Plant Soil
https://doi.org/10.1007/s11104-025-07615-z

RESEARCH ARTICLE

Belowground biomass accumulation in a subtropical anthropogenic archipelago

Yunfan Hu · Tianxiang Li · Xuying Ye · Yuping Zhong · Bin Wang · Dan Long · Mengyuan Chen · Mengsi Zhou · Mingjian Yu · Jinliang Liu

Received: 29 November 2024 / Accepted: 3 June 2025

Abstract

Aims Habitat loss significantly threatens global biodiversity and ecosystem functionality. Forest biomass, encompassing both aboveground and belowground, is key indicator of ecosystem functioning. However, the effects of habitat loss on belowground biomass and the factors driving its distribution in fragmented habitats remain unclear.

Methods We conducted a field planting experiment involving four woody plant species with distinct functional traits (e.g., shade-tolerance and dominance) across edge and interior regions of 11 islands within a subtropical anthropogenic archipelago in China. Belowground biomass accumulation was measured in the growth areas of each species, including root biomass of the planted species and other plants. We then tested the effects of island area, edge effects, and abiotic variables (e.g., soil physicochemical properties and topographic attributes) on belowground biomass.

Results Our results demonstrate that mean belowground biomass increases significantly as island area decreases below a certain threshold. Altitude, litter layer depth, soil bulk density, and soil depth significantly affect belowground biomass. Specifically, belowground biomass accumulation in the growth areas of shade-intolerant species increases significantly as island area decreases before certain threshold. Additionally, mean belowground biomass in edge habitats was significantly greater than in interior habitats, particularly in the growth areas around dominant and shade-intolerant species.

Conclusion These findings suggest that habitat size along with soil physical properties, edge effects, and the species shade tolerance play a critical role in shaping belowground biomass accumulation in fragmented landscapes. This study underscores the importance of integrating belowground biomass dynamics into assessments of ecosystem functionality in fragmented habitats.

Responsible Editor: Zhun Mao.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11104-025-07615-z.

Y. Hu · T. Li · D. Long · M. Chen · M. Zhou · J. Liu (✉)
College of Life and Environmental Science, Wenzhou University, Zhejiang Province, Wenzhou, China
e-mail: jinliang.liu@foxmail.com

X. Ye
Chun'an Forestry Bureau, Zhejiang Province, Hangzhou, China

Y. Zhong · M. Yu
College of Life Sciences, Zhejiang University, Zhejiang Province, Hangzhou, China

Y. Zhong
German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

B. Wang
Xin'an River Ecological Development Group Corporation of Chun'an County, Zhejiang Province, Hangzhou, China

Keywords Habitat fragmentation · Belowground biomass · Edge effect · Ecosystem function · Islands

Introduction

Habitat loss and fragmentation are widely recognized as critical threats to species diversity and ecosystem functions (Ewers et al. 2017; Haddad et al. 2015; Ma et al. 2023; Taubert et al. 2018). Currently, approximately 70% of forests worldwide exist in fragmented habitats, with most areas located less than 1 km away from forest edges (Haddad et al. 2015). Forest fragmentation not only reduces biodiversity by 13% to 75%, but also disrupts critical ecosystem functions (Haddad et al. 2015). Habitat loss and edge effects are major drivers of declines in primary productivity, biomass, and carbon stocks (Nunes et al. 2023; Ziter et al. 2013). Forest biomass, including aboveground and belowground components, constitutes a crucial aspect of ecosystem functionality, aboveground biomass refers to the total mass of living plant material (e.g., stems, leaves, branches, and fruits) above the soil surface, whereas belowground biomass comprises all living plant roots and other below-soil components essential for nutrient absorption and plant stability (Cairns et al. 1997). Although aboveground biomass has been extensively studied, research on belowground biomass remains comparatively underdeveloped (Ma et al. 2021). The effects of habitat fragmentation on plant belowground biomass, in particular, are still not well understood.

Research investigating the effects of habitat fragmentation on ecosystem function has primarily focused on its impacts to the aboveground biomass (Ali and Yan 2017; Hossain and Beierkuhnlein 2018; Nascimento and Laurance 2002). For example, Yan et al. (2024) demonstrated that habitat loss reduces species richness, leading to declines in aboveground biomass. Similarly, Shen et al. (2021) observed that aboveground biomass in subtropical forests decreases with decreasing habitat area. Additionally, edge effects resulting from habitat loss significantly influence biodiversity and ecosystem processes in fragmented forests, playing a pivotal role in shaping biomass dynamics (Bregman et al. 2015; Harper et al. 2005). Overall, habitat loss and edge effects have been shown to cause significant reductions in total biomass within fragmented forests (Nunes et al. 2023). However, responses of aboveground and belowground biomass carbon to environmental changes may differ substantially (Mokany et al. 2006). Whether the response of belowground biomass to habitat area and edge effects is consistent with previous findings on aboveground biomass remains unclear.

Belowground biomass accumulation plays a fundamental role in plant development, interspecific competition, and environmental adaptation (Mokany et al. 2006; Poorter Hendrik and Nagel 2000). Environmental factors, such as soil physicochemical properties and light availability, strongly influence the allocation trade-off between belowground and aboveground biomass (Cleland et al. 2019; Fonseca de Lima et al. 2021). Plants in resource-limited environments could prioritize belowground biomass allocation to optimize soil resource acquisition (Brouwer 1983). Erkin et al. (2023) demonstrated that biomass allocation strategies shift across growth stages under drought conditions, with plants increasing belowground biomass in response to water availability while allocating more biomass aboveground in resource-abundant conditions. Habitat loss and edge effects also exert significant impacts on soil physical and chemical properties (Ewers et al. 2017; Ewers and Didham 2006; Murcia 1995). Smaller habitat fragments, subject to intensified edge effects, are often characterized by reduced soil nutrient availability and water-holding capacity (Harper et al. 2005; Laurance et al. 2002). In fragmented habitats, habitat area loss intensifies environmental filtering, with soil properties—such as thickness, bulk density, and nutrient content—acting as key determinants of species diversity (Liu et al. 2020). This selective pressure underpins a decline in species diversity as habitat area and aboveground biomass decrease (Ewers and Didham 2006). Habitat fragmentation not only alters resource acquisition strategies but also affect root architecture and belowground biomass allocation (Kiaer et al. 2013; Sorenson and Damschen 2019). However, our understanding of the key factors that affect underground biomass accumulation in fragmented habitats remains insufficient. Additionally, it is unclear whether these limiting factors promote or inhibit underground biomass accumulation on islands as habitat area decreases.

