

Research

Island size affects wood decomposition by changing decomposer distribution

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Ecography

44: 456–468, 2021

doi: 10.1111/ecog.05328

Subject Editor: Joaquin Hortal
Editor-in-Chief: Miguel Araújo
Accepted 20 November 2020



Island biogeography theory describes the relationship between island size, isolation and biodiversity, but it does not address the effects on ecosystem processes such as wood decomposition. Wood decomposition rates can be expected to increase with decomposer diversity, which increases with island size and decreases with increasing island isolation. However, island size and isolation effects on wood decomposition may also act by impacting substrate composition, forest composition and biotic interactions among decomposers. In this study, branch-wood decomposition rates of three locally dominant tree species deployed at 154 plots on 15 islands in Thousand Island Lake, China, were measured over one year. The results showed that decomposition rates in coarse-mesh bags where both termites and fungi were allowed access increased with island size for the two tree species preferred by the termites. By contrast, decomposition rates in fine-mesh bags which only fungi could access decreased with island size for the two tree species preferred by fungi. The positive effects of island size on termite feeding activity were mediated by a higher deadwood diversity, a more diverse forest composition and a higher soil moisture content, with forest composition shaping soil moisture. For fungal diversity, the negative effects of island size were attributable to a higher soil moisture content and termite feeding activity. Island isolation decreased fungal diversity but increased wood decomposition rates. Our study indicates that island size affects wood decomposition by altering the distribution of decomposers and their relative contributions to wood decomposition. Size–decomposition relationship further depends on the affinity between substrates and decomposer taxa. In general, our results show that ecosystem processes may be affected by island size and isolation, but the patterns are more complex than expected from the island biogeography theory. This discrepancy is largely due to the different responses and trade-offs among different functional groups.

Keywords: competition, litter–decomposer affinity, microclimate, termites, Thousand Island Lake, wood-decomposing fungi



Introduction

Island biogeography theory predicts that smaller island size and greater island isolation leads to higher extinction rates and lower colonization rates, respectively (MacArthur and Wilson 1963). Therefore, biodiversity is predicted to increase with increasing island size and to decrease with increasing isolation. However, little is known about the effect of increasing island size and isolation on ecosystem processes (Liu et al. 2018a). In a positive biodiversity–ecosystem functioning (BEF) relationship (Loreau et al. 2001), positive effects of larger island size and negative effects of increasing island isolation on ecosystems are expected if biodiversity drives ecosystem processes.

Decomposition is a key ecosystem process that affects element cycling and carbon storage (Bradford et al. 2016). Since decomposer diversity usually decreases with the loss of available micro-habitats like deadwood diversity and amount (Rantalainen et al. 2005, Müller and Bütler 2010, Grilli et al. 2017, Seibold et al. 2017), decomposition may be slower in smaller (Moreno et al. 2014) and more isolated habitats (Spiesman et al. 2018). Yet some studies have reported either null (Bernaschini et al. 2016) or positive (Schleuning et al. 2011, Hertzog et al. 2019) effects of habitat loss and isolation on the decomposition rates in terrestrial systems, suggesting a context–dependent relationship of habitat fragmentation and decomposition. Since decomposition studies are typically conducted in complex terrestrial habitats, the delineation of ‘island’ from matrix and an understanding of the ecological responses to habitat loss and fragmentation may be hard to achieve due to the matrix-type effects (Fahrig 2017, 2020). Moreover, decomposition studies from true islands with a homogeneous water matrix are lacking.

In addition to decomposer diversity, micro-habitat characteristics and biotic interactions among decomposers might also change along the gradients of island size and isolation. These changes may alter decomposer communities and decomposition, thus hampering an appreciation of the generality of relationships between island size, island isolation and decomposition. Decomposers differ in their habitat preferences, including with respect to litter type (Austin et al. 2014) and microclimate (Bässler et al. 2010, Seibold et al. 2016), both of which are shaped by forest composition (Vivanco and Austin 2008, Gottschall et al. 2019), which itself is affected by island size and isolation. For instance, larger islands harbor a higher tree species diversity and more late-successional tree species than do smaller islands (Liu et al. 2019, 2020). Given that substrates under the conspecific tree species might decompose faster than those under different tree species (Freschet et al. 2012, Austin et al. 2014), changes in forest composition along island size/isolation gradients may also affect decomposition rates. These effects may be most pronounced for the substrates preferred by decomposers (Keiser et al. 2014) whereas for the substrates that are less preferred neither island size nor isolation may impact decomposition. Moreover, biotic interactions may change with island size and isolation (Schüepp et al. 2011, LeCraw et al.

2017). While strong competitors increase in diversity and activity with larger island size and decreasing isolation, weak competitors may show the opposite pattern because of competitive exclusion by strong competitors. Consequently, the change in decomposition rates in response to differences in island size and isolation are unclear, given that both strong and weak competitors can drive decomposition.

To study the effects of island size and isolation on the decomposition rates of deadwood, a carbon pool of global relevance (Pan et al. 2011, Giardina 2019), we conducted a wood decomposition experiment at Thousand Island Lake (TIL), China. The study area, a land-bridge island system created by dam construction and inundation from former hilltops, provides a natural ecological laboratory to assess the impacts of fragmentation on biodiversity and ecosystem functioning (Wu et al. 2003, Jones et al. 2016). The ecosystems of the TILs islands are biologically simpler than those of the mainland (Chen et al. 2018) and have a short, common history, since the islands’ forests were clear-cut before flooding in 1959 and have regrown in the years thereafter (Liu et al. 2019).

Fungi and termites are the two most influential wood-decomposing taxa in subtropical forests (Bradford et al. 2014, Ulyshen 2016). Thus, in this study wood was exposed in fine- and coarse-mesh bags to restrict or allow, respectively, the access of termites. Wood decomposition rates, termite feeding activity and fungal diversity were measured after one year. Specifically, the following hypotheses were tested. 1) Smaller island size and higher island isolation have negative effects on termite feeding activity and fungal diversity. These effects may be mediated by changes in deadwood diversity/amount, microclimate, forest composition and forest age (O’Brien et al. 2017) along gradients of island size and isolation (Fig. 1a). 2) The effects of island size and isolation on wood decomposition may be confounded by competition between termites and fungi (Fig. 1b–c), since termites are early wood colonists and outcompete fungi in (sub)tropical forests (Cornwell et al. 2009, Ulyshen 2016, Griffiths et al. 2019). Termites might suppress fungal activity directly by feeding on fungal tissues (Ulyshen 2015; Supporting information) and/or secreting anti-fungal substances (Martin and Bulmer 2018), and/or indirectly through consuming deadwood biomass (Levine 1976; Supporting information). In contrast, meta-analyses show that the presence of fungi in deadwood generally has positive effects on termite aggregation behavior, survival rate and wood consumption (Viana-Junior et al. 2018), due to the fact that some fungi could release attractants for termites after colonizing deadwood (Esenther et al. 1961) and cord-forming fungi translocate nitrogen from rich sources to deadwood (Ulyshen 2015). Thus, termite feeding activity might have some negative effects on fungal diversity and the positive effects of increasing termite feeding activity on wood decomposition might be partially offset by competition with wood-decomposing fungi. 3) The effects of island size and isolation on decomposition via a specific group of decomposer taxa (termites versus fungi) differ between substrate types. For example, for deadwood only accessible to

