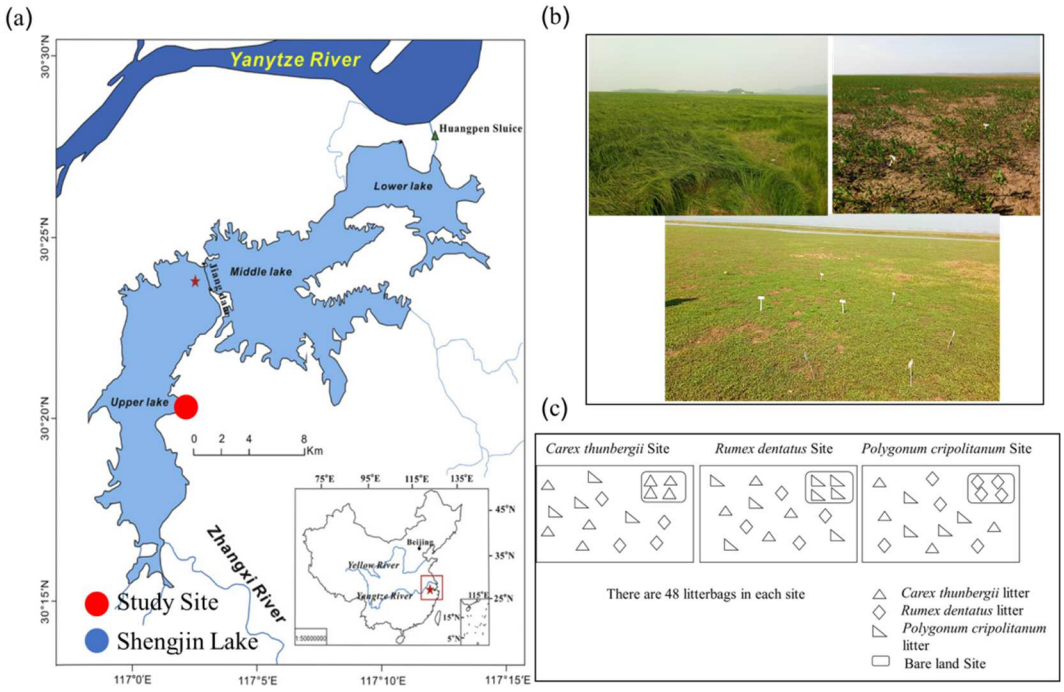

868 **Fig. 1**

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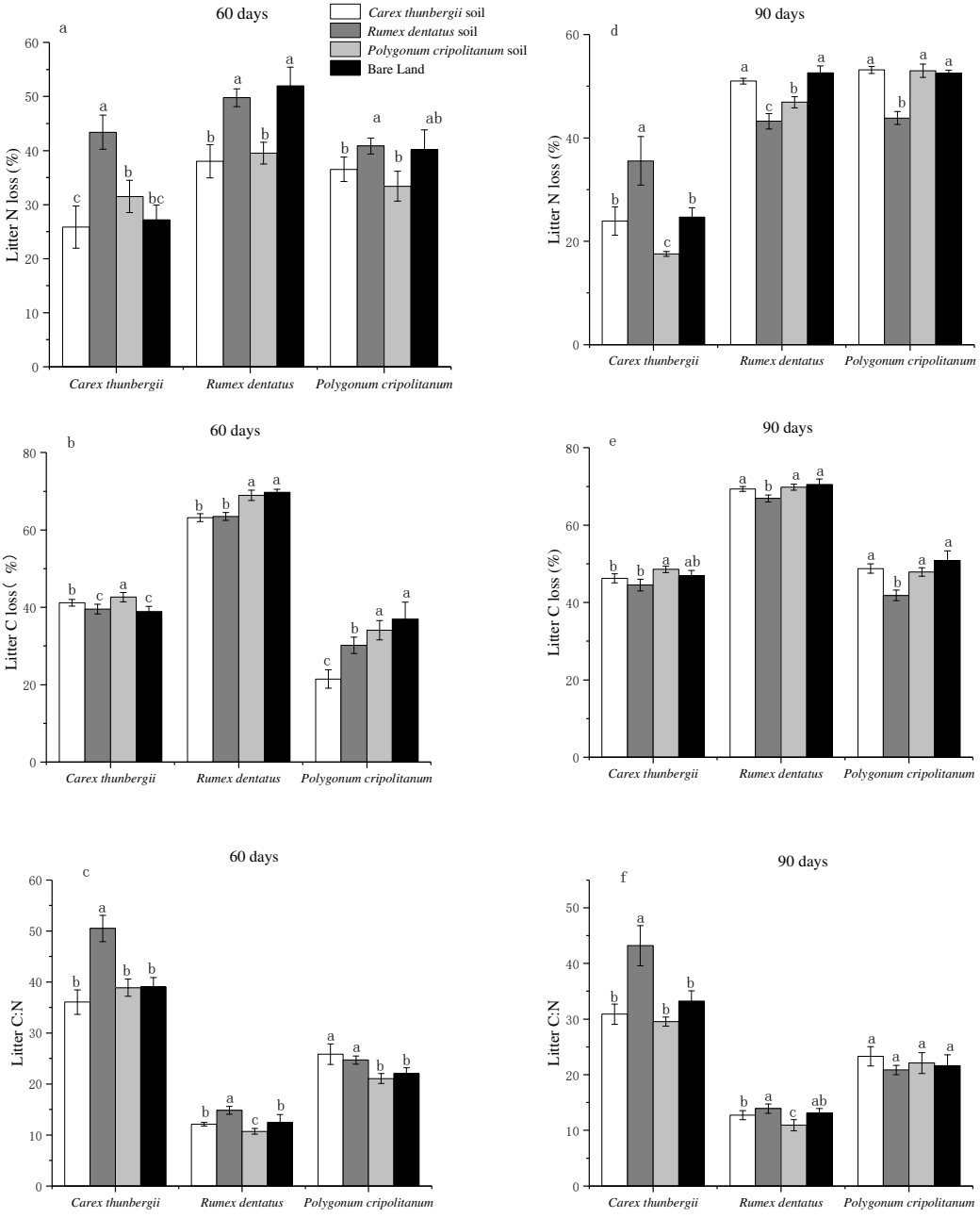

