



# Stronger effects of biodiversity loss and compositional change on forest biomass dynamics at larger spatial scales

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## Abstract

Global environmental changes drive biodiversity loss and community compositional change. Yet whether and how both factors simultaneously impact biomass dynamics in natural ecosystems remains elusive, especially considering their multidimensional effects (e.g., taxonomic, functional, and phylogenetic) over spatial scales. To fill this knowledge gap, we generated an experimental spatial gradient using circular quadrats that vary in radius (2–30 m) in a subtropical forest on Dinghushan Mountain, China. Within each quadrat over 10 years, we calculated the changes in aboveground biomass (i.e., net  $\Delta$ biomass), biodiversity (i.e.,  $\Delta$ biodiversity for richness, Shannon diversity, functional, phylogenetic), and community composition (i.e.,  $\beta$ -diversity for taxonomic, functional, phylogenetic). Based on multi-model inference, we determined the most parsimonious relationships of  $\Delta$ biomass as a function of  $\Delta$ biodiversity and  $\beta$ -diversity and then quantified their standardized coefficients in response to the spatial gradient. Our results showed that  $\Delta$ biomass,  $\Delta$ biodiversity, and  $\beta$ -diversity decreased with quadrat size; the former at an accelerating rate and the latter at decelerating rates. While  $\Delta$ biomass as a function of  $\Delta$ biodiversity and  $\beta$ -diversity had low occurrences across the gradient,  $\Delta$ biomass was strongly related to the change in functional dispersion (i.e.,  $\Delta$ FDIs) and taxonomic  $\beta$ -diversity at larger spatial scales. Our results suggest scale-dependent influences of biodiversity loss and community compositional change on biomass dynamics in natural ecosystems. Further, our results highlight that multiple dimensions of biodiversity should be considered when predicting biomass dynamics at large spatial scales.

**Keywords** Alpha diversity · Beta diversity · Biodiversity-ecosystem functioning · Dinghushan Mountain · Functional diversity · Phylogenetic diversity

## Introduction

Global environmental changes can lead to local plant diversity losses and substantial shifts in the species composition of plant communities (Sala et al. 2000). How such changes

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influence biomass production, a central ecosystem function, remains elusive, especially in natural ecosystems (Mori et al. 2018; van der Plas 2019). Not only are these multi-dimensional relationships spatially variable and temporally dynamic (Reich et al. 2012), but also their underlying drivers can be complicated and context-specific (Hou et al. 2022). Beyond the effects of abiotic and biotic factors (e.g., climate, soil, fungi; Liu et al. 2021, 2022), the spatial scale has been demonstrated as an important mediator that could alter the effects of biodiversity loss and compositional change on forest biomass dynamics (Craven et al. 2020; Gonzalez et al. 2020). Most empirical studies have focused on either one or a comparative spatial scale, such as local vs regional or neighborhood vs community (Bond and Chase 2002; Costanza et al. 2007; Ni et al. 2007; Luo et al. 2019a). Scaling up biodiversity–productivity relationships over various spatial scales has attracted recent attention (Chisholm et al. 2013; Luo et al. 2019b; Barry et al. 2021). Using a wider range of spatial scales, predictions for the landscape-scale consequences of biodiversity loss and community compositional change may improve (Thompson et al. 2018; Qiu and Cardinale 2020).