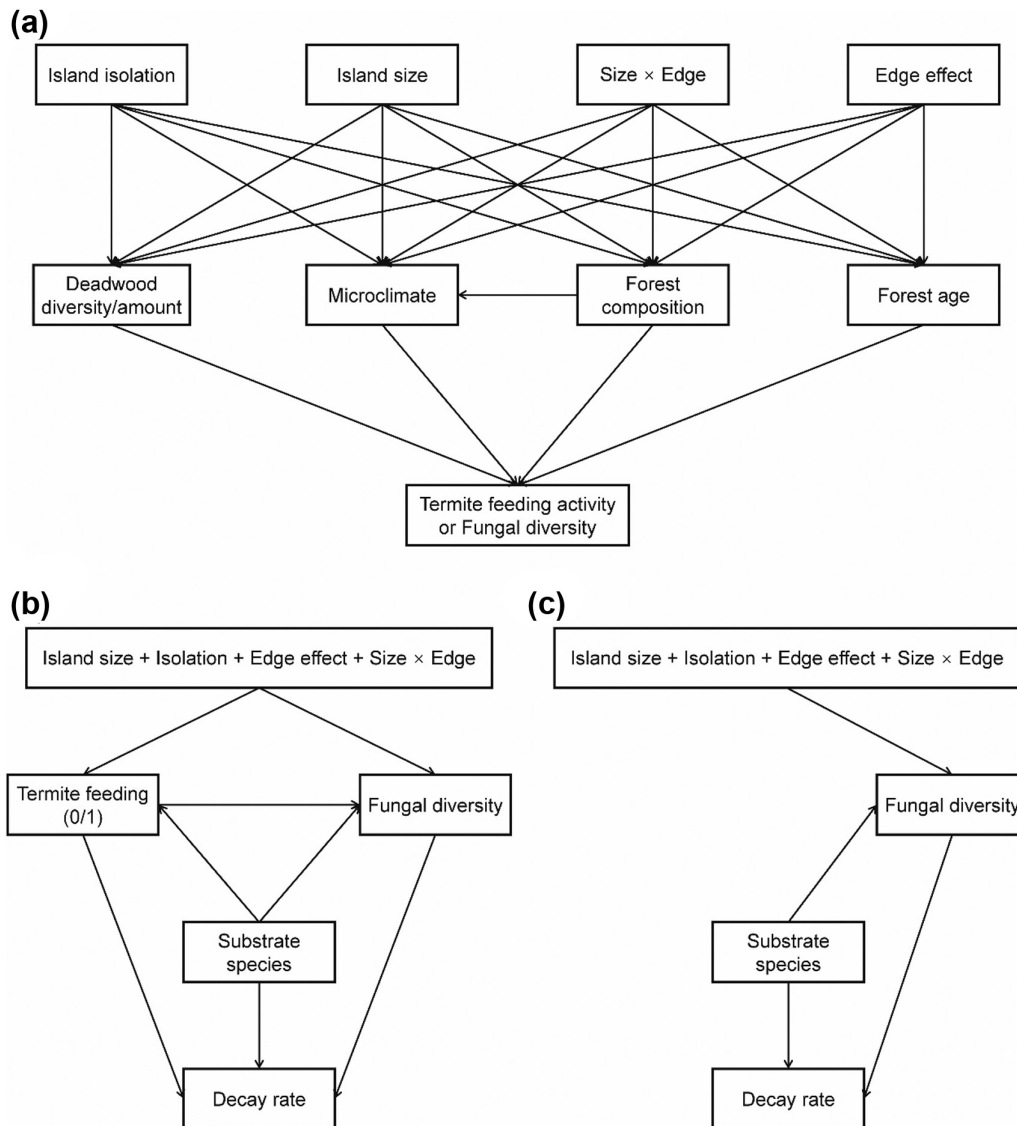


Figure 1. Path models for (a) decomposer activity and diversity at the plot level, (b) decomposition rate at the sample level in coarse-mesh bags and (c) in fine-mesh bags. The substrate species effect is based on a comparison with *L. chinense* (as baseline). Termite feeding is a binary predictor, indicating the deadwood status fed ('1') or not fed ('0') on by termites. Arrows indicate the hypothesized causality.

fungi, only those species preferred by fungi would show responses to a change in island size and isolation. 4) At island margins, environmental conditions could be less ideal (e.g. drier and hotter) such that decomposer activity/diversity and decomposition rates would be lower than that at the island interior. Thus, edge effects on wood decomposition (Crockatt and Bebbler 2015) would be expected.

Material and methods

Study site

Thousand Island Lake (TIL) is an artificial reservoir in Zhejiang Province in eastern China (29°22'–29°50'N, 118°34'–119°15'E; Fig. 2a). The reservoir was formed in

1959 by the damming of the Xin'an River. Prior to flooding, trees of the major canopy layer were completely clear-cut (Liu et al. 2018b). Formation of the lake led to the isolation of > 1000 habitat remnants, referred herein as islands, which have since undergone a secondary succession. Currently, most of the forested areas on the islands (~ 90%) are dominated by *Pinus massoniana* in the canopy and by broad-leaved trees, mainly *Loropetalum chinense*, *Vaccinium carlesii* and *Rhododendron simsii*, in the subcanopy and understory (Hu et al. 2011, Yu et al. 2012, Liu et al. 2018b). Larger islands have a higher tree species diversity (Liu et al. 2020) and a larger number of late-successional trees, e.g. animal-dispersed and shade-tolerant species, than smaller islands (Liu et al. 2019). The climate is subtropical, with monsoons. The mean annual temperature is 17°C; daily temperature extremes range from –7.6°C in January to 41.8°C in July.