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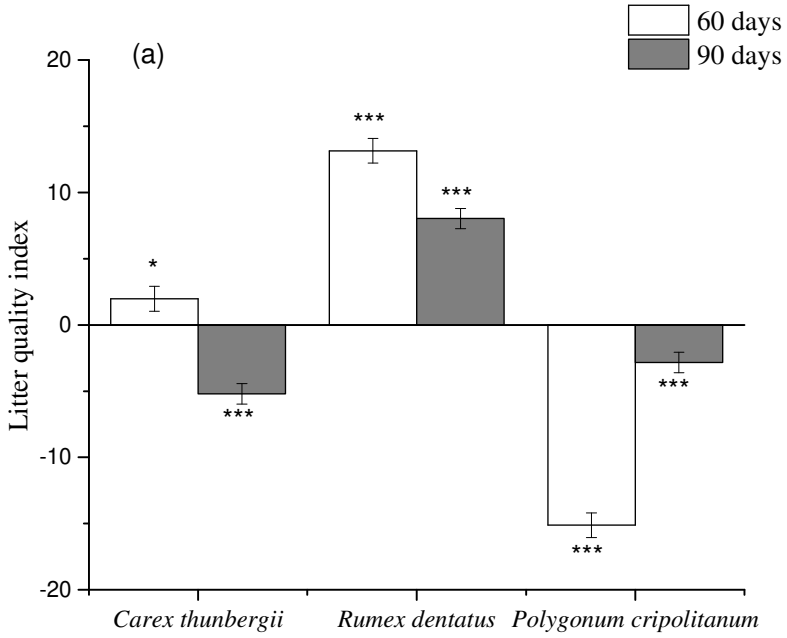

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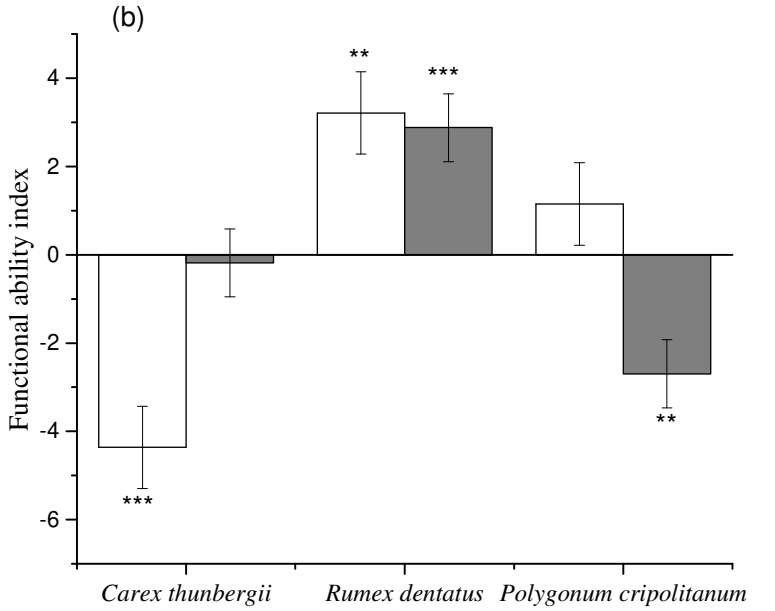