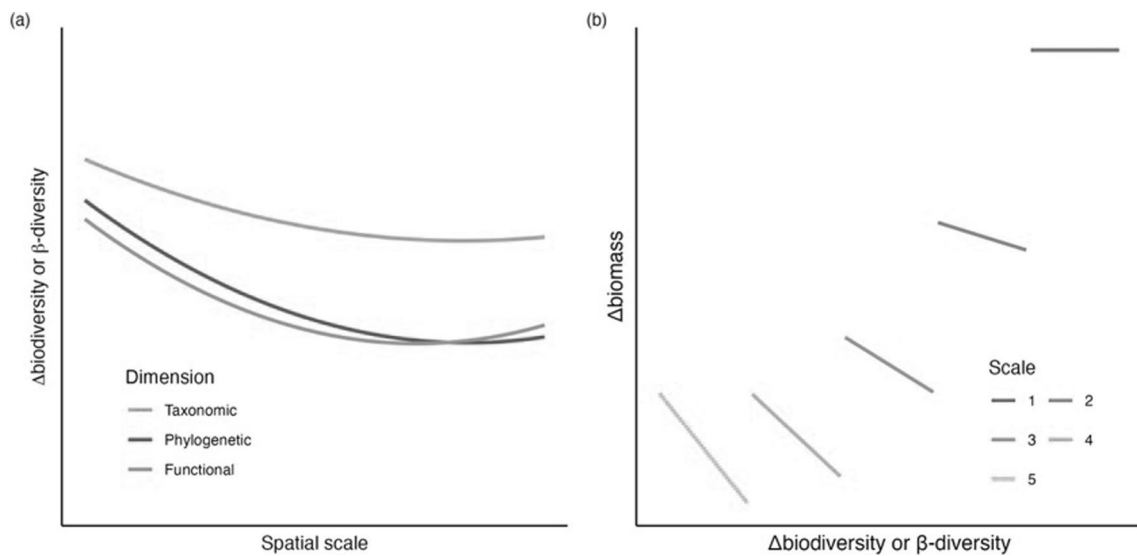
In addition, more empirical research is needed regarding the dimension-dependent effects of biodiversity loss and community compositional change on biomass dynamics in natural ecosystems (e.g., functional or phylogenetic; Naeem et al. 2016). Biodiversity and community composition are inherently multidimensional with taxonomic, functional, and phylogenetic characteristics, emphasizing species identity, traits, and evolutionary history, respectively (Liu et al. 2015; Stevens and Gavilanez 2015). In addition, biodiversity's functional and phylogenetic dimensions might be better predictors than its taxonomic dimensions (e.g., species richness) in explaining the variation in biomass production (Cadotte et al. 2009; Flynn et al. 2011). Given that the different dimensions of biodiversity and community composition are, in general interdependent (Lyashevskaya and Farnsworth 2012), unidimensional approaches (e.g., only species richness) might overestimate or underestimate the impacts of biodiversity loss and community compositional change on biomass dynamics (Liu et al. 2015). Avoiding such biases requires quantifying different dimensions of biodiversity and community composition and assessing their effects on ecosystem functions, which remain poorly investigated (Le Bagousse-Pinguet et al. 2019).

In the current study, we generated a continuous experimental gradient of spatial scale (i.e., a series of circular quadrats ranging from 2 to 30 m in radius) in a 20-ha Forest Dynamic Plot in Dinghushan, China, to understand the critical roles of biodiversity and community structure in ecosystem functioning across spatial scales in the face of global climate change. Within each quadrat, we monitored changes in aboveground biomass (i.e.,  $\Delta$ biomass),

multiple dimensions of biodiversity (i.e.,  $\Delta$ biodiversity for richness, Shannon diversity, functional, and phylogenetic), and community composition (i.e.,  $\beta$ -diversity for taxonomic, functional, and phylogenetic) over 10 years.