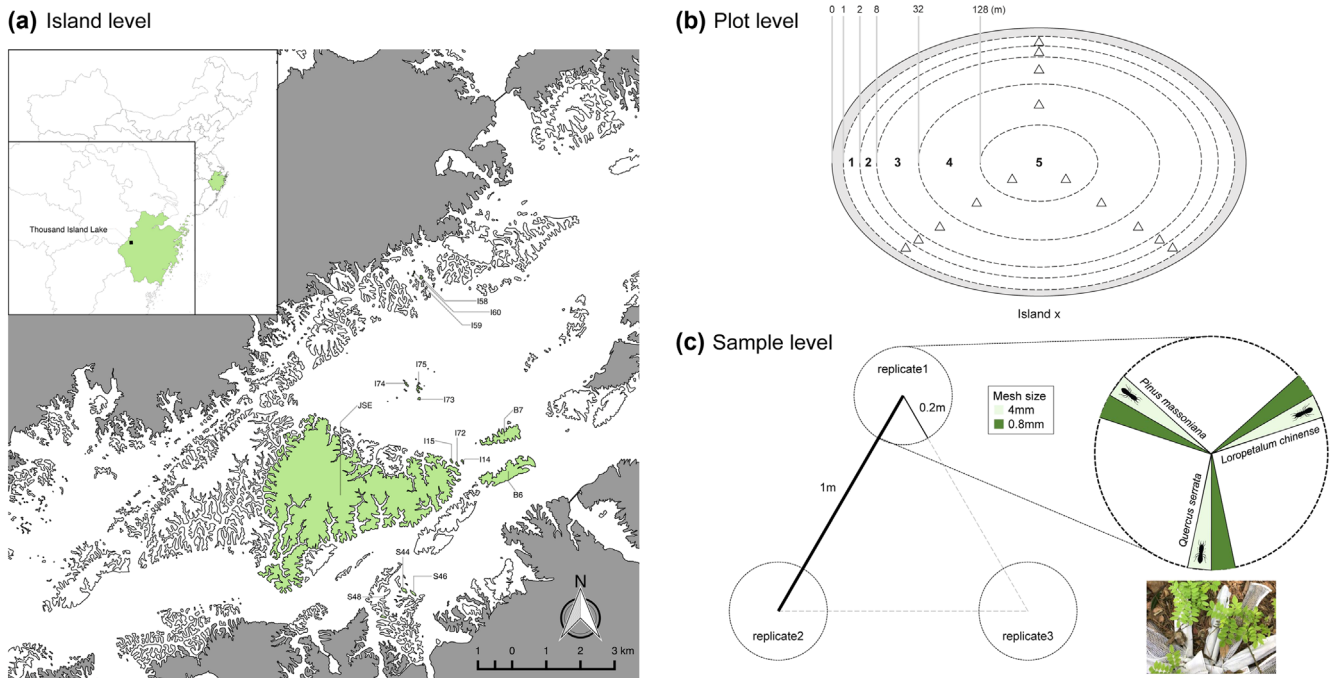


Figure 2. Locations of (a) Thousand Island Lake (TIL) and the 15 studied islands, distributions of (b) triangular plots at each level of edge gradient (1–5) and (c) wood sample arrangements.

Mean annual precipitation is 1430 mm, with 155 d of precipitation per year (Yu et al. 2012). This study was conducted on 15 islands ranging in size from 0.139 ha to 1153.876 ha and isolated from the mainland by distances ranging from 356 m to 4075 m (Fig. 2a).

Plot selection

To account for potential edge effects of island size on wood decomposition processes (Crockatt and Bebbler 2015), wood samples were deployed along an edge gradient extending from the island margins to the island interior (Fig. 2b). Island margins were defined as the outmost trees that formed the envelope lines surrounding the entire island. The islands were divided into six bands based on the distance to the margins: 0–1 ($= 2^0$) m, 1–2 ($= 2^1$) m, 2–8 ($= 2^3$) m, 8–32 ($= 2^5$) m, 32–128 ($= 2^7$) m and > 128 m. Due to seasonal fluctuations of the water level (Xu et al. 2017), the second band rather than the first was chosen as the first level of the edge gradient. The number of edge gradient levels depended on the island size: two levels for the two smallest islands, three for ten medium-sized islands, four for two large islands and five for the largest island, i.e. JSE (Fig. 2a). At each level, three locations differing in their features were selected to set up equilateral triangle plots (side length = 1 m). The centroid of each plot was at the corresponding edge gradient level. For the largest island, the number of plots was doubled because of its large size. For level 5, only four plots were selected due to limited options based on the requirement of distant from the island margin (> 128 m) and without human disturbance (e.g. logging and firebreak). To reduce spatial autocorrelation

among plots, the distance to the nearest plot was ≥ 10 m. A total of 154 plots were established.

Wood decomposition experiment

The branches (diameter = 1.89 ± 0.43 cm; length = 20.03 ± 0.38 cm; mean \pm SD) of three common local tree species served as wood substrates: *Loropetalum chinense* (R. Br.) Oliver (evergreen broad-leaved shrub), *Pinus massoniana* Lamb. (evergreen conifer) and *Quercus serrata* Murray (deciduous broad-leaved tree). These three species represent three major functional groups in Chinese subtropical forests (Kröber et al. 2012, Jin et al. 2018) and rank 1st, 3rd and 8th, respectively, in abundance among the 76 woody plant species found at TIL (Supporting information) (Hu et al. 2011, Liu et al. 2020). Fresh branches were harvested from healthy trees on the largest island (JSE) in January 2018. All samples were oven-dried for 48 h at 60°C to achieve a constant weight. The initial sample volume was calculated as a cylinder. Sample diameter was measured twice orthogonally at both ends of the sample, such that the mean was calculated from four reads. Since wood decomposition depends on wood traits such as wood density, the C:N ratio and the lignin content (Weedon et al. 2009, Van Geffen et al. 2010, Liu et al. 2015, Kahl et al. 2017), these traits were measured in all three species. Wood density (g cm^{-3}) equaled the dry weight divided by the sample volume. To determine whether the lignin content and C:N ratio of the three tree species differed, five branches per tree from 60 trees were additionally sampled for each of the three species. After the branches had dried to a constant weight, an electric drill was used to obtain

wood powder (five drills per branch) from five branches of the same tree, yielding 60 powder samples per tree species. The C:N ratio was measured using an elemental analyzer. The lignin content was determined based on the revised Klason method (Yang et al. 2014) and was similar between the three tree species (Supporting information). However, *Quercus ser-rata* had the lowest C:N ratio (richest in nitrogen), *Pinus mas-soniana* the lowest wood density and *Loropetalum chinense* the highest wood density.

The maximum head width of worker castes of all termite species measured in the TIL was > 0.8 mm (Supporting information). The contribution of termites to wood decomposition (Ulyshen and Wagner 2013) was distinguished using fine (exclusion; mesh size = 0.8 mm) and coarse (control; mesh size = 4 mm) mesh bags (Fig. 2c). Two mesh size treatments per species were made comparable with respect to sample size by carefully matching the samples so that the diameter ratio between the coarse- and fine-mesh samples was close to one (Supporting information). Prior to their deposition in the field, the samples were tagged, placed in mesh bags and closed with cable ties. In each plot, 18 samples were deployed. Six samples, including one fine- and one coarse-mesh sample for each of the three species, were tied together as one bundle. In case a wood sample was on top of another and thus without soil contact, the leaf litter underneath the wood sample was removed so that the shallow pits held the samples more firmly (Supporting information). In addition, the knot made in each bundle was fixed using an aluminum nail such that the wood samples were deployed in a radial arrangement. Three bundles were separately deployed at the three vertexes of the triangular plot (Fig. 2c). In total, 2772 samples were deployed in 154 plots on 15 islands in January 2018.