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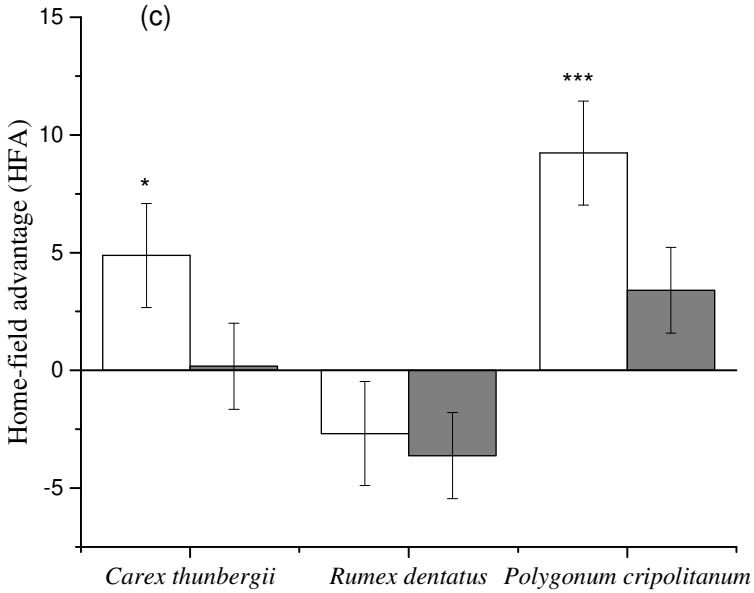

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883 **Fig. 3**

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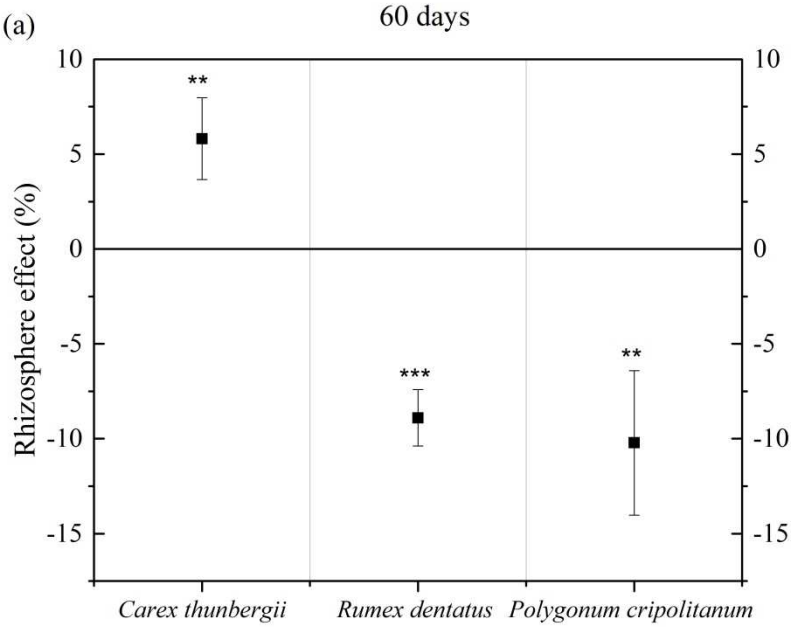