Variations in root structures, functional traits, and resource adaptation strategies, result in species specific differences in belowground biomass under varying environmental conditions (Comas et al. 2013;

Poorter et al. 2012). For example, Sell et al. (2024) reported that increased air humidity altered biomass allocation and fine root morphology in trees, with species exhibiting distinct adaptive responses. Similarly, Zhang et al. (2020) observed that two *Gentiana* species displayed significant differences in aboveground and belowground biomass distribution along an elevation gradient, underscoring the influence of environmental factors on biomass allocation strategies. Interspecific root competition also exerts a significant influence on belowground biomass allocation in neighboring plants (Armas and Pugnaire 2011). Lak et al. (2020), using competitive root boxes to study interactions between *Fagus* and *Acer* species, found that interspecific competition significantly reduced the fine root growth in *Fagus*. Conversely, *Acer* exhibited greater root plasticity, allowing it to better adapt to competitive pressure. Furthermore, shade tolerance is a critical trait influencing belowground biomass allocation, with shade-tolerant species allocating proportionally more resources to belowground biomass compared to shade-intolerant species (Kitajima 1994). According to the functional equilibrium theory (Brouwer 1983), shade-intolerant plants allocate more biomass to aboveground structures in resource-rich environments to enhance their competitive advantages for light capture. This strategy may reduce belowground competition and promote the growth of surrounding plant roots. Smaller fragments, subject to intensified edge effects, are often dominated by shade-intolerant species and characterized by higher light availability (Liu et al. 2019), which may facilitate the growth of other plant roots (e.g., herbs and shade-tolerant woody plants) around these species. These findings underscore the potential for habitat loss and edge effects to differentially impact belowground biomass across species. The extent of belowground biomass accumulation in growth areas may vary depending on species-specific traits and their responses to environmental conditions and competition dynamics.

In this study, we investigated the effects of habitat loss and edge dynamics on belowground biomass through a field planting experiment conducted on 11 islands within a subtropical anthropogenic archipelago in China (Li et al. 2022, 2023). Previous research in this archipelago has shown that island area, rather than isolation, significantly influences plant species diversity and ecosystem function due to environmental filtering processes, such as soil bulk density and soil depth (Liu et al. 2020). Using data on belowground biomass from both planted species and other species, along with abiotic data (e.g., soil physicochemical properties and topographic attributes) collected from edge and interior sites on islands, we aimed to address the following questions: (1) What is the relationship between plant belowground biomass and island area? (2) Which factors significantly affect belowground biomass accumulation on islands, and do these factors enhance or inhibit belowground biomass accumulation as island area decreases? (3) Do species with different shade tolerances exhibit differential responses in belowground biomass accumulation within their growth areas to island area and edge effects?

Methods

Study site

The root growth monitoring experiment was conducted at Thousand Island Lake (TIL) in Zhejiang Province, eastern China. This artificial lake, covering an area of 581 km^2, was created as a result of flooding caused by the construction of a dam on the Xin'an River. The inundation led to the emergence of 1,078 islands, each exceeding 0.25 ha in size, from the peaks of former mountains (Liu et al. 2020). Prior to the flooding, forests on these hilltops were clear-cut; however, natural regeneration of the vegetation occurred following the lake's formation (Liu et al. 2018a, b). Since 1962, TIL has been designated as a national park, and most islands have remained largely undisturbed by human activity. The region experiences a subtropical monsoon climate, characterized by hot, humid summers and cool, dry winters. The mean annual temperature is 17.0 °C, with seasonal extremes ranging from −7.6 °C in January to 41.8 °C in July. Average annual precipitation totals 1,430 mm, occurring over 155 rainy days, with the majority of rainfall concentrated between April and June (Liu et al. 2018a, b).

Experimental design

Island areas were measured using ArcGIS 10.8 to quantify habitat size. To investigate the effects of island size and edge effect on seedling root growth and belowground biomass, we conducted an experiment on 11 islands varying in size from 1.06 to 1153.88 ha (Appendix S1). Experimental sites were established based on island size: two sites were placed on each small island (< 5 ha, six islands), and four sites were placed on each large island (> 20 ha, five islands), resulting in a total of 32 experimental sites across all islands. At each experimental site, we established a 20 m× 20 m plot. According to previous research in TIL, plots located within 40 m of the island edge were classified as an "edge plots", while those further inland were classified as an "interior plot" (Li et al. 2022). On small islands, no interior plots could be set because the interior habitats on the islands are less than 40 m away from the island edge, so two edge plots were established. On large islands, two replicated plots were established on the edge and interior of each island (Fig. 1). In total, we established 22 edge plots and 11 interior plots on 11 islands. Within each, three subplots were aligned diagonally, and four plant species were grown in flowerpots within each subplot. To replicate natural germination conditions, 2 cm holes were drilled into the sides of the flowerpots, enabling the roots of neighboring plants to grow inward and interact with one another when the pots were buried in the ground (Fig. 1).

Species selection

To test whether the species with different shade tolerances exhibit differential responses in belowground biomass accumulation within their growth areas to island area and edge effects, we selected two shade-intolerant species (*Cinnamomum camphora* and *Loropetalum chinense*) and two shade-tolerant species (*Cyclobalanopsis glauca* and *Schima superba*). According to their relative abundance on the islands in TIL, *L. chinense* is a dominant species, and *S. superba* is a common species, while C. *camphora* and *C. glauca* are rare species on island.

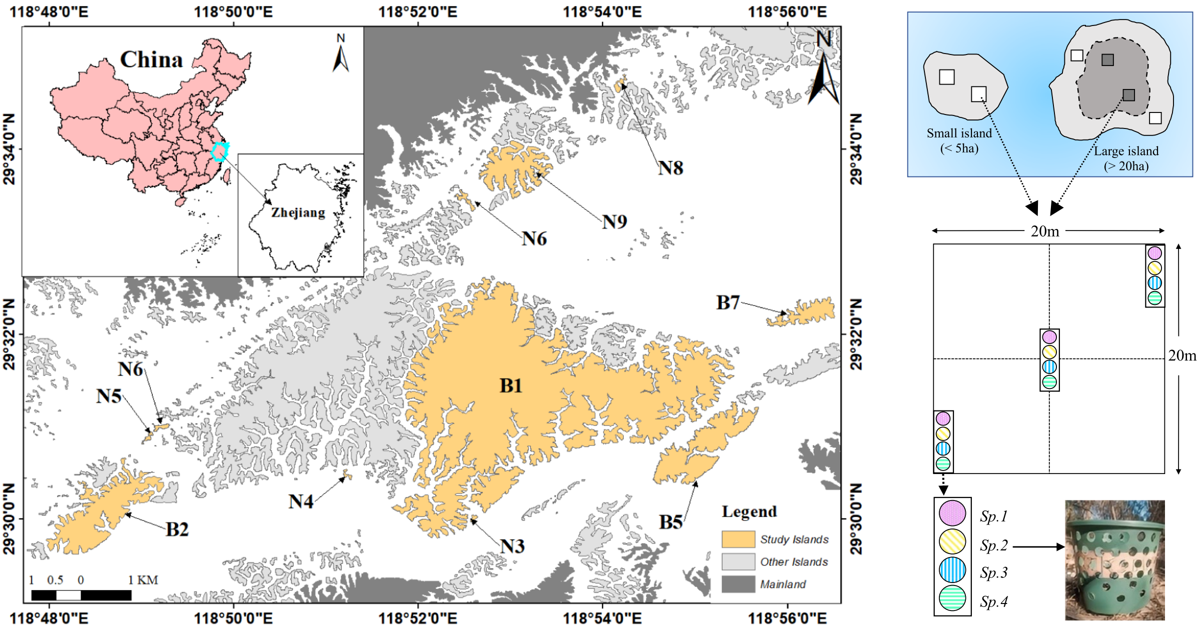

Fig. 1 Experimental design for the root growth monitoring experiment. This experiment was conducted on six small islands (< 5 ha) and five large islands (> 20 ha). Two edge plots (20 m× 20 m, located within 40 m of the island edge) were established on all islands, while an additional two interior plots (> 40 m from the island edge) were set up on large islands. Each plot contained three replicate subplots, each with four perforated flowerpots designed to allow roots from surrounding plants to grow into the pots. All flowerpots were open at the bottom, and each flowerpot was planted with a single species