One year later, in January 2019, each sample was retrieved in a zip-lock plastic bag, which maintained the wood moisture level, prevented saproxylic insects from escaping and protected the fruit bodies from damage and desiccation. In the laboratory, large fruiting bodies as well as insects and soil material on and in the samples were removed to avoid an overestimation of the sample weight. Each sample was placed in a paper bag and dried to a constant weight at 60°C for 48 h. The exponential decomposition rate k (yr⁻¹) for each sample was then calculated (Olson 1963).

Termites

For each sample, two indices were recorded: termite feeding, i.e. the presence/absence of termite feeding marks; termite occurrence, i.e. the presence/absence of live termites. Termite feeding marks included soil sheets on the wood surface, mud in hollowed wood and complex tunnels and galleries with a mottled lining of light brown fecal material (Haverty and Nutting 1975, Ulyshen and Wagner 2013). In September 2018, plot-level termite feeding activity was investigated. All woody debris (diameter \geq 1 cm) within the 5 × 5 m range of the central experimental wood samples was searched for termite feeding marks. Termite feeding activity was calculated

as the ratio of the number of woody debris items fed on by termites to the total number of woody debris items.

Wood-decomposing fungi

Due to the large sample size ($n = 2772$), fungal DNA for each sample could not be sequenced. Instead, as an alternative estimate of diversity, the number of fruit body types emerging on deadwood was determined, although this traditional method may underestimate the true diversity of fungi inhabiting deadwood (Abrego et al. 2017, Dawson et al. 2019). Nevertheless, fruiting species are also the most abundant and active fungal species (Ovaskainen et al. 2013). A single survey can efficiently estimate the composition and diversity of major and active wood-decomposing fungi (Abrego et al. 2016) and at the stand scale may rival sequencing in its accuracy (Runnel et al. 2015).

Fruit body type is a categorical trait defined by the shape, size, texture and structure of the fruit body and its mode of attachment to the resource unit (Zanne et al. 2020). Nine fruit body types have been recognized: agaricoid, resupinate corticioid, discomycetoid, pileate corticioid, pileate polyporoid, resupinate polyporoid, ramarioid, stromatoid and tremelloid. Fungal diversity was calculated as the number of fruit body types for each wood sample. By pooling nine fine-mesh-bag samples (three species × three replicates) from the same plot, plot-level fungal diversity could also be calculated. The coarse-mesh-bag samples were not included in the calculations of plot-level fungal diversity because they were accessible to termites and thus subject to competition, since termite feeding can substantially alter fungal community composition and even reduce fungal diversity (Ulyshen et al. 2016), which was not considered in the path model for plot-level fungal diversity (Fig. 1a).

Because fruit body morphology is closely linked to environmental niche (Halbwachs et al. 2016), the diversity metric based on fungal morphotypes is closely related to functional aspects. Species of the same fruit body type do not necessarily have closer evolutionary histories and thus do not strictly map onto a fungal phylogeny. For example, corticioid fungi distribute across most of the orders comprising the class Agaricomycetes (Hibbett et al. 2014). Nevertheless, there are several distinctions in the taxonomy of the nine morphotypes. For instance, stromatoid and discomycetoid morphotype are found only in Ascomycetes while the other seven morphotypes belong to Basidiomycetes (Dawson et al. 2019).

Forest composition, deadwood diversity/amount and forest age

The diameter at breast height (DBH) and species identity of all tree individuals (DBH \geq 1 cm) within the 5 × 5 m range of the central experimental wood samples were recorded. Stem numbers for each of the three substrate tree species were summed to represent the forest composition. The total basal area ($= \sum \pi \times \text{DBH}^2/4$) of each tree species was calculated to estimate its biomass. *Pinus massoniana* had the highest basal

area and the 5th highest stem number among the 64 tree species identified in the 154 plots; *L. chinense* had the highest stem number and ranked 2nd in basal area and *Q. serrata* had the 5th highest basal area and ranked 11th in stem number (Supporting information).

Species identity, length and two reads of diameter (smallest and largest) for deadwood with a minimum diameter > 1 cm were recorded. Deadwood diversity per plot was then calculated as the number of different deadwood types for tree species in the same plot. Deadwood amount was calculated as the sum of deadwood volume (in cylinder shape). Tree core data showed that the DBH of *P. massoniana* correlated strongly with tree age ($\text{age} = 0.8062 \times \text{DBH} + 4.6087$; $R^2 = 0.74$, $p < 0.001$, $n = 231$). The DBH of the largest tree per plot (*P. massoniana* in 89 of the 154 plots) was used to calculate the forest age.

Soil microclimate

The diurnal soil microclimate was measured four times, in late January, mid-April, late July and late November. Soil temperature and moisture at a 5-cm depth were recorded daily from 10 am to 2 pm using a WET-2 sensor kit (Delta-T, Cambridge, UK) after removing the litter layer. The sensor was inserted into the soil under each pair of treatments (fine/coarse mesh) of the same species, resulting in nine measurements (three species \times three vertexes) per plot. Plot-level soil temperature and moisture were calculated as the mean values of the nine measurements across four seasons. The time span of measurements made on the same island were controlled within one hour to ensure that the data among plots along the edge gradients were comparable.

Statistical analyses

All statistical analyses were conducted using R ver. 3.5.0 (R Core Team). To improve normality, island size, isolation and forest age were \log_{10} -transformed, and the deadwood amount was $\log(1+x)$ -transformed. Considering that the number of edge gradient levels increased with island size, an interaction between island size and edge gradient was included as a fixed effect (Fig. 1). The initial model is shown in Fig. 1, with the directions of the arrows indicating the causal relationship between variables. Island isolation, island size, edge effect and the interaction between the latter two were treated as exogenous variables (Fig. 1). Termite feeding happened in the past while fungal diversity was documented at the end of experiment. Therefore, we supposed that there was a causal effect from termite feeding to fungal diversity (Fig. 1b). Piecewise structural equation modeling (R package 'piecewiseSEM', Lefcheck 2016) and linear mixed-effect models (R package 'lme4', Bates et al. 2015) were used to test the hypotheses. Based on $|r| > 0.7$ as the indicator of high collinearity (Dormann et al. 2013), none of the pairwise correlation coefficients among plot-level predictors exceeded this value (Supporting information). Island identity was treated as a random effect. For sample-level models (Fig. 1b–c),

generalized linear mixed models with binomial (for termite feeding) and Gaussian (for fungal diversity and wood decomposition rate) errors were used as candidate models. Plot identity was treated as a random effect. Poisson models were not used for count data (fungal diversity) because it followed a near-normal distribution (Supporting information). Fisher's C statistic and Shipley's test of d-separation were used to evaluate the overall fit of the model (Shipley 2013). The removal or inclusion of a path in 'piecewiseSEM' depended firstly on its significance ($p < 0.05$). The AICc (Akaike information criterion corrected for small sample sizes) values of the new and the original model were then compared. If the AICc of the new model was > 2 units lower than that of the original model then the new model was retained. Otherwise, the new model was rejected and the original model retained. This procedure was continued until the model with the lowest AICc value remained (Luo et al. 2019). Standardized coefficients were scaled by the relevant range of the data, because the path coefficients of the binomial models could not be scaled by the standard deviation (Grace and Bollen 2005, Grace et al. 2012).

