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Soil fertility underlies the positive relationship between island area and litter decomposition in a fragmented subtropical forest landscape

Xian Yang [a,c,1], Yating Wang [b,1], Qianna Xu [c], Weixing Liu [d], Lingli Liu [d], Yujia Wu [b], Lin Jiang [c,*], Jianbo Lu [b,*]

[a] State Key Laboratory of Biocontrol, School of Ecology, Sun Yat-sen University, Guangzhou 510275, China
[b] College of Life and Environmental Sciences, Hangzhou Normal University, Hangzhou 311121, China
[c] School of Biological Sciences, Georgia Institute of Technology, Atlanta, GA 30332, USA
[d] Institute of Botany, Chinese Academy of Sciences, Beijing, China

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ABSTRACT

Habitat fragmentation has transformed many once contiguous habitats into smaller patches varying in size, especially in forest ecosystems. However, while the consequences of habitat fragmentation for biodiversity and ecosystem functioning (e.g., productivity) have been widely documented, we know much less about how habitat fragmentation affects litter decomposition, a key component of biogeochemical cycling. Here we investigated the effect of forest fragment size on leaf litter decomposition by conducting a litterbag experiment on a group of land-bridge islands in the Thousand Island Lake in subtropical China. We also explored the mechanisms underlying litter decomposition-island area relationship by assessing the bottom-up (via soil nutrients) and top-down (via soil fauna) effects on litter decomposition. We found that the leaf litter of six common plant species with different litter quality, including *Castanopsis sclerophylla*, *Dalbergia hupeana*, *Liquidambar formosana*, *Pinus massoniana*, *Quercus fabri, and Schima superba*, consistently decomposed faster on larger islands, where greater soil fertility facilitated decomposition. Soil faunal diversity also enhanced litter decomposition, but its effect was mainly associated with litter quality and unaffected by island size. Our study demonstrates the deleterious effect of habitat fragmentation on litter decomposition, as well as the importance of bottom-up regulation by soil fertility in modulating habitat fragmentation effect on biogeochemical processes.

1. Introduction

The ever-increasing anthropogenic activities have fundamentally altered Earth's ecosystems. Habitat fragmentation, as an important aspect of anthropogenic environmental changes, is transforming once intact habitats into smaller patches. The impacts of habitat fragmentation on various ecological processes, such as species persistence (e.g., Stouffer et al., 2011), biomass production and carbon sequestration (e.g., Berenguer et al., 2014; Pütz et al., 2014; Chaplin-Kramer et al., 2015), ecological succession (e.g., Schweiger et al., 2000; Cook et al., 2005), trophic dynamics (e.g., Fáveri et al., 2008), and soil nutrient retention (e.g., Billings and Gaydess, 2008), have been widely reported. By contrast, litter decomposition, a key component of terrestrial carbon and nutrient cycling (Gessner et al., 2010), has received less attention (Wardle, 1997; Cuke and Srivastava, 2016; Yeong, 2016). Given that more than half of the net primary production is returned to soil through the decomposition of plant litter in terrestrial ecosystems (Wardle et al., 2004), it is imperative to elucidate how litter decomposition and its driving factors change in the face of widespread habitat fragmentation.

The process of litter decomposition, fuelled by soil microbial activities, is influenced from the bottom by resource quality and from the top by soil macroinvertebrates and the trophic cascades initiated by their predators (Milton and Kaspari, 2007; LeCrawet al., 2017). Reduced habitat size, as one of the most noteworthy aspects of habitat fragmentation, could affect both soil fertility and faunal communities, and therefore potentially alter bottom-up and top-down regulation of litter decomposition. On the one hand, reduced habitat size and the increased proportion of edge habitats could alter environmental conditions, such as soil temperature, moisture, and nutrients (Didham and Lawton, 1999; Haddad et al., 2015; Li et al., 2020), which could have direct impacts on

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* Corresponding authors.
E-mail addresses: lin.jiang@biology.gatech.edu (L. Jiang), jianbo.lu@hznu.edu.cn (J. Lu).
[1] Xian Yang and Yating Wang have contributed equally to this work.