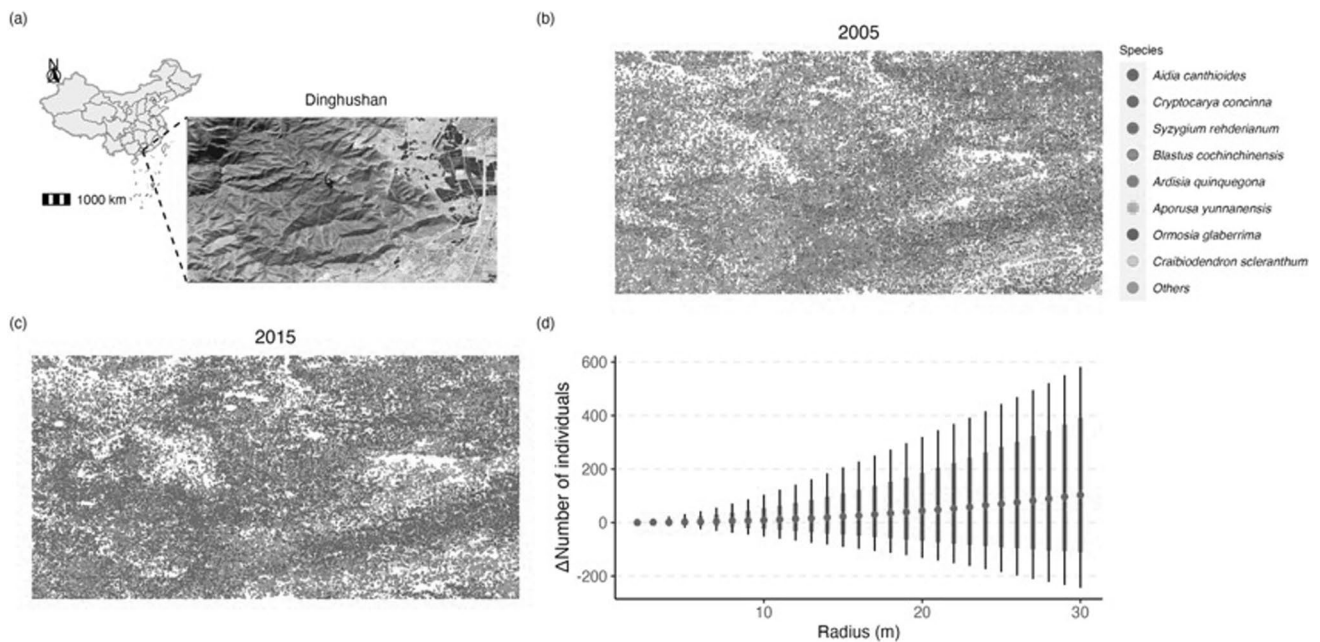
In our system, we make a series of predictions. Firstly,  $\Delta$ biodiversity and  $\beta$ -diversity will drop steeply and then decelerate with spatial scale due mostly to environmental changes (Fig. 1a; Keil et al. 2018; Pimiento et al. 2020). Species–area relationships typically show that biodiversity rises steeply and then decelerates with increasing spatial scale in natural ecosystems (Arrhenius 1921; Gleason 1922), primarily due to the presence of common species at small scales and an increase in rare species at larger scales (Tjørve et al. 2008). Moreover, we expect scale-dependent mismatches among the different dimensions of  $\Delta$ biodiversity and  $\beta$ -diversity (Fig. 1a; Wang et al. 2013; Mirochnitchenko et al. 2021). For example, species richness and Shannon diversity can have a decreasing correlation with spatial scale (Zhang et al. 2012). Consequently, the influences of  $\Delta$ biodiversity and  $\beta$ -diversity on  $\Delta$ biomass will vary with spatial scale and among different dimensions (Qiao et al. 2021).

Secondly, we predict  $\Delta$ biodiversity and  $\beta$ -diversity will have weak or no relationships with  $\Delta$ biomass at small spatial scales (Fig. 1b). On the one hand, high correlations among their different dimensions are probably due to low species redundancy resulting from the intense competition (i.e., limiting similarity hypothesis; MacArthur and Levins 1967), implying that their influences might be consistently weak or strong. On the other hand, high dominance means that the majority of  $\Delta$ biomass could be ascribed to one or a few dominant species, i.e., sampling or selection effects (Loreau and Hector 2001). However, due to high species turnover, those dominant species might over-yield or under-yield (i.e., through positive or negative selection), thus potentially resulting in neutral or weak relationships between  $\Delta$ biomass and  $\Delta$ biodiversity or  $\beta$ -diversity (Smith and Knapp 2003; Sasaki and Lauenroth 2011; Lohbeck et al. 2016). With increased spatial scale,  $\Delta$ biodiversity and  $\beta$ -diversity will have stronger relationships with  $\Delta$ biomass probably due to increasing complementarity effects (Isbell et al. 2018). That is, at large spatial scales, the higher number of lost species and stronger compositional shift means a greater variety of resources (e.g., water, nutrients, or pollinators) cannot be fully reutilized, thus resulting in a higher decline in biomass (Thompson et al. 2021). Hence, we expect that the dimensions of  $\Delta$ biodiversity and  $\beta$ -diversity more related to resource utilization (e.g., functional) and species' rarity (e.g., Shannon diversity or taxonomic  $\beta$ -diversity) will have stronger relationships with  $\Delta$ biomass at large spatial scales (Fig. 1b; Qiao et al. 2021).