To control for edge effects in the analyses of how island size and isolation effects on wood decomposition depend on species identity and treatment (independent of the SEM analysis), two scenarios were used to compare the wood decomposition rates across the 15 islands: 1) island margins suffered the strongest edge effects and 2) island interior least affected by edge effects. The sample sizes in the two scenarios were comparable (three plots per island; except JSE, $n = 6$ at island margins and $n = 4$ in the island interior). In this analysis, linear mixed-effects models were used, with substrate species, mesh treatment, island size, island isolation and their interactions (i.e. 'species \times treatment \times island size' and 'species \times treatment \times island isolation') as fixed effects while plot identity served as a random effect. Model selection was based on backwards selection and the AIC (Anderson and Burnham 2004) in the R package 'lmerTest' (Kuznetsova et al. 2017). Changing the baseline pair of substrate species and mesh size allowed pair-specific parameter estimates and a determination of the significance of size/isolation effects. To visualize island size/isolation effects on each pair of substrate species and treatment, the function 'plot_model' in the R package 'sjPlot' (Lüdtke 2018) was used to plot predicted mean values and confidence intervals of the wood decomposition rates.

Results

From the 2772 samples, 2769 were successfully retrieved. *Quercus serrata* had the highest mean wood decomposition rate (k , yr^{-1}) in both the fine-mesh bags ($0.61 \pm 0.31 \text{ yr}^{-1}$; mean \pm SD) and the coarse-mesh bags ($0.63 \pm 0.30 \text{ yr}^{-1}$; Fig. 3a), followed by *Loropetalum chinense* (fine, $0.53 \pm 0.22 \text{ yr}^{-1}$; coarse, $0.52 \pm 0.19 \text{ yr}^{-1}$), and *Pinus massoniana* (fine, $0.20 \pm 0.20 \text{ yr}^{-1}$; coarse, $0.19 \pm 0.19 \text{ yr}^{-1}$). The difference

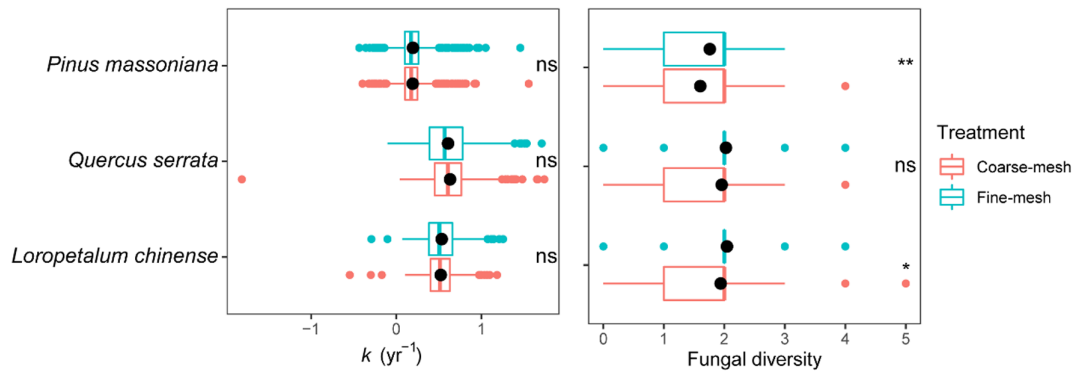


Figure 3. Distributions of (a) the wood decomposition rate and (b) fungal diversity per species and treatment. Significance of difference between treatments is indicated by: $p > 0.05$ (ns); < 0.05 (*) and < 0.01 (**). Black filled circles denote the mean values.

between the decomposition rates in the fine and coarse mesh bags per species was insignificant (Fig. 3a).

Island size did not correlate with island isolation ($r = -0.016$, $p = 0.955$). Deadwood diversity increased and the stem number of *L. chinense* decreased with increasing island size, but neither variable was affected by island isolation, which was removed after AIC model selection (Fig. 4a–b; see Supporting information for summaries of final and initial plot-level models). Neither island size nor island isolation significantly influenced the microclimate, forest age, deadwood amount or stem number of *P. massoniana* or *Q. serrata*. After model selection, both the edge gradient and its interaction with island size were removed as they had no significant effects on micro-habitat characteristics, decomposers or decomposition rates (Fig. 4; also see Supporting information for summaries of the final and initial sample-level models).

Effects of substrate type, island size and island isolation on termites and fungi

Termites (detected in 1.95% of 1384 coarse-mesh bag samples) belonged to three wood-consuming genera: *Macrotermes*, *Odontotermes* and *Reticulitermes*. Marks of termite feeding were detected on 264 of the 1384 coarse-mesh bag samples, and more frequently on branches of *P. massoniana* and *Q. serrata* than on those of *L. chinense* (Fig. 4c). For fungi, eight of the nine fruit body types (except ramarioid) were identified in 95.52% of the 1384 coarse-mesh bag samples and 98.34% of the 1385 fine-mesh bag samples, with sample-level and plot-level diversity ranging from 0 to 5 and from 0 to 6, respectively (Fig. 3b and Supporting information). Sample-level fungal diversity was higher on the branches of *L. chinense* and *Q. serrata* than on those of *P. massoniana* (Fig. 4c–d), regardless of the mesh size. A comparison of the fine-mesh and coarse-mesh bag samples of the same species showed that only those of *Q. serrata* did not differ in fungal diversity, which for the other two tree species was higher in the fine-mesh bags (Fig. 3b).

Island size had opposing effects on termites and fungi (Fig. 4). For termites, island size indirectly increased their plot-level feeding activity by increasing deadwood diversity,

which had positive effects on termite feeding activity, and by decreasing the stem number of *L. chinense*, which had negative effects on termite feeding activity. In addition, the stem number of *L. chinense* had negative effects on soil moisture which increased termite feeding activity (Fig. 4a). By contrast, island size indirectly decreased fungal diversity, as a higher soil moisture content under the lower stem number of *L. chinense* had negative effects on fungal diversity (Fig. 4b). In accordance with the plot-level results, positive and negative effects of island size on sample-level were found for termite feeding and fungal diversity, respectively (Fig. 4c–d).

Island isolation had no significant effect on either plot-level or sample-level termite feeding activity (Fig. 4a, c), but it decreased sample-level fungal diversity in both the coarse-mesh and the fine-mesh bags (Fig. 4c–d).