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soil detritivores and litter microbial decomposition (Williams-Linera, 1990; Kaposet al., 1997). On the other hand, habitat size could affect several aspects of soil faunal communities, including diversity, population sizes, and food web structure (Benderet al., 1998; Post et al., 2000). These changes in the soil faunal communities may lead to changes in the activities of soil microorganisms, given the demonstrated importance of soil fauna for nutrient mineralization and litter fragmentation (Gessner et al., 2010; García-Palacios et al., 2013; Handa et al., 2014). In addition, changes in soil properties and soil faunal communities may also influence litter decomposition indirectly by altering the diversity and composition of soil microbial communities (Wardle et al., 2004; Hättenschwiler et al., 2005).

To understand the role of habitat area on leaf litter decomposition and the underlying mechanisms in the context of habitat fragmentation, we conducted a litter decomposition experiment in fragmented subtropical forests on a group of land-bridge islands in the Thousand-Island Lake (TIL) in China. The TIL was formed by dam construction in 1959, and the previously continuous landscape in this area was transformed into forest-inhabiting islands surrounded by water. These islands vary substantially in size (Fig. S1, Table S1) and have been subjected to little human interference since their formation, making them ideal for exploring the effects of habitat size on ecosystem processes such as litter decomposition. Previous studies on islands created by dam construction have shown that both soil properties and soil fauna communities could be affected by island size (Feer and Hingrat, 2005; Li et al., 2020). Here, we aimed to answer two specific questions. First, how does litter decomposition vary with island size? Second, how do two opposing mechanisms, including bottom-up regulation by soil properties and top-down regulation by soil fauna, contribute to the effects of island area on litter decomposition in the fragmented subtropical forest landscape?

2. Material and methods

2.1. Study site

Our experiment was conducted on the islands in the TIL, located in Chun'an County of Zhejiang Province, China (29°22′N to 29°50′N and 118°34′E to 119°15′E) (Fig. S1). The region has a subtropical monsoonal-type climate, with an average annual rainfall of 1430 mm, an average annual temperature of 15–17 °C, and relative humidity of 76% (Hu et al., 2012). After damming in 1959, the historically continuous landscape in the TIL region was fragmented into 1078 islands with areas greater than 0.25 ha when the water level reaches 108 m above sea level, qualifying the freshwater lake as one with the most islands in the world (Hu et al., 2012). The island area varies substantially, ranging from less than 1 ha to 1154 ha. These islands are covered by subtropical forests dominated by *Pinus massoniana* in the canopy and evergreen broad-leaved plants *Castanopsis sclerophylla*, *Cyclobalanopsis glauca*, and *Lithocarpus glaber* in the subcanopy (Lu et al., 2011; Liu et al., 2019). The herbaceous layer was dominated by *Pteridium aquilinum*.

2.2. Experimental design

We selected a total of nine islands (Fig. S1, Table S1), which range in area from 0.12 ha to 1154 ha and thus formed a strong area gradient for our study. On each island, a 5 m × 5 m experimental plot was established. The plots were located less than 20 m from the edge of the islands, and characterized by similar geographical conditions (i.e., similar aspect, slope, and elevation). We deployed 20 × 20 cm litterbags in the experimental plot on each of our study islands. All litterbags were 20 cm apart from each other to avoid interactions. The litterbags were made of polyester fabric with mesh size of 5 mm, which granted access for most soil fauna to the enclosed litter. Litterbags contained litter from one of six common tree species in the TIL area, including *Castanopsis sclerophylla* (Lindl.) Schott, *Dalbergia hupeana* Hance, *Liquidambar formosana*, *Pinus massoniana* Lamb., *Quercus fabri* Hance, and *Schima superba* Gardn. et Champ. All leaf litters were collected at the same location from the nearby mainland. The initial litter mass in each litterbag was 10 g.