**Fig. 1** Conceptual diagram outlining the changes in the multiple dimensions of biodiversity (i.e.,  $\Delta$ biodiversity) and community composition (i.e.,  $\beta$ -diversity) along a gradient of spatial scale (a) and their potential effects on net biomass change (i.e.,  $\Delta$ biomass) with

spatial scales (b). The different colors in the first plot represent the different dimensions of  $\Delta$ biodiversity and  $\beta$ -diversity including taxonomic, phylogenetic, and functional. The different colors in the second plot represent a gradient of spatial scale. (Color figure online)



**Fig. 2** Dinghushan Mountain in China (a), the spatial point patterns of species in a subtropical forest plot of 20 hectares in Dinghushan Mountain in 2005 (b) and 2015 (c), and the difference in the number of individuals (i.e.,  $\Delta$ number of individuals) sampled across an experimental gradient of spatial scale in both years (d). The species

in the spatial point patterns are ranked by their abundance and represented by different colors. The points, short, and long bars represent the median values, 75%, and 95% CIs of the  $\Delta$ number of individuals randomly sampled 10,000 times in both years

## Methods

### Study site

Our study site is a subtropical long-term forest plot of 20 ha (i.e., 400 m × 500 m) located in the Dinghushan Nature Reserve (23°09′21″–23°11′30″ N, 112°30′39″–112°33′41″ E), Guangdong Province, China (Fig. 2a). The vegetation in the plot is a natural mature evergreen broadleaved forest, which has been well-protected for over 400 years (Li et al. 2019a). The climate is a typical subtropical monsoon, with a mean annual temperature of about 21.0 °C. The annual precipitation is about 1927 mm and mainly distributes between April and September. The soil is classified as red and yellow with a small amount of humus according to the soil classification of China (Gong 1999). The common plants include *Aidia canthioides*, *Cryptocarya concinna*, *Syzygium rehderianum*, and *Blastus cochinchinensis*.

The forest plot was established in November 2004 and then surveyed in 2005 and 2015. In each survey, all living and standing woody vegetation (i.e., trees and shrubs) with a diameter at breast height (DBH) > 1 cm were identified as species. Their height and DBH were measured, and their positions were recorded. After standardizing species names with the Flora of China (<http://www.iplant.cn>) and The Plant List (<http://www.theplantlist.org>), the first survey recorded a total of 71,452 individuals, belonging to 193 species, 115 genera, and 56 families; the second survey recorded a total of 80,283 individuals, belonging to 174 species, 105 genera, and 53 families. The two surveys reflected extreme climate fluctuations, including the cold and hot spells in 2008 and a prolonged drought from 2010 to 2013 (Li et al. 2021). As a result, the plot underwent an evident shift in species composition and distribution (Fig. 2b, c).

### Random sampling

To create a continuous gradient of spatial scale, we set a series of circular quadrats of different radii ranging from 2 to 30 m (size interval as 1-m), each having thirty replicates randomly arranged in the whole plot. The minimum radius was set to avoid too many empty quadrats, and the maximum radius was established to guarantee that replicates fell wholly within the plot. To ensure the random and non-overlapped distribution of the replicates, we used the function “rmh” in the R package spatstat (Baddeley and Turner 2005) to assume that they follow a Gibbs hard-core point process (Ratcliffe et al. 2015). Within each replicate, species composition in the two surveys was recorded, and aboveground biomass production was

estimated. Averagely, the number of individuals in each size of sampling quadrat ranged from 4 to 1018 across the whole gradient of spatial scale and was generally similar between the two surveys (Fig. 2d).

### Net biomass change and its components

For each individual recorded in replicate, we estimated its aboveground biomass using the function “computeAGB” in the R package BIOMASS (Réjou-Méchain et al. 2017) based on the field measurements (e.g., dbh, height, species identity). Because of the massive missing plant height data, aboveground biomass was estimated using an improved allometric equation provided by Chave et al. (2014), i.e.,

$$AGB = e^{(-2.024 - 0.896 \times E + 0.920 \times \log WD + 2.795 \times \log D - 0.0461 \times (\log D)^2)}, \quad (1)$$

where  $E$  is a measure of environmental stress,  $D$  is DBH (cm), and  $WD$  is wood density ( $g/cm^3$ ). Wood density was estimated for all the species recorded except 110 species using the function “getWoodDensity” in the R package BIOMASS (Réjou-Méchain et al. 2017). The estimation of aboveground biomass was summed over all the individuals recorded in a quadrat as aboveground community biomass (Mg). Then, the net change of aboveground community biomass in a quadrat between the two surveys (i.e.,  $\Delta biomass_{2015-2005}$ ) was calculated and then partitioned into the amounts of decreased and increased biomass as the following:

$$\begin{aligned} \Delta biomass_{2015-2005} &= biomass_{2015} - biomass_{2005} \\ &= increment + decrement. \end{aligned} \quad (2)$$