Measurement of belowground biomass

Seeds for the experiment were collected in the autumn 2020 for the TIL region. In early March 2021, 20 seeds from each of the four selected species were sown into individual flowerpots. Before sowing, the leaf litter and existing rooted plants were removed, the soil surface was scarified, and the seeds were gently tamped into the soil to enhance seed-soil contact. Seed viability was confirmed prior to planting through exposure to a 5% TTC dye (2,3,5-triphenyltetrazolium chloride) solution, which indicated all seeds were viable. Flowerpots were installed from December 2020 to January 2021, several months before seed sowing. This installation period allowed roots from surrounding vegetation to grow into the perforated flowerpots, simulating natural root interaction conditions.

The experiment concluded in April 2022, after which the root biomass of both the planted seedlings and other plants that had grown into the flowerpots was measured. Each flowerpot was removed from the soil, and the soil attached to the plant roots was cleaned and removed. Initially, the roots of the planted species were carefully extracted from the flowerpots by visual assessment. Subsequently, the roots were categorized into two groups: those belonging to the planted species and miscellaneous roots from other species. All root samples were dried in an oven at 75 °C for at least 72 h until a constant weight was achieved. Once dried, the roots were weighed using an analytical balance to ensure precision in biomass measurement.

Measurement of environmental factors

To evaluate the influence of environmental factors on belowground biomass across the islands, five soil cores (0–10 cm deep) were collected evenly across each 20 ×20 m plot after removing the litter layer. These soil cores were combined and sieved through a 2-mm mesh to create a composite sample for the analysis of soil chemical properties. The chemical properties assessed include total carbon (TC, %), total nitrogen (TN, mg/kg), ammonium nitrogen (NH_4^+-N, mg/kg), nitrate nitrogen (NO_3^--N, mg/kg), total phosphorus (TP, mg/kg), available phosphorus (AP, mg/kg) and soil pH (Li et al. 2023). TC and TN was quantified using an Element Analyzer (CN model, Vario MACRO Cube, Elementar, Langenselbold, Germany). NH_4^+-N and NO_3^--N were extracted with 2 mol/L KCl solutions and determined using a Continuous Flow analyzer (San + +, Skalar, Breda, Holland). TP was extracted with H_2SO_4 and $HClO_4$ and analyzed using an ICP-OES (Optima 8300, Perkin Elmer, USA). AP was extracted with a 0.03 mol/L NH_4F-0.1 mol/L HCl solution and also measured by ICP-OES.

Additionally, the gravimetric soil water content (SWC, g/kg), and soil bulk density (SDEN, g/cm^3) were measured using the cutting ring method (Viji and Rajesh 2011). Soil depth (SDEP, cm) and litter layer depth (LLP, cm) were recorded at each subplot using a steel needle penetration method. Altitude (m) was calculated as a proxy for the distance of the sampling site from the island edge, with higher altitudes indicating greater distances from the edge. Canopy openness (%) for each site was quantified using hemispherical photographs taken at a height of 1.3 m above the soil surface. These photographs were captured with a Canon 6D MARK II digital camera equipped with a Sigma 4.5-mm fisheye lens mounted on a tripod. The images were processed using Hemiview v. 2.1 software. To ensure consistent lighting conditions, all photographs were taken early in the morning in July under uniformly overcast skies. Environmental variables were averaged across three subplots within each plot to estimate representative values for the entire plot.

Data analysis

The belowground biomass of the plant community in each plot (20 m× 20 m) was determined by summing the root mass (g) of both the planted species and other plants within the flowerpots in the plot, represented as the total root mass in pots per plot (M_{plot}, g). Additionally, the belowground biomass within the growth areas of each planted species was calculated in each plot, incorporating the root mass of both the planted species and other plants in the flowerpots. The total root mass in pots per plot (M_{plot}) was calculated as follows:

$$M_{plot} = \sum_{i=1}^{n} M_i \tag{1}$$

In Eq. (1), M_i represents the root mass in flowerpot i within the plot, and n denotes the total number of flowerpots in the plot, either for all planted species combined or for each individual species.

To determine the mean belowground biomass of the plant community on the island, the total root mass in pots per plot (M_{plot}) was averaged across all plots on the island, resulting in the mean root mass (M_{island}, g). Similarly, the mean belowground biomass within the growth areas of each planted species on the island was calculated by averaging the M_{plot} from the corresponding plots for each species across the island.

To investigate the relationship between belowground biomass of the plant community and island area, we first applied a log transformation to the island area and fitted a simple generalized linear model using a Gaussian distribution on the mean root mass. To assess potential shifts in mean root mass across the island area threshold, we also implemented a segmented regression model from the "segmented" package (Muggeo 2017) to detect any breakpoints along the log-transformed island area gradient. The parsimony of the segmented regression model was compared to a simple linear model using the Akaike information criterion (AICc) from the "MuMIn" package (Bartoń, 2024). In the segmented regression model, we calculated the slope (representing the fitted model's slope before the breakpoint), and the U1 parameter, which represents the difference in slope before and after the breakpoint, along with its associated *P*-value. We conducted the Davies' test using "*davies.test()*" function to test for a significant difference in slope. If the *P*-value from the Davies' test was greater than 0.05, it indicated that there was no evidence to support the use of a segmented model for these data. In these models, the mean root mass on the island, for both all species and individual species, were treated as response variable, with island area serving as the explanatory variable.

To examine species-specific belowground biomass responses to environmental factors, we employed a linear mixed-effects (LME) model. The total root mass in pots per plot on island was treated as the response variable, so island was included as a random effect to account for potential within-island dependencies between plots, while environmental factors—including canopy openness, altitude, slope, aspect, SDEP, LLP, SBD, SDEN, SWC, TP, AP, NH_4^+-N, NO_3^--N, soil pH, and the total carbon-to-nitrogen ratio (TC/TN)—were treated as fixed effects. Multicollinearity among explanatory variables was assessed using variance inflation factors (VIF), ensuring that all VIF values remained below 5, indicating no significant multicollinearity. Model selection was performed using the AICc to select the best-fitting model, and only the variables retained in the final best model are presented. We tested the relationship between the retained variables in the best-fitting models and island area using the segmented regression model.

To evaluate the impact of edge effects on belowground biomass, we utilized a linear mixed-effects (LME) model to compare the total root mass in pots per plot between edge and interior plots. The analysis was conducted for all plots across all islands, as well as only including plots on large islands. Plot location (edge vs. interior) was included as a fixed effect, while island was treated as a random effect to account for the lack of independence among plots within the same island (Li et al. 2023). We also tested relationships between island area and the mean root mass of edge plots and interior plots for all species and each species through model selection of the simple linear model and segmented regression model.