Island size increases termite-mediated but decreases fungal-mediated wood decomposition rates

Sample-level termite feeding and fungal diversity had similar contributions (0.42 versus 0.44) to the wood decomposition rates (Fig. 4c) but they increased and decreased with island size, respectively (Fig. 4c–d). Island size increased termite feeding while decreasing fungal diversity both directly and, on larger islands, indirectly, by increasing termite feeding. Island isolation increased wood decomposition rates irrespective of mesh treatment (Fig. 4c–d). Together, the direct and indirect effects suggested that in the coarse-mesh bags island size (net effect = $[-0.03] + [0.17] \times [-0.52] = -0.1184$) was slightly more influential than island isolation (-0.07) in decreasing fungal diversity whereas in the fine-mesh bags its negative effect on fungal diversity (-0.02) was weaker than that of island isolation (-0.09).

The effect of island size on wood decomposition rates depends on both substrate species and mesh treatment

Given that the number of edge gradients was imbalanced among islands, samples at the island interior (Fig. 5a) and at the island margins (Fig. 5b) were compared to control for the confounding effects of edge gradients in tests of an effect

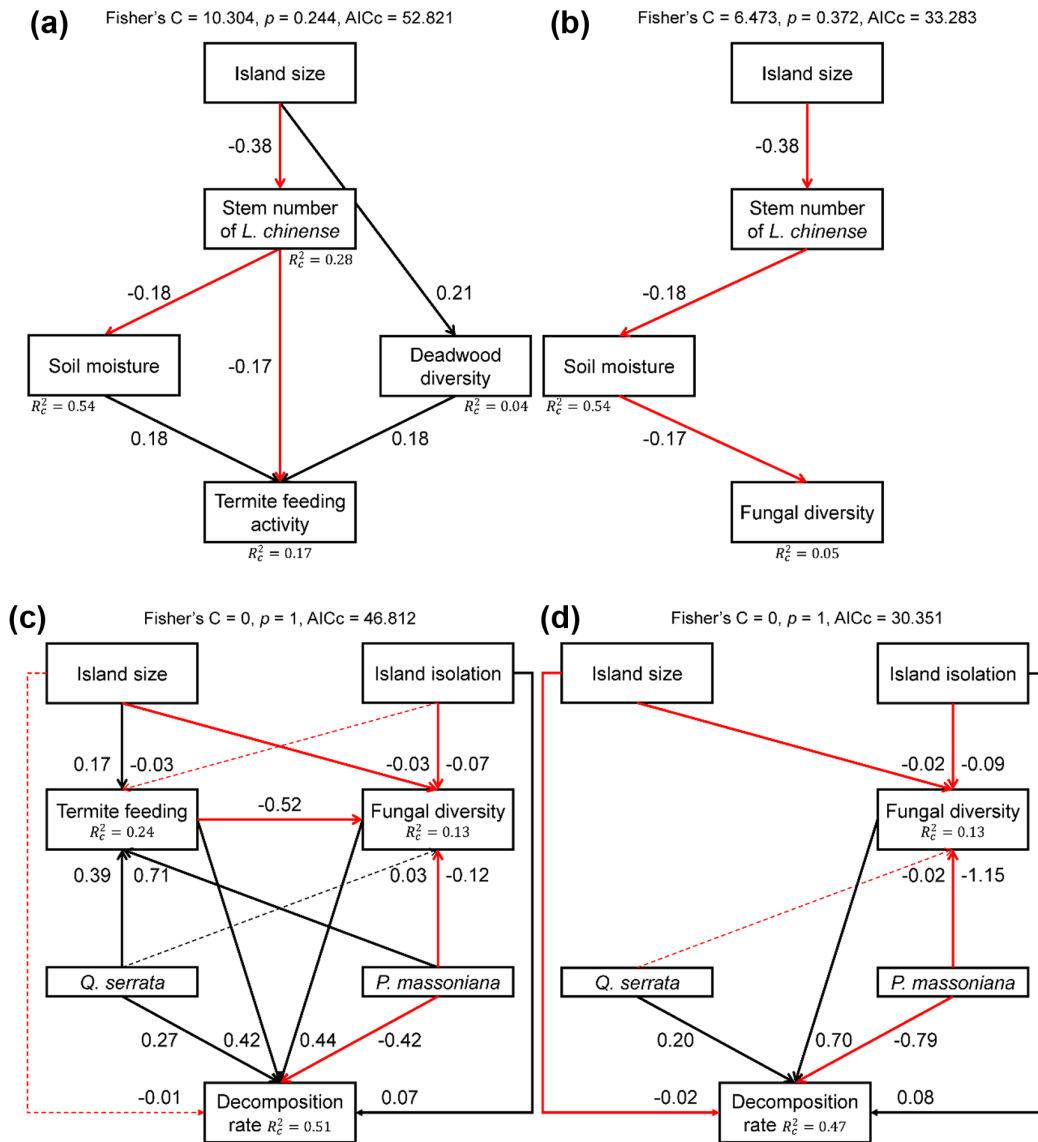


Figure 4. Path model results for (a) termite feeding activity, (b) fungal diversity at the plot-level and (c) the wood decomposition rate at the sample level in coarse-mesh bags and (d) that in fine-mesh bags. Standardized coefficients and the explained conditional variance (R_c^2) are reported. Dashed/solid arrow indicates significant/insignificant effect, and red/black arrow indicates negative/positive effect. The substrate species effects (*Q. serrata* and *P. massoniana*) were based on a comparison with *L. chinense*. Supporting information for final model summaries.

of island size and isolation on wood decomposition rates. Combining the results from the island interior and margins showed that wood decomposition rates in the fine-mesh bag samples decreased with larger island size, except in the case of *P. massoniana*. In the coarse-mesh bag samples, wood decomposition rates increased with larger island size, with the exception of *L. chinense*. Island isolation had positive effects on wood decomposition rates, independent of substrate species and mesh treatment (Table 1, Fig. 4c–d).

Discussion

Wood decomposition is a critical process that contributes to carbon flux and nutrient cycling in forest ecosystems

(Cornwell et al. 2009, Giardina 2019), but how it is affected by island size and isolation in true-island systems is unclear. Our study showed that: 1) island size has contrasting effects on the distribution of termites and fungi and thus on their relative contributions to wood decomposition, by changing forest composition and through competitive exclusion among decomposers; 2) island size affects wood decomposition and its effects further depend on the affinities of substrate-decomposers; 3) island isolation has negative effects on the diversity of wood-decomposing fungi but positive effects on wood decomposition.