We established four replicates for each litter species treatment on each island, resulting in 216 litterbags (6 species × 9 islands × 4 replicates). The litterbags were nailed to the ground in the experimental plots in February 2015, and one replicate of each treatment was retrieved from each island every three months during the following year (i.e. May 2015, August 2015, November 2015, and February 2016). The retrieved litters were carefully rinsed with distilled water to remove soil particles and other impurities. They were then air dried at room temperature before being incubated continuously at 65 °C until achieving a constant weight. The samples were then weighed. For each plot, we took four soil cores (5 cm diameter to 10 cm depth) randomly distributed across the plot and mixed them to form one composite soil sample each time when the litterbags were retrieved from the field.

Soil fauna in the litterbags was extracted immediately after the litter bags were transferred to the laboratory. Macrofauna were picked out manually, and other soil animals were extracted using the Berlese-Tullgren funnel method (Jeffery et al., 2010). Soil animals were identified morphologically under a dissecting microscope according to Yin (1998). Soil fauna richness, defined as the number of families, and total abundance of soil animals in each litterbag were recorded.

2.3. Chemical analyses

We quantified the concentrations of carbon (C), nitrogen (N), and lignin of the leaf litters before deploying the litterbags. The litter samples were oven-dried at 65 °C until achieving a constant weight and grounded into fine powder. The C and N concentrations were measured using an elemental analyser (EA3000, EuroVector, Pavia, Italy). The lignin concentration of the litter was determined using the Van Soest extraction protocol (Van Soest, 1994).

The collected soil samples were divided into two portions, with one portion air-dried at room temperature for estimating the N and P concentrations and soil organic C concentration (SOC), and the other portion stored in a refrigerator at 4 °C for a week for estimating soil microbial biomass carbon (MBC). The air-dried soil was crushed with a soil pulverizer and passed through a 100-mesh (0.15 mm) sieve. The inorganic C in the soil samples was removed using 2 $\mathrm{mol \cdot l^{-1}}$ hydrochloric acid, and the soil organic C and N concentrations were then measured using an elemental analyser (EA3000, EuroVector, Pavia, Italy). The P concentration was measured using the molybdate/ascorbic acid method with a 722-type ultraviolet and visible spectrophotometer at 700 nm (Shanghai Jingke Scientific Instrument, Shanghai, China) for colorimetric analysis, after H_2SO_4–H_2O_2 digestion at a constant volume of 100 ml. For the soil samples stored at 4 °C, we first removed stones, fine plant roots, and other impurities by hand; the soil was then passed through a 2 mm mesh screen to be mixed. The MBC of the soil microorganisms was estimated using the fumigation extraction method (Joergensen, 1996).

2.4. Data analysis

Litter mass loss was expressed as the percentage of litter weight loss during the experimental period (one year). Litter decomposition rate (k) was estimated based on the equation $M_t/M_0 = e^{-kt}$ (Olson 1963), where M_t is the litter mass at time t and M_0 is the initial litter mass. We calculated average values of soil abiotic and biotic variables, including soil organic C, N, and P concentrations, MBC and soil fauna richness and abundance, across four sampling time points. We used bivariate regressions to examine the relationship between island area and litter decomposition rate for all plant species considered together as well as for each plant species separately. We then used bivariate regressions to examine the relationship between island area and soil fertility (soil organic C, N, and P concentrations), soil MBC, and soil faunal richness and abundance, as well as between these soil abiotic and biotic variables and litter mass loss.

We used a piecewise structural equation modelling (piecewise SEM) approach (Shipley, 2009) to assess the direct and indirect effects of island area and soil abiotic and biotic variables on litter mass loss and decomposition rate. The initial piecewise SEM was constructed based on the schematic diagram in Fig. A2 (Fig. S2), where island area and litter quality (lignin concentration and C: N ratio) could influence litter decomposition through affecting soil fertility, microbial activity, and soil fauna communities (Fig. S2). We used principal component analysis (PCA) to reduce the dimension of soil chemical variables (soil organic C, N, and P concentrations); the first principal component, which accounted for 78.2% of the variation in the data (Table S2), was used in the SEM to represent soil fertility. Starting with the initial piecewise SEM model, we eliminated the paths whose loss resulted in the reduction of AIC (Akaike Information Criterion; Shipley, 2013) and repeated this process until no further path could be removed. The overall fit of the piecewise SEM was evaluated using Fisher's C test. All statistical analyses were performed using R version 3.4.3 (R Core Team, 2019), with SEM conducted with the piecewiseSEM package (Lefcheck, 2016).