All statistical analyses were performed in R version 4.3.3 (R Core Team 2024).

Results

The mean belowground biomass (i.e., mean root mass) of all species exhibited significant threshold effects: the mean root mass decreased significantly with increasing island area before the threshold, and then stabilized afterward (Fig. 2a: breakpoint estimate $=0.86$ ha, CI $=0.35$–1.37 ha, slope difference $P= 0.006$). (Fig. 2a; Table S1 and S2 in Appendix S2). However, the mean root mass of planted species did not exhibit a significant correlation with island area (Fig. S1 in Appendix S2). Notably, the total root mass in pots per plot of all species was significantly correlated with the total root mass in pots per plot of other plants but not with that of the planted species (Fig. S2).

When examining the effects of environmental factors on belowground biomass, we found that altitude, litter layer depth, soil bulk density, and soil depth had significant effect on the total root mass in pots per plot for all species (Table 1). Species-specific analyses revealed that the total root mass in pots per plot

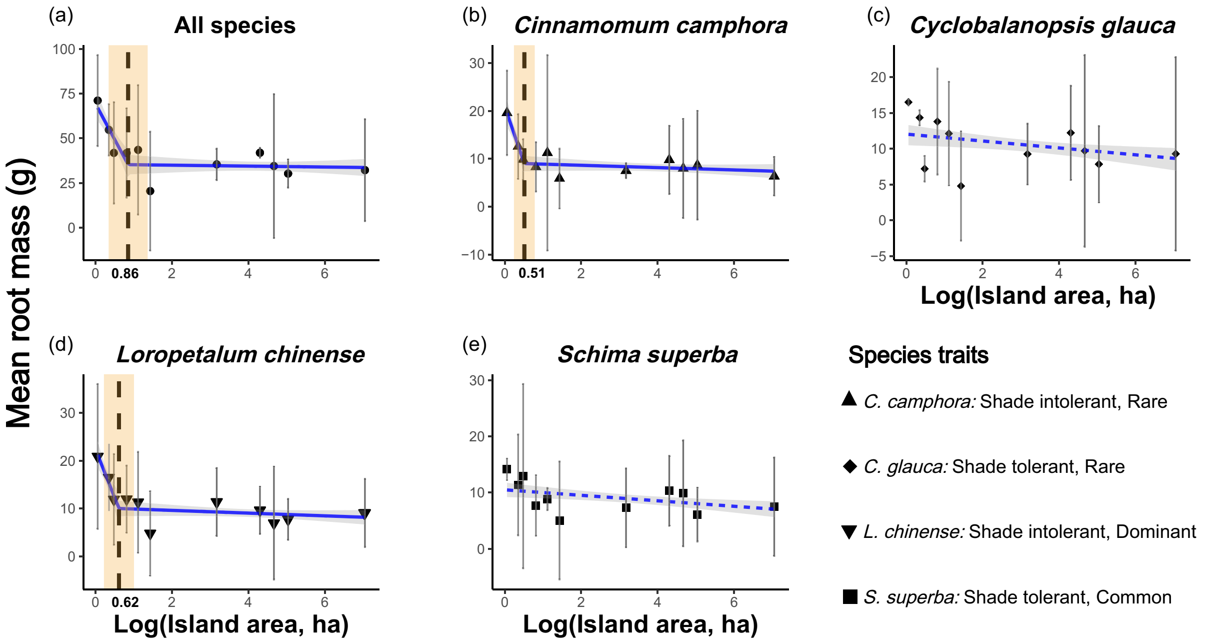

Fig. 2 Relationships between island area and (**a**) mean root mass for all species, and the mean root mass in the growth areas of each planted species for (**b**) *Cinnamomum camphora*, (**c**) *Cyclobalanopsis glauca*, (**d**) *Loropetalum chinense*, and (**e**) *Schima superba*. Error bars represent the standard deviation of the mean total root mass in pots per plot across all plots on the island. The blue line indicates the best-fit model (either a simple linear regression model or a segmented regression model), selected based on the lowest AICc value. The light grey shaded area represents the 95% confidence interval (CI) predicted from the best-fit model. Dashed lines indicate non-significant relationships, while solid lines represent significant relationships ($P \leq$ 0.05). The estimated significant breakpoint ($P \leq$ 0.05) in each relationship is represented by the dotted vertical black line, and the light purple shaded area represents the 95% CI around the breakpoint. The light grey shaded area illustrates the 95% CI predicted from the segmented regression

in the growth areas of *C. camphora*, *C. glauca*, and *L. chinense*, was significantly influenced by altitude, whereas no such effect was observed for *S. superba*. However, the total root mass in pots per plot in the growth areas of *S. superba* was significantly affected by soil bulk density (t= −4.539, P< 0.001). Additionally, litter layer depth, soil depth, and total phosphorus were found to influence the total root mass in pots per plot of *C. glauca* (Table 1). When the island area is less than a certain threshold, the smaller islands have higher litter depth, and lower soil bulk density (Fig. S3).

Further analysis revealed that the mean root mass in the growth areas of the shade-intolerant species *C. camphora* (breakpoint =0.51 ha, CI =0.24–0.78 ha, slope difference P= 0.023) and *L. chinense* (breakpoint =0.62 ha, CI =0.22–1.01 ha, slope difference P= 0.005) decreased significantly with increasing island area before the threshold (Fig. 2; Table S1 and S2). In contrast, the mean root mass in the growth areas of the shade-tolerant species *C. glauca* and *S. superba* was not significantly correlated with island area (Fig. 2; Table S2).

The total root mass in pots per plot in edge habitats was significantly higher than that in interior habitats on the island (Fig. 3). Examining the effects of different species on belowground biomass accumulation in edge and interior regions revealed distinct patterns. Across all islands, the total root mass in pots per plot in the growth areas of all species (t= −2.189, P= 0.031), *C. camphora* (t= −2.176, P= 0.029), *C. glauca* (t= −1.996, P= 0.046), and *L. chinense* (t= −1.965, P= 0.049) was significantly higher in edge habitats compared to interior habitats (Fig. 3a). However, no significant difference in total root mass in pots per plot was observed for *S. superba* (t= −0.799, P= 0.424) between edge and interior regions (Fig. 3a). When considering only large islands, the total root mass in pots per plot in the growth areas of all species (t= −2.219, P= 0.026), *C. glauca* (t=

Table 1 Results of the influence of abiotic factors on the total root mass in pots per plot for all species and for species *Cinnamomum camphora*, *Cyclobalanopsis glauca*, *Loropetalum chinense*, and *Schima superba* using generalized linear mixed-effect models