Consistent with the general species–area relationship and previous observations of wood-inhabiting beetles in terrestrial systems (Seibold et al. 2017), we found positive effects of island size on termites. However, contrary to

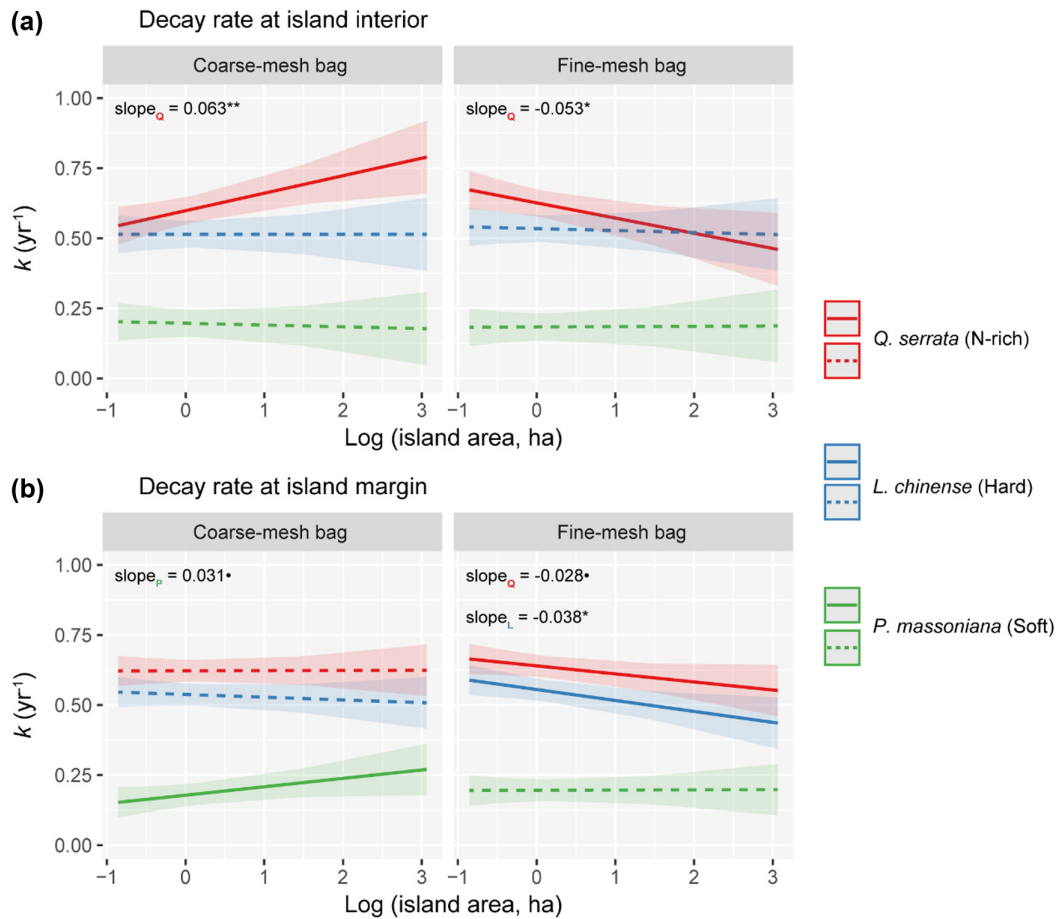


Figure 5. Island size effect on the wood decomposition rate for each pair of substrate species and mesh size. Comparisons across 15 islands were made at the island interior (a) and island margins (b). Predictions of the mean value and the confidence interval of the wood decomposition rate (k , yr^{-1}) based on the results of a linear mixed-effects model (Table 1) are shown. The parameter estimates ($p < 0.1$) of the effect of island size on the wood decomposition rate are indicated by solid lines, and the neutral effects of island size by dashed lines. Significance: $\bullet p < 0.1$, $*p < 0.05$, $**p < 0.01$.

previous studies demonstrating positive effects of habitat availability on fungal diversity (Abrego and Salcedo 2014, Ylisirniö et al. 2016), in this study fungal diversity decreased with increasing island size. In a recent study also conducted in TIL, soil fungal diversity within the same volume of soil was not responsive to changes in island size, whereas soil bacterial diversity increased (Li et al. 2020). These results indicate that responses to island size vary among taxa (Didham et al. 2012).

Forest composition was the primary factor influencing the taxon-specific responses of decomposers to island size. *Loropetalum chinense*, one of the most dominant tree species on the TILs islands, was more abundant on small islands (Liu et al. 2020). This species has a wide ecological niche (Gong et al. 2016), prefers sun-exposed locations (Jin et al. 2018) and has the ability to regenerate from seeds and through resprouting, which together contribute to its dominance in early successional forests (Wang et al. 2007) and its gradual replacement by other tree species during forest succession (Supporting information). In addition, the wood of *L. chinense* seems to be less preferred by termites, most

likely because of its high density and low nitrogen content (Liu et al. 2015, Ulyshen 2015). Therefore, the amount of preferred wood for termites (i.e. from tree species other than *L. chinense*) may increase with increasing island size, resulting in higher termite feeding activity. Second, tree species identity alters the understory microclimate, thereby changing both decomposer community and decomposition rates (Augusto et al. 2015, Gottschall et al. 2019). In the islands of TIL, where forests were once clear-cut, the unshaded conditions exposed fungi to dryness, thus selecting for dry-adapted species in this region (Peay et al. 2016). This observation is partially supported by a recent finding that soil fungal diversity did not increase with higher soil moisture on the larger islands of TIL (Li et al. 2020). By contrast, termites are more sensitive to desiccation in disturbed forests, especially for dominant wood-feeding species like fungus-grower (Woon et al. 2019). In summary, the opposing preferences of termites and fungi for the wood of *L. chinense* and the lower moisture conditions induced by this tree species may explain the opposing responses of these two groups of organisms to island size gradients.

Table 1. Selection results of a linear mixed model of the wood decomposition rate at the island interior (a) and margins (b). Significant predictors ($p < 0.05$) are shown in bold. The wood decomposition rate in the coarse-mesh-bag samples of *Loropetalum chinense* served as the baseline category.

Predictor	Est. \pm SE	t	p
(a) Decomposition rate at island interior			
Intercept	0.219 \pm 0.127	1.719	0.093
<i>Quercus serrata</i>	0.084 \pm 0.027	3.076	0.002
<i>Pinus massoniana</i>	-0.318 \pm 0.027	-11.587	< 0.001
Fine-mesh bag	0.020 \pm 0.027	0.742	0.458
Island size	0.001 \pm 0.022	0.037	0.970
Island isolation	0.098 \pm 0.042	2.358	0.023
Fine mesh bag: <i>Q. serrata</i>	0.007 \pm 0.039	0.193	0.847
Fine mesh bag: <i>P. massoniana</i>	-0.034 \pm 0.039	-0.864	0.388
Island size: <i>Q. serrata</i>	0.063 \pm 0.024	2.565	0.010
Island size: <i>P. massoniana</i>	-0.006 \pm 0.024	-0.256	0.798
Island size: fine-mesh bag	-0.003 \pm 0.010	-0.281	0.779
Island size: fine-mesh bag: <i>Q. serrata</i>	-0.110 \pm 0.034	-3.187	0.002
Island size: fine mesh bag: <i>P. massoniana</i>	0.014 \pm 0.034	0.415	0.678
(b) Decomposition rate at island margin			
Intercept	0.342 \pm 0.108	3.177	0.003
<i>Q. serrata</i>	0.084 \pm 0.020	4.233	< 0.001
<i>P. massoniana</i>	-0.360 \pm 0.020	-17.984	< 0.001
Fine-mesh bag	0.018 \pm 0.016	1.083	0.279
Island size	-0.009 \pm 0.016	-0.570	0.570
Island isolation	0.065 \pm 0.035	1.848	0.071
Island size: <i>Q. serrata</i>	0.010 \pm 0.016	0.657	0.511
Island size: <i>P. massoniana</i>	0.040 \pm 0.016	2.523	0.012
Island size: fine-mesh bag	-0.029 \pm 0.013	-2.280	0.023