3. Results

The initial litter chemistry of the six plant species varied substantially, with carbon/nitrogen ratio ranging from 16.85 to 32.25 and lignin concentration ranging from 36.7% to 53.1% (Fig. 1a). For soil fauna, we found a total of 6340 individuals, classified into 11 classes, 21 orders, and 89 families (Fig. S3).

Litter experienced continuous weight loss over time (Fig. S4). After one-year incubation, a significant positive relationship was found between litter mass loss and island area when all species were considered together (Fig. 1b; $R^2 = 0.64$, $p < 0.001$). Likewise, litter decomposition rate (k) was significantly positively related to island area (Fig. 1c; $R^2 = 0.52$, $p < 0.001$). Similar positive relationships between island area and decomposition were found for each individual litter species (Fig. 1b, c).

Island area significantly affected soil fertility, with larger islands exhibiting marginally higher soil organic C and significantly higher soil N and P concentrations (Fig. 2a,b,c). Larger islands also supported greater soil MBC (Fig. 2d) and marginally higher soil faunal richness (Fig. 2e). These factors were, in turn, positively associated with litter mass loss (Fig. 3a-e). Soil faunal abundance, however, was unaffected by island area (Fig. 2f), and unrelated to litter mass loss (Fig. 3f).

SEM revealed that the positive relationship between island area and litter decomposition was primarily driven by greater soil fertility, which promoted litter decomposition directly (standardized path coefficient = 0.52 × 0.49 = 0.26 and 0.52 × 0.44 = 0.23 for litter mass loss and decomposition rate, respectively) as well as indirectly via increasing soil MBC (standardized path coefficient = 0.52 × 0.29 × 0.42 = 0.06 and 0.52 × 0.29 × 0.38 = 0.06 for litter mass loss and decomposition rate, respectively), on larger islands (Fig. 4). Soil faunal richness, which was lower for litter with higher lignin concentration, also had a positive effect on litter decomposition through increasing soil MBC (standardized path coefficient = 0.32 × 0.42 = 0.13 and 0.32 × 0.38 = 0.12 for litter mass loss and decomposition rate, respectively). Soil faunal richness, however, did not respond to changes in island area (Fig. 4).

4. Discussion

Litter decomposition is an important ecosystem process carried out by soil microbes, which are influenced by both bottom-up forces through resource availability and top-down forces through soil macroinvertebrate detritivores (Milton and Kaspari 2007; LeCraw et al., 2017). Few studies, however, have compared the relative importance of bottom-up and top-down regulation of litter microbial decomposition (but see LeCraw et al., 2017 for an aquatic study).

On our study islands, the bottom-up control of litter decomposition emerged as litter decayed faster on larger islands with higher soil fertility (i.e., higher organic C, N and P concentrations; Fig. 4). This result is consistent with studies reporting positive effects of soil fertility on litter decomposition (e.g., Bonanomi et al., 2017; Blesh and Ying, 2020), but at odds with studies reporting negative effects of soil fertility on litter decomposition (e.g., Craine et al., 2007; Frey et al., 2014). One possible mechanism for the positive effects of soil fertility on litter decomposition is that greater soil C, N and P availability could promote litter decomposition by providing high quality substrates for microbial growth, which supports higher microbial biomass and enhances extracellular hydrolytic enzyme activities (Bastida et al., 2007; Kanchikerimath and Singh, 2001; Sinsabaugh et al., 2014). On the other hand, high N concentration in soil may also inhibit litter decomposition by reducing ligninolytic enzyme activities (Carreiro et al., 2000). It remains to be seen whether this negative effect of soil fertility on decomposition would emerge in longer experiments on the TIL islands, as the less degradable lignin often accumulates during the later stages of decomposition (Knorr et al., 2005).