	Estimate	Std. Error	*t* Value	*p*Value
All species				
Altitude	−0.317	0.106	−2.968	0.005
Litter layer depth	0.456	0.151	3.018	0.005
Soil bulk density	−0.652	0.113	−5.766	< 0.001
Soil depth	−0.607	0.163	−3.712	< 0.001
Cinnamomum camphora				
Altitude	−0.326	0.151	−2.150	0.039
Soil bulk density	−0.445	0.152	−2.914	0.006
Cyclobalanopsis glauca				
Altitude	−0.375	0.132	−2.833	0.008
Aspect	−0.504	0.121	−4.141	< 0.001
Litter layer depth	0.495	0.175	2.817	0.008
Soil depth	−0.495	0.177	−2.783	0.009
Total phosphorus	0.409	0.133	3.067	0.004
Loropetalum chinense				
Altitude	−0.220	0.107	−2.051	0.049
Litter layer depth	0.590	0.151	3.886	< 0.001
Soil bulk density	−0.669	0.113	−5.920	< 0.001
Soil depth	−0.567	0.163	−3.455	0.001
Schima superba				
Soil bulk density	−0.656	0.144	−4.539	< 0.001
Gravimetric soil water content	−0.268	0.144	−1.856	0.073

The abiotic features included: canopy openness, altitude, slope, aspect, soil depth, litter layer depth, soil bulk density, gravimetric soil water content, total phosphorus, available phosphorus, ammonium nitrogen, nitrate nitrogen, soil pH, and total C/total N. Model selection was performed using the AICc to select the best-fitting model, and only the variables retained in the final model are presented

−1.816, $P = 0.069$), and *L. chinense* ($t = -2.267$, $P = 0.023$) remained significantly higher in edge habitats compared to interior habitats. In contrast, the total root mass in pots per plot in the growth areas of *C. camphora* ($t = -1.060$, $P = 0.289$) and *S. superba* ($t = -0.840$, $P = 0.401$) showed no significant differences between edge and interior habitats (Fig. 3b). Additionally, the mean root mass of edge plot including all species (breakpoint = 0.58 ha, CI = 0.23–0.94 ha, $P = 0.007$), and in the growth areas of *L. chinense* (breakpoint = 0.60 ha, CI = 0.19–1.01 ha, $P = 0.019$), and *C. camphora* (breakpoint = 0.51 ha, CI = 0.21–0.80 ha, $P = 0.057$) decreased significantly with increasing island area below the threshold area in edge habitats (Fig. 4, Table S3 and S4). However, no significant correlation was observed between the mean root mass of interior plot and island area (Fig. 4; Table S3 and S4).

Discussion

Given the uncertain effects of habitat fragmentation on plant belowground biomass (Klimešová et al. 2018; Mokany et al. 2006), this study provides evidence that island area and edge effects significantly influence belowground root biomass. Specifically, belowground root biomass tends to increase as island area decreases below a threshold island area and as proximity to the island edge increases. Additionally, the studied species with differing shade-tolerance exhibited variable responses in belowground biomass to reductions in island area and the influence of edge effects.

Here, we observed smaller islands exhibited higher belowground biomass compared to large islands, especially below a threshold island area (Fig. 2a). Notably, the mean root mass of planted species did not exhibit a significant correlation with island area (Fig. S1), and the mean root mass was significantly correlated with the mean root mass of other plants but not with that of the planted species (Fig. S2). This finding suggests that the mean belowground biomass in the growth areas of each species primarily reflects the root growth of other plants rather than the planted species. Previous studies have shown that aboveground biomass decreases with the decrease of island area (Broadbent et al. 2008), the finding, combined with our results, highlights the ability of plants to respond to habitat area loss by adjusting biomass allocation trade-offs between aboveground and belowground structures. Consequently, the increased belowground biomass below a threshold area may represent an adaptive strategy by other plants not planted species to optimize resource acquisition under environmental conditions.

Abiotic factors, including altitude, soil bulk density, litter layer depth and soil depth, significantly influence plant belowground biomass (Table 1). Additionally, our findings demonstrate that soil physical properties, such as litter layer depth, soil

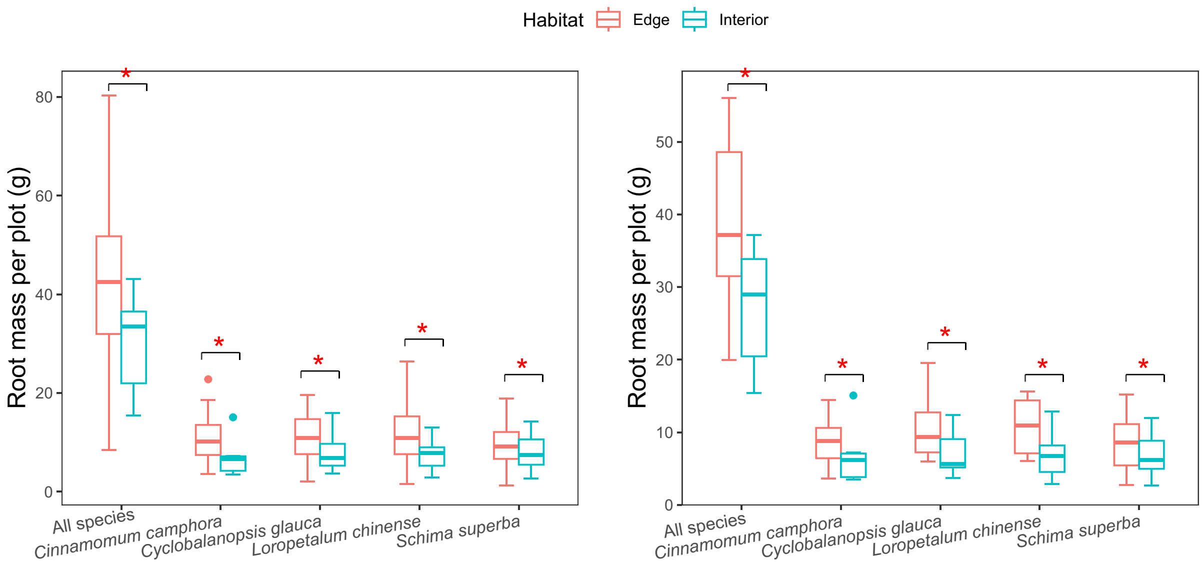

Fig. 3 The differences in the total root mass in pots per plot (g) and the total root mass in pots per plot within the growth areas of each planted species between edge (red color) and interior plot (blue color) when (**a**) including all plots or (**b**) only including plots on large islands."*"indicates a significant difference with $P \leq 0.05$ according to the results of linear mixed effect models, and"NS"denotes no significant difference

depth, and soil bulk density, significantly impact belowground biomass accumulation (Table 1). Both litter layer depth and soil depth positively impact root development. Litter layer depth often serves as an indicator of organic content in the topsoil, providing essential for root nourishment (Prescott 2002). Soil depth functions as a long-term reservoir of water and nutrients, supporting sustained root growth and enabling plants to accumulate more belowground biomass in deeper soils. Soil bulk density, as an indicator of soil compactness, also plays a crucial role in root growth. Higher soil bulk density reduces pore space between soil particles, restricting root expansion, particularly under conditions of limited water and oxygen flow (Jackson et al. 1996). Consequently, soil bulk density has a significant negative effect on belowground biomass. We further found that when the island area falls below a certain threshold, smaller islands exhibit greater litter depth and lower soil bulk density (Fig. S3), suggesting that higher belowground biomass accumulation on smaller islands below this threshold area is linked to increased litter layer depth and reduced soil bulk density. This result also implies that root mass accumulation growth is not promoted on island with limited resources.