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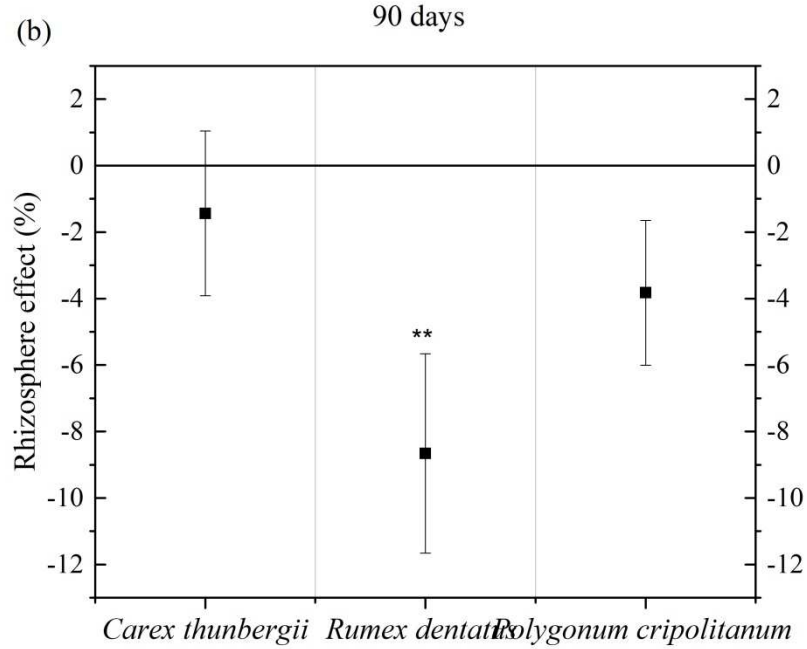

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890 **Fig. 4**

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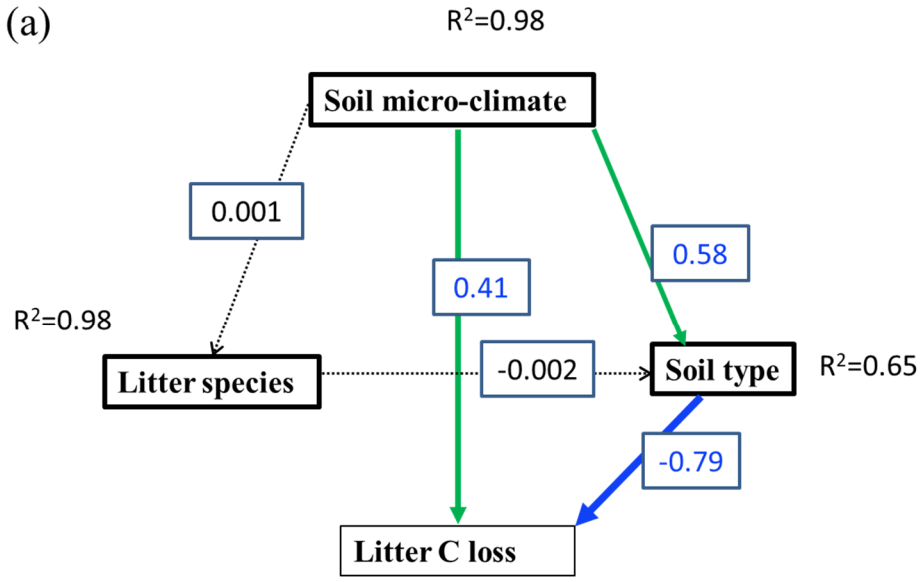

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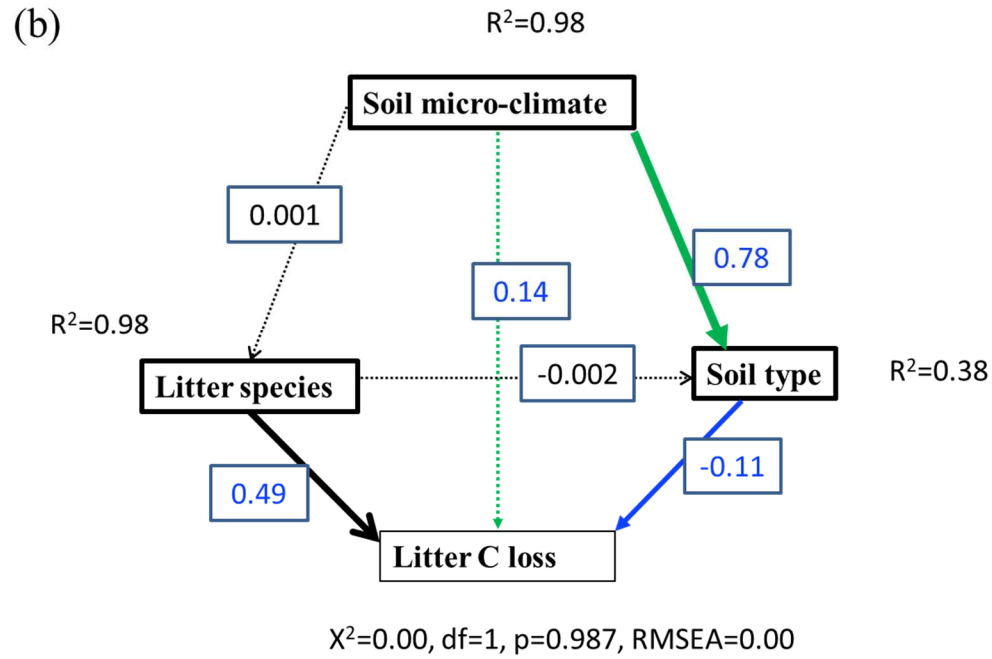