The greater soil nutrient availability on the larger TIL islands may be attributed to several factors. One possibility is that smaller islands, due to their lower statue, tend to experience more frequent flooding caused by both water discharge from dam and seasonal water level fluctuation. The occurrence of floods may have increased the nutrient loss from the smaller islands (Mubyana et al., 2003). Another possible explanation for

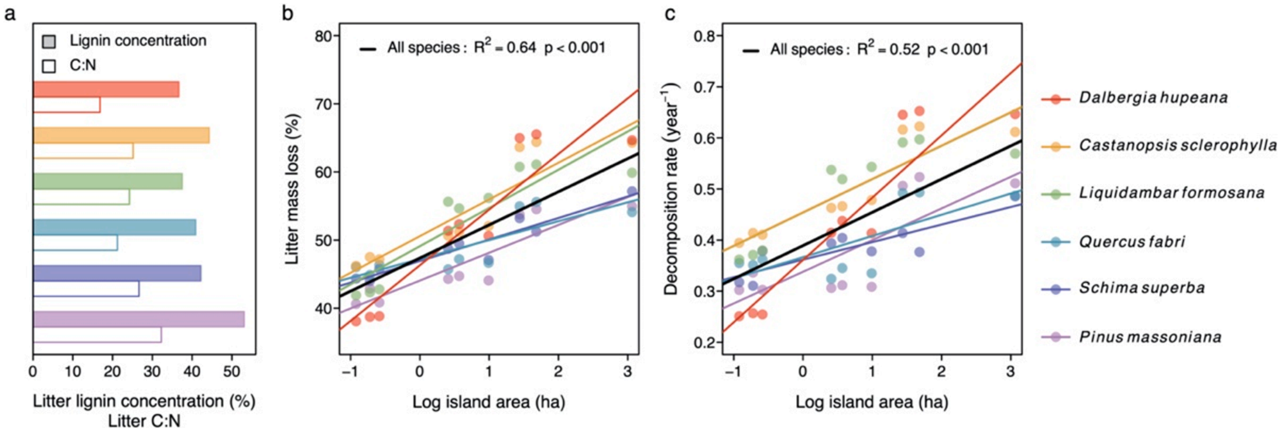

Fig. 1. (a) Litter initial lignin concentration and carbon nitrogen (C:N) ratio, and relationships between island area and (b) litter mass loss and (c) litter decomposition rate for each species and all species pooled. Island area was log 10 transformed. Solid lines represent regressions significant at $p < 0.001$. Black lines are regression lines for all species consider together, and coloured lines are regressions lines for individual species.