In addition to the soil physicochemical properties, environmental conditions, such as light availability also influence the species interactions, with foundational traits playing a critical role in determining how species affect the root growth of others (Comas et al. 2013; Kitajima 1994; Lak et al. 2020). In this study, we found that the accumulation of belowground biomass in the growth areas of shade-intolerant species *C. camphora* and *L. chinense* decreased significantly with increasing island area below a threshold area. Moreover, belowground biomass accumulation in the growth areas was significantly correlated with the root biomass of other plants but not with the root biomass of the planted species. These findings suggest that the roots of other plants surrounding shade-intolerant species *L. chinense* and *C. camphora* grow more vigorously on smaller islands below a certain threshold. Smaller islands in this system are characterized by a greater prevalence of shade-intolerant, early-successional woody species compared to larger fragments, even after 50 years of secondary succession (Liu et al. 2019). The abundance of sunlight on smaller islands provides shade-intolerant species, such as *L. chinense*, with a competitive advantage (Poorter Hendrik and Nagel 2000). These species rely on sunlight for rapid growth and typically allocate more biomass to aboveground structures to enhance

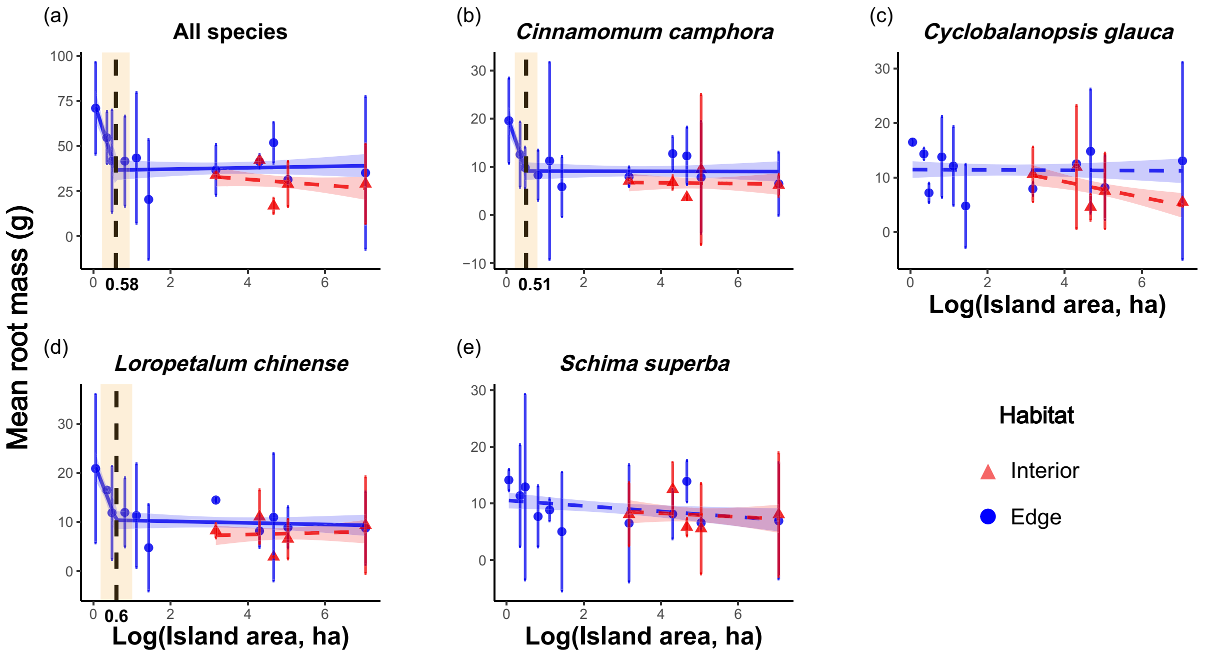

Fig. 4 Relationships between island area and (**a**) mean root mass of all species, and the mean root mass within the growth areas of each planted species for (**b**) *Cinnamomum camphora*, (**c**) *Cyclobalanopsis glauca*, (**d**) *Loropetalum chinense*, and (**e**) *Schima superba* in edge plots (red triangle) and interior plots (blue dot). Error bars represent the standard deviation of mean root mass for edge plots or interior plots on the island. The blue line represents the best-fit model (either a simple linear regression model or a segmented regression model), selected based on the lowest AICc value. The light grey shaded area represents the 95% confidence interval (CI) predicted from the best-fit model. Dashed lines indicate non-significant relationships, while solid lines indicate significant relationships ($P \leq 0.05$). The estimated significant breakpoint ($P \leq 0.05$) in each relationship is represented by the dotted vertical black line, and the light purple shaded area represents the 95% CI around the breakpoint. The light grey shaded area shows the 95% CI predicted from the segmented regression

light capture in resource-rich light environments. When light availability is abundant, shade-intolerant species prioritize resource allocation to aboveground biomass to maximize photosynthetic capacity (Brouwer 1983). As such, increased light promote the vigorous growth of shade-intolerant species, such as *L. chinense*, leading to a greater allocation of biomass aboveground, resulting in relatively weaker root competition compared to shade-tolerant species, thereby allowing roots from other species to penetrate into the pots (Laurance et al. 1998; Ries et al. 2004). Therefore, shade-intolerant species, *L. chinense* and *C. camphora*, exhibit weaker belowground competition with other plants on smaller islands, enabling the roots of neighboring plants to expand. Specifically, shade-intolerant species, which dominate smaller islands (Liu et al. 2019), promote the accumulation of belowground biomass of surrounding plants, thereby contributing to the higher belowground biomass observed on smaller islands.

As island size decreases, plant growth becomes increasingly influenced by edge effects (Liu et al. 2023; Kerr et al. 2021; Murcia 1995). Edge effects could significantly enhance shade-intolerant species growth rates and increase the number of new recruits in edge habitats, although these new recruits are often smaller species with lower aboveground biomass (Broadbent et al. 2008). Here, the mean belowground biomass of plants in edge habitats was significantly higher than that in interior habitats on islands (Fig. 3). In addition, higher altitude on islands often indicates a greater distance from the site to the island edge, which can reflect variations in temperature, humidity, and light exposure. Our results also reveal that the belowground biomass are negatively significantly affected by altitude (Table 1). These results highlight the critical role of edge effects in increasing belowground biomass, suggesting that edge effects contribute to the elevated belowground biomass observed on small islands. Notably, the belowground root mass of non-planted species in this study includes both woody and herbaceous plants, but the experiment did not distinguish between these two groups in flowerpots. Herbaceous plants are known to exhibit pronounced habitat preferences in fragmented landscapes (Tian et al. 2023). According to Siebert et al. (2002), herbaceous plants thrive in well-lit environments, such as edge habitats, where they exhibit greater adaptability compared to low-light areas. This adaptability likely contributes to higher belowground root biomass at edges relative to interior habitats. Based on this, we hypothesize that herbaceous root biomass at edges significantly exceeds that in interior habitats, thereby contributing to the overall increase in belowground biomass in edge environments. Additionally, our results showed that the accumulation of belowground biomass in the growth areas of *L. chinense* decreased with increasing island area below a threshold area in the edge habitats, while no such trend was observed in interior habitats (Fig. 4). *L. chinense* is one of the most dominant species on the island, with the highest relative abundance (Liu et al. 2020). As we have discussed earlier, shade-intolerant species tend to exhibit weaker belowground competition with other plants on smaller islands, allowing other plant roots to grow. Therefore, as a dominant and the shade-intolerant species, *L. chinense* may positively contribute to the belowground biomass accumulation in its growth area on island edges.