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896 **Fig. 5**

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899 ***Figure captions:***

900 **Fig. 1** (a) The location of the study area, (b) examples of the field quadrat setup, illustrating *Carex*
901 *thunbergii* (left), *Rumex dentatus* (right), *Polygonum cripolitanum* stand (below), respectively, and
902 (c) an illustration of the sampling schematic.

903

904 **Fig. 2** Litter C loss, litter N loss, and the changes of litter C: N ratio of the three litter species in
905 different soil types (*C. thunbergii*-stand soil, *R. dentatus*-stand soil, *P. cripolitanum*-stand soil and
906 bare land) after (a, b, c) 60 days and (d, e, f) 90 days. Different lowercase letters above the bars
907 show significant differences at $P = 0.05$ within same litter species.

908

909 **Fig. 3** Parameters estimated from the Decomposer Ability Regression Test (DART) model
910 proposed by Keiser et al. (2014) for (a) litter quality index on the litter C loss (a ranking of the
911 chemical quality / decomposability of litters regardless of the soil type), (b) functional ability
912 index (the functional capacity of the decomposer community in breaking down litter) and (c)
913 home-field advantage (HFA, the strength of a soil decomposer community in decomposing litter
914 species that originate from "home" soil type compared to other soil types ("away")) index (mean ±
915 1SE, $n = 6$). *, ** and *** represents $P < 0.05$, $P < 0.01$ and $P < 0.001$ from zero, respectively.

916

917 **Fig. 4** The rhizosphere effect (RE, %) calculated from litter C loss. The positive value represents
918 the positive influence of plants on the C loss of litters, and *vice versa*. According to *t*-test, ** and
919 *** shows there is significant difference from zero at $P = 0.05$ and $P = 0.01$, respectively, and
920 each value represents mean ±1SE ($n = 6$).

921

922 **Fig. 5** Result of SEM explaining variation in litter C loss at 60 (a) and 90 days (b) of incubation.
923 Numbers next to lines represent standardized path coefficients and are indicative of the effect size
924 of the relationship. Line width indicates the strength of the causal relationship. Solid lines
925 represent significant effects ($P < 0.05$) while dashed ones are indicative of non-significant
926 relationships. Percentage (R^2) associated with response variables indicates the proportion of the
927 variation explained by other variables.

928

Tables

Table 1 Initial chemical characteristics of the three litter species

	Total N (%)	Total C (%)	C:N	Neutral detergent fiber (%)	Acid detergent fiber (%)	Acid detergent lignin (%)	Lignin: N
Carex thunbergii	0.96 ± 0.04c	45.53±0.49a	46.47±1.71a	69.1±5.7a	27.0±1.7b	7.2±1.3b	7.51±0.31b
Polygonum cripolitanum	1.69 ± 0.07b	36.40±0.63c	20.95±1.21b	61.2±0.5b	44.8±0.4a	21.7±0.7a	12.83±0.57a
Rumex dentatus	2.02 ± 0.04a	41.09 ±0.72b	20.37±0.25b	40.4±1.4c	23.3±0.4c	8.6±0.4b	4.24±0.07c

Values represent the mean ± 1SE (n = 6). Values within same column sharing different lowercase letters are different at P = 0.05.

854

855 **Table 2** Statistical results from ANOVA with the percentage of sums of squares explained (%SS)
856 on the effects of litter species (*C. thunbergii*, *R. dentatus* or *P. cripolitanum*), incubation site (*C.*
857 *thunbergii* soil, *R. dentatus* soil, *P. cripolitanum* soil, bare land) and time (60 days, 90 days) on
858 the elements loss, and decomposition constant.