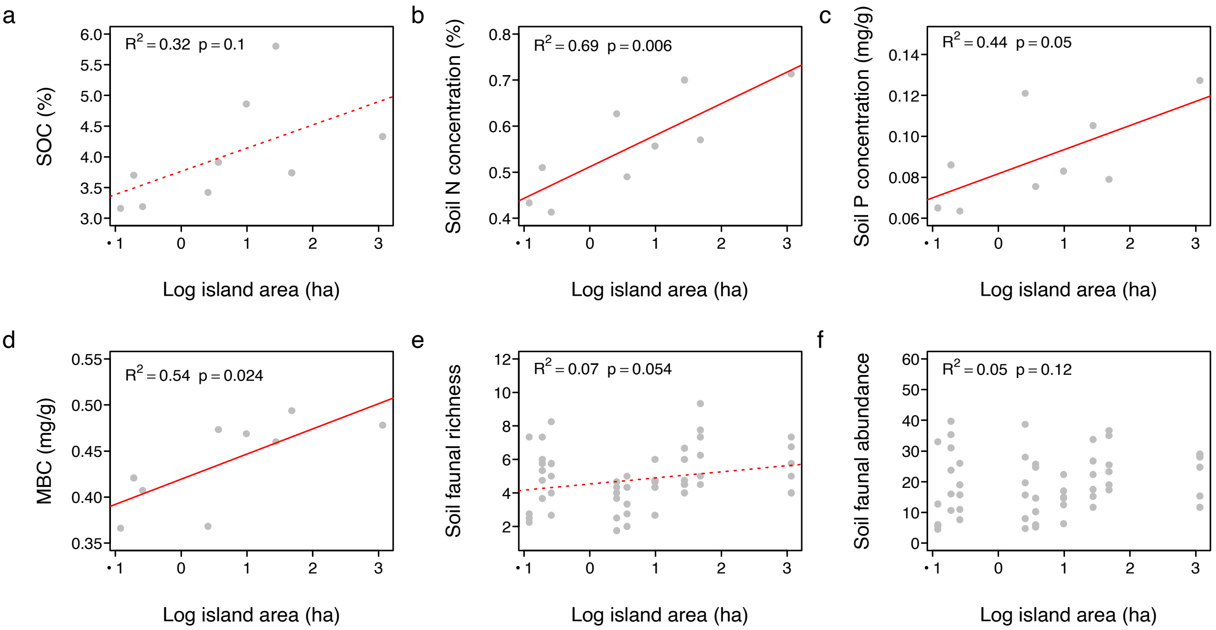

Fig. 2. Relationships between island area and (a) soil organic carbon (SOC), (b) soil nitrogen N) concentration, (c) soil phosphorous (P) concentration, (d) soil microbial biomass carbon (MBC), (e) soil faunal richness, and (f) soil faunal abundance. Island area was log 10 transformed. Solid lines represent significant regressions ($p < 0.05$). Dashed lines represent marginally significant regressions ($p < 0.1$).

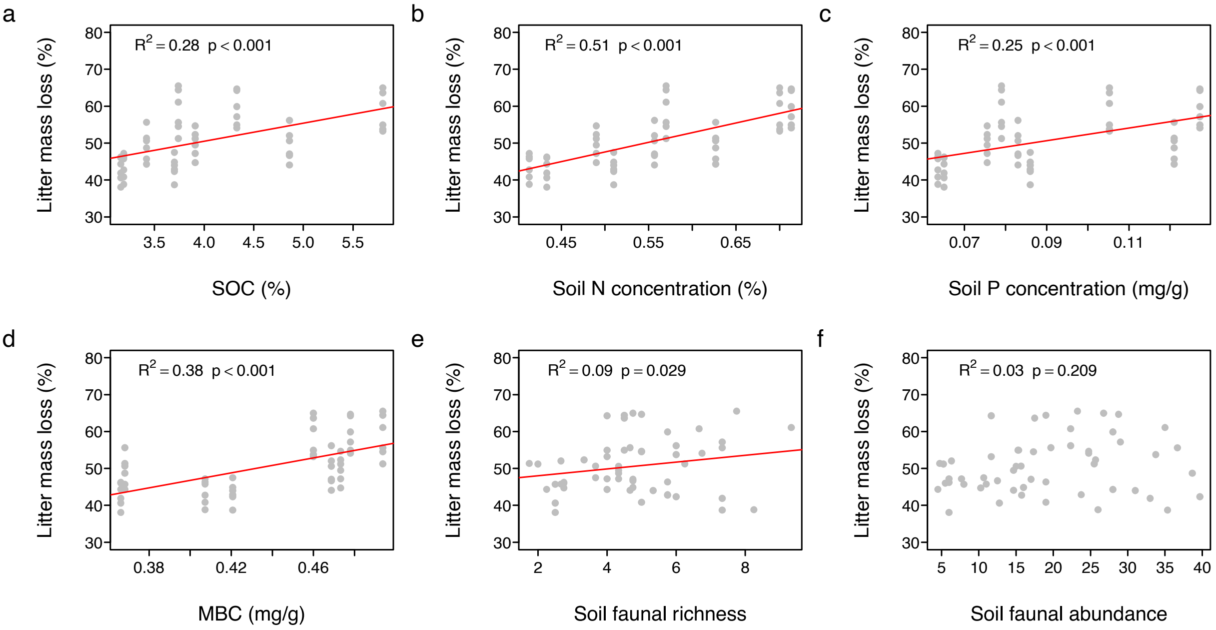

Fig. 3. Relationships between (a) soil organic carbon (SOC), (b) soil nitrogen (N) concentration, (c) soil phosphorus (P) concentration, (d) soil microbial biomass carbon (MBC), (e) soil faunal richness, and (f) soil faunal abundance and litter weight loss. Solid lines represent significant regressions ($p < 0.05$).