Conclusion

In summary, our results demonstrate that belowground biomass increases as island area decreases below a certain threshold. Further analysis revealed that litter layer depth, soil bulk density, and soil depth significantly affect the belowground biomass accumulation. Higher belowground biomass accumulation on smaller islands below this threshold was associated with increased litter layer depth and reduced soil bulk density. The response of belowground biomass in the growth areas of species with varying shade tolerance differs with habitat loss and edge effects. Specifically, root growth in the growth areas of dominant shade-intolerant species contributes to increased belowground biomass accumulation at the island edges on smaller islands. This study advances the understanding of belowground biomass accumulation and its driving factors in fragmented habitats. Our findings underscore the importance of habitat size, edge effects, and species'shade tolerance as key factors shaping belowground biomass accumulation in fragmented landscapes. These findings highlight the necessity of incorporating belowground biomass dynamics into assessments of ecosystem functions in fragmented habitats.

Acknowledgements We thank Xue Li, Wenjie Deng, Tengteng Liu, and Weiyong Liu and many students at the Wenzhou University and Zhejiang University, and many local farmers for their contribution to the fieldwork. We thank Xin'an River Ecological Development Group Corporation and the Forestry Bureau of Chun'an County for the permits necessary to conduct our research in Thousand Island Lake. This research was funded by the National Natural Science Foundation of China (32271606, 31901104), and "Pioneer" and "Leading Goose"R&D Program of Zhejiang (2023C03137).

Author contributions All authors contributed to the study conception and design. Conceptualization of the project was led by Jinliang Liu and Mingjian Yu. Data collection and analysis were performed by Yunfan Hu, Tianxiang Li, Xuying Ye, Yuping Zhong, Bin Wang, Dan Long, Mengyuan Chen, Mengsi Zhou and Mingjian Yu. Data analysis was performed by Yunfan Hu and Jinliang Liu. The first draft of the manuscript was written by Jinliang Liu and Yunfan Hu. All authors commented on previous versions of the manuscript and gave final approval for publication.

Funding This research was funded by the National Natural Science Foundation of China (32271606, 31901104), and "Pioneer" and "Leading Goose"R&D Program of Zhejiang (2023C03137).

Data availability The data presented in this study are available in the supplementary material.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

References

Ali A, Yan ER (2017) The forest strata-dependent relationship between biodiversity and aboveground biomass within a subtropical forest. For Ecol Manage 401:125–134. https://doi.org/10.1016/j.foreco.2017.06.056

Armas C, Pugnaire FI (2011) Plant neighbour identity matters to belowground interactions under controlled conditions. PLoS ONE 6(11):7. https://doi.org/10.1371/journal.pone.0027791

Bartoń K (2024) MuMIn: multi-model inference. R package version 1.48.4. https://doi.org/10.32614/CRAN.package.MuMIn

Bregman TP, Lees AC, Seddon N et al (2015) Species interactions regulate the collapse of biodiversity and ecosystem function in tropical forest fragments. Ecology 96(10):2692–2704. https://doi.org/10.1890/14-1731.1.sm

Broadbent EN, Asner GP, Keller M et al (2008) Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. Biol Conserv 141(7):1745–1757. https://doi.org/10.1016/j.biocon.2008.04.024

Brouwer R (1983) Functional equilibrium: sense or nonsense? Netherlands J Agricultural Science 31(4):335–348. https://doi.org/10.18174/njas.v31i4.16938

Cairns MA, Brown S, Helmer EH, Baumgardner GA (1997) Root biomass allocation in the world's upland forests. Oecologia (Berlin) 111(1):1–11. https://doi.org/10.1007/s004420050201

Cleland EE, Lind EM, DeCrappeo NM et al (2019) Belowground biomass response to nutrient enrichment depends on light limitation across globally distributed grasslands. Ecosystems 22:1466–1477. https://doi.org/10.1007/s10021-019-00350-4

Comas LH, Becker SR, Cruz VMV, Byrne PF, Dierig DA (2013) Root traits contributing to plant productivity under drought. Front Plant Sci 4:442. https://doi.org/10.3389/fpls.2013.00442

Erkin F, Yue D, Abdureyim A, Huang WY, Tayir M (2023) Link between the aboveground and belowground biomass allocation with growing of Tamarix sp. seedlings in the hinterland of Taklimakan Desert, China. Plos One 18(8):16. https://doi.org/10.1371/journal.pone.0289670

Ewers RM, Didham RK (2006) Confounding factors in the detection of species responses to habitat fragmentation. Biol Rev 81(1):117–142. https://doi.org/10.1017/S1464793105006949

Ewers RM, Andrade A, Laurance SG et al (2017) Predicted trajectories of tree community change in Amazonian rainforest fragments. Ecography 40(1):26–35. https://doi.org/10.1111/ecog.02585

Fonseca de Lima CF, Kleine-Vehn J, De Smet I, Feraru E (2021) Getting to the root of belowground high temperature responses in plants. J Exp Bot 72(21):7404–7413. https://doi.org/10.1093/jxb/erab202

Haddad NM, Brudvig LA, Clobert J et al (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci Adv 1(2):9. https://doi.org/10.1126/sciadv.1500052

Harper KA, Macdonald SE, Burton PJ et al (2005) Edge influence on forest structure and composition in fragmented landscapes. Conserv Biol 19(3):768–782. https://doi.org/10.1111/j.1523-1739.2005.00045.x

Hossain ML, Beierkuhnlein C (2018) Enhanced aboveground biomass by increased precipitation in a central European grassland. Ecol Process 7:13. https://doi.org/10.1186/s13717-018-0149-1

Jackson RB, Canadell J, Ehleringer JR et al (1996) A global analysis of root distributions for terrestrial biomes. Oecologia (Berlin) 108(3):389–411. https://doi.org/10.1007/bf00333714

Kerr KL, Zenes N, Trugman AT, Anderegg WRL (2021) Testing the effects of species interactions and water limitation on tree seedling biomass allocation and physiology. Tree Physiol 41(8):1323–1335. https://doi.org/10.1093/treephys/tpab005

Kiaer LP, Weisbach AN, Weiner J (2013) Root and shoot competition: a meta-analysis. J Ecol 101(5):1298–1312. https://doi.org/10.1111/1365-2745.12129

Kitajima K (1994) Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. Oecologia (Berlin) 98(3–4):419–428. https://doi.org/10.1007/bf00324232

Klimešová J, Martínková J, Ottaviani G (2018) Belowground plant functional ecology: Towards an integrated perspective. Funct Ecol 32(9):2115–2126. https://doi.org/10.1111/1365-2435.13145