Competitive exclusion was the second most relevant factor contributing to the taxon-specific responses of decomposers to island size in our study. Termites can outcompete wood-decomposing fungi (Ulyshen et al. 2016) because they consume fungal tissue, i.e. intraguild predation (Moore et al. 2004), and secrete anti-fungal substances (Ulyshen 2015, Martin and Bulmer 2018). Moreover, wood consumption rates of termites may be higher than those of fungi (Griffiths et al. 2019). Further evidence that termites are able to outcompete fungi in utilizing deadwood was the significantly higher fungal diversity in the fine-mesh than in the coarse-mesh bags containing *L. chinense* and *P. massoniana*, which suggested that termite exclusion led to a significant increase of fungal diversity. Thus, the increase of termite feeding activity with increasing island size may have decreased fungal diversity via competitive exclusion. This finding is to some extent consistent with the trophic theory of island biogeography, which predicts that species with a higher trophic rank (e.g. termites) are more strongly limited by food resources, which generally increase with island size (Gravel et al. 2011, Roslin et al. 2014). It is also in accordance with our observation of an increased termite feeding activity in the presence of a higher deadwood diversity on larger islands. However, it may also be the case that species at a lower trophic rank (e.g. fungi) do not positively correlate with island size, instead depending on the accompanying change of biotic interactions (Godsoe et al. 2017). This negative relationship between fungal diversity and island size could be due to the density compensation, which predicts that a given species is more abundant, and

has a broader niche, on a species-poor small island than on a species-rich larger island, where interspecific competition for the same resources is stronger (MacArthur et al. 1972).

With the increase in island size, termite-mediated decomposition increased while fungal-mediated decomposition decreased. This shift in the decomposer contribution made the net effects of island size on wood decomposition rates further subject to other factors such as litter-decomposer affinity (Austin et al. 2014). For *Q. serrata*, a species preferred by both termites and fungi, decomposition rates decreased in the fine-mesh bags and increased in the coarse-mesh bag with increasing island size, consistent with the decrease in fungal diversity and the increase in termite feeding activity with larger island size, respectively. Since fungi preferred hard wood (*L. chinense*) and termites soft wood (*P. massoniana*), with larger island size the decomposition rate decreased in the fine-mesh bags for *L. chinense* and increased in the coarse-mesh bag for *P. massoniana*. These results indicated that island size effect on decomposition rate occurs only for those substrate types preferred by the respective decomposer taxa.

As predicted by the island biogeography theory (MacArthur and Wilson 1963), island isolation had negative effects on fungal diversity. However, inconsistent with the BEF relationship (Loreau et al. 2001, Bardgett and van der Putten 2014), island isolation had positive effects on the wood decomposition rates in TIL. This is similar to results from temperate forests, where litter decomposition rates were higher near the forest edge in small and isolated forest fragments (Hertzog et al. 2019). Thus, island isolation

in TIL may affect wood decomposition via pathways other than those involving decomposer diversity and activity, e.g. changing environmental conditions (Liu et al. 2018a) and/or functional characteristics of decomposer communities (Maynard et al. 2019). However, none of the micro-habitat characteristics examined in our study were associated with island isolation, such that the environmental causes for the positive effect of island isolation on decomposition remain unclear. Quantifying the species-specific capacity of fungi to decompose wood, e.g. the hyphal extension rate of fungi (Lustenhouwer et al. 2020), may lead to a better understanding of island size and isolation effects apart from those leading to a change in species diversity.

Previous studies reported negative relationships between fungal diversity and wood decomposition (Fukami et al. 2010, Yang et al. 2016), in contrast to our findings. The discrepancy may be due to differences in fungal community composition and biotic interactions. Highly even community has positive richness–decomposition relationships and uneven community negative or null relationships (Maynard et al. 2018). The effect of richness on fungal functions was experimentally shown to strongly depend on two properties of the competitive network: its intransitivity (‘rock–paper–scissors’) and the average competitive ability. Notably, in highly intransitive communities with weak competitors the diversity–function relationship is positive, while in weakly intransitive communities with strong competitors it is negative (Maynard et al. 2017). Hence, it is possible that the fungal communities in our study were evenly structured, strongly intransitive and mainly composed of weak competitors, which merits further testing.

We found that the patterns of decomposer communities and wood decomposition along gradients of island size and isolation did not follow simple predictions based on the island biogeography theory and a positive BEF relationship. Instead, the effects of island size differed between wood-decomposing fungi and termites, leading to a shift in relative importance, from fungi to termites, with increasing island size. Furthermore, litter–decomposer affinity and biotic interactions among decomposers can result in context-dependent effects of island size and isolation on wood decomposition.

Data availability statement

Some data is acquired from other collaborators, which is not allowed for the public repository.

Acknowledgements – We thank Qianqian Wu, Shenhao Yao, Boliang Wei, Tiantian Zhang and other students in Zhejiang Univ., and many local farmers for their contributions to the field work. We also thank Aiyang Zhang and Yuchu Xie for giving helpful comments for the manuscript.

Funding – This work was supported by Major Project of Zhejiang Provincial Natural Science Foundation (LD19C030001), International Collaborative Project of National Key R & D Plan of China (2018YFE0112800), and National Natural Science Foundation of China (31930073).

Conflicts of interest – All authors declare no conflicts of interest.

Permits – This manuscript describes an original analysis of data from a fragmented forest landscape in eastern China. We declare that the authors collected and have the appropriate authority to use these data. The work conforms to the legal requirements of China, where it was carried out, including those related to conservation and welfare, as well as to Ecology’s policies.

Author contributions

Donghao Wu: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (equal); Methodology (lead); Project administration (equal); Software (equal); Validation (lead); Visualization (lead); Writing – original draft (lead). **Sebastian Seibold:** Conceptualization (supporting); Formal analysis (supporting); Methodology (lead); Software (equal); Validation (supporting); Visualization (supporting); Writing – review and editing (lead). **Zhen Ruan:** Data curation (supporting); Investigation (equal); Project administration (equal); Resources (supporting); Validation (supporting). **Changlu Weng:** Data curation (supporting); Investigation (supporting); Project administration (supporting); Resources (supporting). **Mingjian Yu:** Conceptualization (supporting); Funding acquisition (lead); Project administration (supporting); Resources (lead); Supervision (lead); Writing – review and editing (supporting).

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