the greater soil fertility on larger TIL islands is that later successional broad-leaved tree species (e.g., *C. sclerophylla*, *C. glauca*, *L. glaber*) are more abundant on larger islands (Liu et al., 2019). Compared with small islands, soils on large TIL islands, which tend to contain higher moisture (Li et al., 2020; Fig. S5), could better support the growth of later successional plant species (Liu et al., 2019). Larger TIL islands may thus have higher concentrations of soil organic C and N because of the accumulation of organic matter on forest floor in later successional forests (Brais et al., 1995; Negrete-Yankelevich et al., 2007; Hume et al., 2016). Note that although here we examined the effect of soil fertility on litter decomposition, higher decomposition rate on larger islands may have contributed to increased soil fertility. Future studies that directly manipulate soil fertility within islands would provide independent tests of our results. While out of the scope of the present study, an interesting question to ask next is whether litter collected from different islands would decompose more rapidly on larger islands, similar to what we found here, or on their home islands, as predicted by the home-field advantage hypothesis (Ayres et al., 2009; Freschet et al., 2012).

Many experiments have demonstrated the importance of soil fauna for litter decomposition (González and Seastedt, 2001; Kampichler and Bruckner, 2009; García-Palacios et al., 2013). Accordingly, our study recognized a positive soil faunal diversity, not abundance, effect on litter

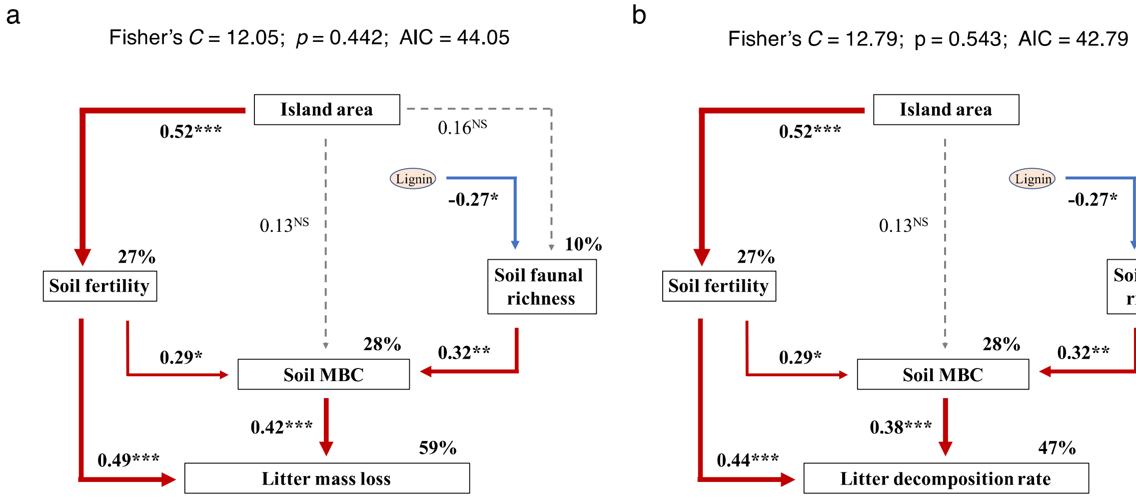

Fig. 4. Structural equation models (SEM) of the effects of island area on (a) litter mass loss and (b) litter decomposition rate (*k*). Soil nutrient was represented by the first principal component (PC1) of all soil nutrient variables measured. Solid red arrows represent significantly positive paths ($p < 0.05$), and solid blue arrows represent significantly negative paths ($p < 0.05$). Dotted arrows represent non-significant paths. We report the path coefficients as standardized effect sizes. Overall fit of the piecewise SEM was evaluated using Shipley's test of d-separation and Akaike information criterion (AIC). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