Source of variation		N loss	C loss	C:N	decomposition constant (*k*)
	df	2	2	2	2
Litter species	F	68.749	266.379	431.988	282.475
	P	< 0.001	< 0.001	< 0.001	< 0.001
	%SS	13.0	16.6	17.9	16.7
	df	3	3	3	3
Incubation site	F	2.207	1.871	1.367	1.674
	P	0.093	0.138	0.256	0.176
	%SS	1.5	0.9	0.7	0.8
	df	1	1	1	1
Time	F	2.253	9.298	1.039	6.428
	P	0.115	0.003	0.310	0.012
	%SS	0.6	1.5	0.2	1.0
	df	5	5	5	5
Litter species × Incubation site	F	38.656	130.109	232.703	128.224

	P	< 0.001	< 0.001	< 0.001	< 0.001
	%SS	14.8	17.2	18.5	17.1
Error	df	115	115	115	115
	%SS	6.5	3.0	1.8	3.3
	df	3	3	3	3
Litter species × Time	F	45.841	341.502	322.193	280.366
	P	< 0.001	< 0.001	< 0.001	< 0.001
	%SS	13.0	18.2	18.1	17.8
Error	df	115	115	115	115
	%SS	8.2	2.0	2.2	2.6
	df	4	4	4	4
Incubation site × Time	F	2.299	3.665	1.318	2.998
	P	0.065	0.008	0.268	0.021
	%SS	2.1	2.3	0.9	1.8
Error	df	115	115	115	115
	%SS	19.2	17.9	19.4	18.6
	df	6	6	6	6
Litter species × Incubation site × Time	F	32.101	222.485	227.859	171.609
	P	< 0.001	< 0.001	< 0.001	< 0.001
	%SS	14.8	18.7	18.8	18.2
	df	115	115	115	115

Error		%SS	6.4	1.6	1.6	2.2

859

860 **Table 3** Decomposition constant (*k*), time in years taken for 50 percentage C loss ($t_{0.5}$), and time

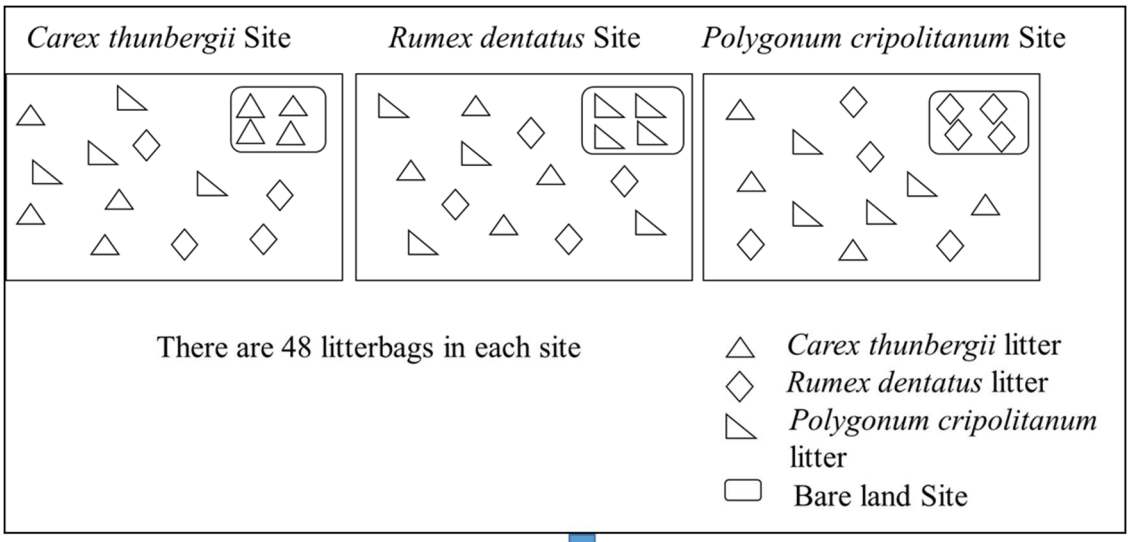
861 taken for 95 percentage C loss ($t_{0.95}$) of litter from *Carex thunbergii* , *Carex thunbergii* and