Lak ZA, Sandén H, Mayer M, Godbold DL, Rewald B (2020) Plasticity of root traits under competition for a nutrient-rich patch depends on tree species and possesses a large congruency between intra- and interspecific situations. Forests 11(5):19. https://doi.org/10.3390/f11050528

Laurance WF, Ferreira LV, Rankin-De-Merona JM, Laurance SG (1998) Rain forest fragmentation and the dynamics of amazonian tree communities. Ecology 79(6):2032–2040. https://doi.org/10.2307/176707

Laurance WF, Lovejoy TE, Vasconcelos HL et al (2002) Ecosystem decay of amazonian forest fragments: A 22-year investigation. Conserv Biol 16(3):605–618. https://doi.org/10.1046/j.1523-1739.2002.01025.x

Li T, Li X, Wu C et al (2022) Herbivory rather than root competition and environmental factors determines plant establishment in fragmented forests. Forests 13(5):767. https://doi.org/10.3390/f13050767

Li X, Li T, Zhong L et al (2023) Species diversity of arbuscular mycorrhizal but not ectomycorrhizal plants decreases with habitat loss due to environmental filtering. Plant Soil 489(1–2):211–224. https://doi.org/10.1007/s11104-023-06007-5

Liu J, Coomes DA, Hu G et al (2019) Larger fragments have more late-successional species of woody plants than smaller fragments after 50 years of secondary succession. J Ecol 107(2):582–594. https://doi.org/10.1111/1365-2745.13071

Liu JJ, Wilson M, Hu G et al (2018) How does habitat fragmentation affect the biodiversity and ecosystem functioning relationship? Landsc Ecol 33(3):341–352. https://doi.org/10.1007/s10980-018-0620-5

Liu JL, Vellend M, Wang ZH, Yu MJ (2018) High beta diversity among small islands is due to environmental heterogeneity rather than ecological drift. J Biogeogr 45(10):2252–2261. https://doi.org/10.1111/jbi.13404

Liu JL, Matthews TJ, Zhong L et al (2020) Environmental filtering underpins the island species-area relationship in a subtropical anthropogenic archipelago. J Ecol 108(2):424–432. https://doi.org/10.1111/1365-2745.13272

Liu JL, Liu TT, Zhou YY et al (2023) Plant diversity on islands in the Anthropocene: integrating the effects of the theory of island biogeography and human activities. Basic Appl

Ecol 72:45–53. https://doi.org/10.1016/j.baae.2023.07.006

Ma HZ, Mo LD, Crowther TW et al (2021) The global distribution and environmental drivers of aboveground versus belowground plant biomass. Nat Ecol Evol 5(8):1110–1122. https://doi.org/10.1038/s41559-021-01485-1

Ma J, Li JW, Wu WB, Liu JJ (2023) Global forest fragmentation change from 2000 to 2020. Nat Commun 14(1):10. https://doi.org/10.1038/s41467-023-39221-x

Mokany K, Raison RJ, Prokushkin AS (2006) Critical analysis of root: shoot ratios in terrestrial biomes. Glob Change Biol 12(1):84–96. https://doi.org/10.1111/j.1365-2486.2005.001043.x

Muggeo VMR (2017) Interval estimation for the breakpoint in segmented regression: a smoothed score-based approach. Aust N Z J Stat 59:311–322. https://doi.org/10.1111/anzs.12200

Murcia C (1995) Edge effects in fragmented forests: implications for conservation. Trends Ecol Evol 10(2):58–62. https://doi.org/10.1016/S0169-5347(00)88977-6

Nascimento HEM, Laurance WF (2002) Total aboveground biomass in central Amazonian rainforests: a landscape-scale study. For Ecol Manage 168(1–3):311–321. https://doi.org/10.1016/s0378-1127(01)00749-6

Nunes MH, Vaz MC, Camargo JLC et al (2023) Edge effects on tree architecture exacerbate biomass loss of fragmented Amazonian forests. Nat Commun 14(1):13. https://doi.org/10.1038/s41467-023-44004-5

Poorter H, Nagel O (2000) The role of biomass allocation in the growth response of plants to different levels of light, CO2, nutrients and water: a quantitative review. Aust J Plant Physiol 27(6):595–607. https://doi.org/10.1071/PP99173_CO

Poorter H, Niklas KJ, Reich PB et al (2012) Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. New Phytol 193(1):30–50. https://doi.org/10.1111/j.1469-8137.2011.03952.x

Prescott CE (2002) The influence of the forest canopy on nutrient cycling. Tree Physiol 22(15–16):1193–1200. https://doi.org/10.1093/treephys/22.15-16.1193

R Core Team (2024) R: a language and environment for statistical computing. Retrieved from http://www.R-project.org/. Accessed 29 Feb 2024

Ries L, Fletcher RJ, Battin J, Sisk TD (2004) Ecological responses to habitat edges: mechanisms, models, and variability explained. Annu Rev Ecol Evol Syst 35:491–522. https://doi.org/10.1146/annurev.ecolsys.35.112202.130148

Sell M, Rohula-Okunev G, Kupper P, Ostonen I (2024) Adapting to climate change: responses of fine root traits and C exudation in five tree species with different light-use strategy. Front Plant Sci 15:1389569. https://doi.org/10.3389/fpls.2024.1389569

Shen CY, Shi NN, Fu SL et al (2021) Decline in aboveground biomass due to fragmentation in subtropical forests of China. Forests 12(5):12. https://doi.org/10.3390/f12050617

Siebert SF (2002) From shade-to sun-grown perennial crops in Sulawesi, Indonesia: implications for biodiversity conservation and soil fertility. Biodivers Conserv 11:1889–1902. https://doi.org/10.1023/A:1020804611740

Sorenson QM, Damschen EI (2019) The mechanisms affecting seedling establishment in restored savanna understories are seasonally dependent. J Appl Ecol 56(5):1140–1151. https://doi.org/10.1111/1365-2664.13354

Taubert F, Fischer R, Groeneveld J et al (2018) Global patterns of tropical forest fragmentation. Nature 554(7693):519–522. https://doi.org/10.1038/nature25508

Tian K, Chai PT, Wang YQ et al (2023) Species diversity pattern and its drivers of the understory herbaceous plants in a Chinese subtropical forest. Front Ecol Evol 10:12. https://doi.org/10.3389/fevo.2022.1113742

Viji R, Rajesh PP (2011) Assessment of water holding capacity of major soil series of Lalgudi, Trichy, India. Journal of Environmental Research and Development 7:393–398

Yan YZ, Jarvie S, Zhang Q (2024) Habitat loss weakens the positive relationship between grassland plant richness and above-ground biomass. eLife 12:15. https://doi.org/10.7554/eLife.91193

Zhang J, Wang YZ, Gao HK et al (2020) Different strategies in biomass allocation across elevation in two *Gentiana* plants on the Yunnan-Guizhou Plateau. China J Mt Sci 17(11):2750–2757. https://doi.org/10.1007/s11629-020-6253-6

Ziter C, Bennett EM, Gonzalez A (2013) Functional diversity and management mediate aboveground carbon stocks in small forest fragments. Ecosphere 4(7):21. https://doi.org/10.1890/es13-00135.1