decomposition (see also Heneghan et al., 1999). Higher soil faunal diversity promoted litter decomposition mainly via its positive effect on microbial biomass (Fig. 4; see also Bradford et al., 2002; Mikola et al., 2002). This effect arose presumably because soil detritivores, through the digestion and fragmentation of the litter, make litter more accessible to microorganisms (Petersen and Luxton, 1982), facilitating microbial growth and in turn, litter decomposition. An alternative explanation is that soil fauna, when feeding on microflora, promote nutrient recycling as a result of their stoichiometric differences, potentially resulting in increased microbial activities (Wang et al., 2009; Kong, et al., 2018). Note that fewer faunal species were found on lower-quality (i.e., containing more lignin) litter, regardless of island area (Fig. S6). This is presumably because soil fauna tends to prefer litter with higher quality (Zhang et al., 2015; Sauvadet et al., 2016), and only a limited number of faunal species could subsist on recalcitrant litters. Importantly, we note that the top-down regulation of litter decomposition by soil fauna diversity, although statistically significant, was not responsible for the observed positive litter decomposition-island area relationship (Fig. 4), due to the lack of the effect of island area on the diversity of soil fauna inhabiting litterbags deployed on the TIL islands (Fig. 2e). The total abundance of soil fauna did not affect litter decomposition rate in our study, probably because different soil fauna species contribute differently to this process. Previous study has found that the abundance of key soil fauna groups, rather than the total abundance, was more important in driving litter mass loss (Wang et al., 2009). It is possible that more diverse soil fauna community are more likely to contain these species.

Our study is the first, to our knowledge, to compare the importance of bottom-up and top-down regulation of relationships between habitat size and litter decomposition in a terrestrial ecosystem. Several terrestrial studies have examined relationships between habitat size and litter decomposition, but did not attempt to disentangle the role of top-down and bottom-up forces (Wardle et al., 1997; Didham, 1998; Moreno et al., 2014). The only other study that explored the topic was conducted in an aquatic system—the water-filled leaf wells of bromeliads (LeCraw et al., 2017), where habitat size-decomposition relationships were strongly shaped from the top down by macroinvertebrates (LeCraw et al., 2017). The contrasting results between our and LeCraw et al.,'s (2017) studies may be potentially explained by the generally stronger top-down control in aquatic than terrestrial systems (Shurin et al., 2002, 2006), and higher sensitivity of species at high trophic levels to habitat size variation in aquatic than terrestrial systems (Holt, 1999; Drakare et al., 2006; LeCraw et al., 2017). Clearly, the validity of this explanation and the generality of the findings of our study and LeCraw et al., (2017) would need to be examined in various terrestrial and aquatic systems.

We acknowledge three limitations in our experiment. First, we measured a limited number of litter quality and soil properties in this study. Other factors that were believed to affect soil microbial activities and litter decomposition, including concentrations of litter phenolic compounds, litter tannins, soil temperature and moisture, soil pH, and concentrations of other soil mineral elements (Canessa et al., 2021), were not measured. Future studies should consider more litter and soil properties to evaluate the robustness of our results. Second, in addition to microbial biomass, the diversity and taxonomic composition of microbial communities are known to influence litter decomposition (e.g., Strickland et al., 2009). Future studies should thus consider the potential effects of variation in bacterial and fungal community structure on the decomposition of litters. On a related note, future studies may also need to quantify extracellular enzyme activities that reflect microbial decomposition of organic compounds to better understand the mechanisms underlying the observed effect of soil fertility on microbial activities.

5. Conclusion

Litter decomposition is a key process affecting carbon and nutrient cycling in terrestrial ecosystems. However, how habitat fragmentation affects little decomposition remains poorly understood. By conducting a leaf litter decomposition experiment in fragmented forests on the islands of the TIL in subtropical China, we found a consistently positive effect of habitat area on litter decomposition. Mechanistically, this positive decomposition-area relationship was not driven from the top-down by soil fauna, but from the bottom-up by soil fertility, which was higher on larger islands. Our study illustrates the deleterious effect of habitat fragmentation on litter decomposition, as well as the importance of bottom-up regulation of the relationships between habitat size and this important ecosystem process in a fragmented landscape.

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Authors contributions

JL conceived the project; YW performed the experiment; XY analysed the data; XY, LJ, and JL led the writing; all authors critically revised the article and contributed to its final version.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.catena.2021.105414.

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