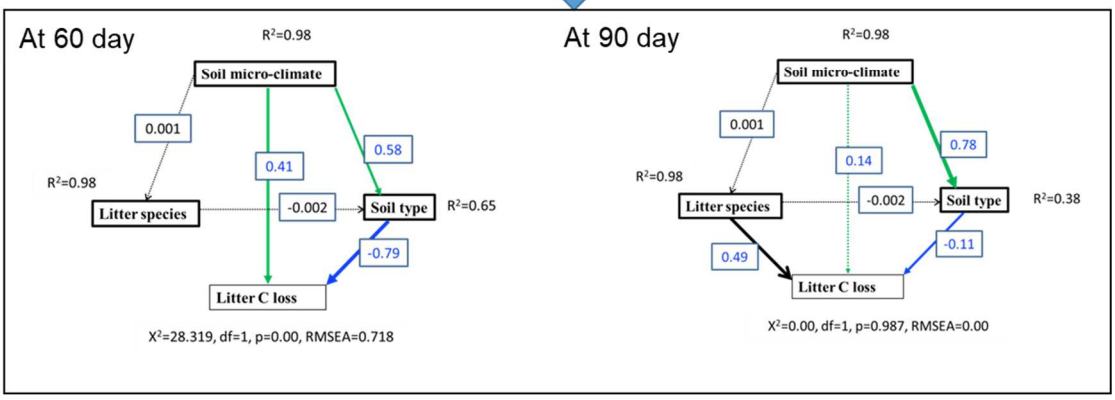
862 *Polygonum cripolitanum* after 60 and 90 days.

Litter species		*Carex thunbergii*	*Rumex dentatus*	*Polygonum cripolitanum*
Carex thunbergii soil	60d			
	k	3.23±0.09b	6.08±0.17b	1.47±0.19c
	$t_{0.5}$(years)	0.21	0.11	0.47
	$t_{0.95}$(years)	0.93	0.49	2.03
	90d			
	k	2.65±0.18a	4.80±0.02b	2.71±0.10a
	$t_{0.5}$(years)	0.26	0.14	0.26
	$t_{0.95}$(years)	1.13	0.63	1.11
Rumex dentatus soil	60d			
	k	3.06±0.13c	6.13±0.17b	2.19±0.18b
	$t_{0.5}$(years)	0.23	0.11	0.32
	$t_{0.95}$(years)	0.98	0.49	1.37
	90d			
	k	2.39±.011b	4.31±0.25c	2.13±0.18b
	$t_{0.5}$(years)	0.29	0.16	0.33

	$t_{0.95}$(years)	1.25	0.70	1.41
	60d			
	k	3.38±0.13a	7.13±0.26a	2.54±0.23b
	$t_{0.5}$(years)	0.20	0.10	0.27
Polygonum	$t_{0.95}$(years)	0.89	0.42	1.18
cripolitanum soil	90d			
	k	2.70±0.01a	4.86±0.10ab	2.64±0.08a
	$t_{0.5}$(years)	0.26	0.14	0.26
	$t_{0.95}$(years)	1.11	0.62	1.13
	60d			
	k	3.00±0.13c	7.26±0.17a	3.02±0.57a
	$t_{0.5}$(years)	0.23	0.10	0.23
	$t_{0.95}$(years)	1.00	0.41	0.99
Bare land	90d			
	k	2.57±0.10a	5.11±0.28a	2.88±0.21a
	$t_{0.5}$(years)	0.27	0.14	0.24
	$t_{0.95}$(years)	1.17	0.59	1.04

All *k v*alues were determined from litter C loss based on Olson (1963). Different letters following *k* values indicate a significant difference among different decomposing sites at $P = 0.05$.


Carex thunbergii Site
Rumex dentatus Site
Polygonum cripolitanum Site
There are 48 litterbags in each site
Carex thunbergii litter
Rumex dentatus litter
Polygonum cripolitanum litter
Bare land Site


At 60 day
R^2=0.98
Soil micro-climate
0.001
0.41
0.58
R^2=0.98
Litter species
-0.002
Soil type
R^2=0.65
-0.79
Litter C loss
X^2=28.319, df=1, p=0.00, RMSEA=0.718
At 90 day
R^2=0.98
Soil micro-climate
0.001
0.14
0.78
R^2=0.98
Litter species
-0.002
Soil type
R^2=0.38
0.49
-0.11
Litter C loss
X^2=0.00, df=1, p=0.987, RMSEA=0.00