### Molecular phylogeny

For the species recorded, we constructed a molecular phylogeny using three different universal DNA barcodes, including *rbcL*, *matK*, and ITS, since their combination can provide substantial discriminatory power for the close-related species in our system (Liu et al. 2019a). After extraction and sequencing (Jin et al. 2022), *rbcL* and *matK* were aligned using the MAFFT (Version 7; Katoh and Standley 2013). ITS sequences were aligned separately by order or closely related orders, then combined and edited manually in Geneious R11.1.5 (Biomatters Ltd., Auckland, New Zealand). The three alignments were concatenated to build a super-matrix, and then a maximum likelihood molecular phylogeny was constructed using RAxML (Version 8.2.12, Stamatakis 2014). Two gymnosperm species (*Nageia fleuryi* and *Pinus massoniana*) were chosen as outgroups. Using the inferred divergence times in Magallón et al. (2015) as secondary calibrations, the phylogeny was transformed into an

ultra-metric tree by automatically estimating the divergence time in treePL (Smith and O'Meara 2012). Then the 1000 bootstrap replicates of the super-matrix were run to evaluate node support for the phylogenetic topology constructed. In our molecular phylogeny, the average node support (median) is 100%, and the proportion of nodes with a high support rate ( $\geq 80\%$ ) is greater than 75% (Appendix: Fig. 6).

## Functional traits

For the species recorded, we assembled seventeen different functional traits important for the aboveground biomass production of forests. Those traits included leaf area ( $\text{cm}^2$ ), leaf dry matter content (%), specific leaf area ( $\text{cm}^2 \text{g}^{-1}$ ), petiole length (m), petiole density ( $\text{g cm}^{-2}$ ), petiole dry matter content ( $\text{mg g}^{-1}$ ), leaf nitrogen content ( $\text{mg g}^{-1}$ ), leaf phosphorus content ( $\text{mg g}^{-1}$ ), photosynthetic nitrogen use efficiency ( $\mu\text{mol mol}^{-1} \text{s}^{-1}$ ), photosynthetic phosphorus use efficiency ( $\text{mmol mol}^{-1} \text{s}^{-1}$ ), leaf chlorophyll content ( $\mu\text{g l}^{-1}$ ), stem conductance ( $\text{kg m}^{-1} \text{MPa}^{-1} \text{s}^{-1}$ ), leaf conductance ( $10^{-4} \text{kg m}^{-1} \text{MPa}^{-1} \text{s}^{-1}$ ), stomatal conductance per unit area ( $\text{mmol m}^{-2} \text{s}^{-1}$ ), stomatal conductance per unit mass ( $\text{mmol g}^{-1} \text{s}^{-1}$ ), instantaneous water use efficiency ( $\mu\text{mol mol}^{-1}$ ), and leaf expansion loss point (Mpa) (Jones et al. 2015; Li et al. 2015a). Part of the trait data was assembled from literature (Liu et al. 2019b; Zhang et al. 2019) and characterized based on the TRY database (Kattge et al. 2011). The remaining trait data were estimated using Multiple Imputations with Chained Equations (MICE), as implemented in the R package mice (van Buuren and Groothuis-Oudshoorn 2011).

## Biodiversity loss and community compositional change

For a replicate of sampling quadrat at each given scale, we estimated its biodiversity loss between the two surveys as the following:

$$\Delta \text{biodiversity}_i = \text{biodiversity}_{i,2015} - \text{biodiversity}_{i,2005} \quad (3)$$

where  $i$  represents one dimension of biodiversity. The multiple dimensions of biodiversity were calculated, including species richness (i.e., number of species;  $S$ ), Shannon's diversity ( $H'$ ), and functional and phylogenetic diversity. Shannon's diversity was calculated following

$$H' = \sum_{i=1}^S \frac{n_i}{N} \log \left( \frac{n_i}{N} \right) \quad (4)$$

where  $N$  is the number of individuals,  $S$  is the number of species, and  $n_i$  is the abundance of species  $i$ . Functional diversity was measured as the mean distance of each species to the abundance-weighted centroid of the multivariate space composed of the functional traits considered (i.e., functional dispersion abbreviated as FDis; Laliberté and Legendre 2010), using the function "dbFD" in the R package FD (Laliberté et al. 2014). Phylogenetic diversity measures included three metrics: Faith's PD, which sums the branch lengths that connect component species in a community (Faith 1992); abundance-weighted mean pairwise distance (MPD), which is the abundance-weighted phylogenetic distance separating all pairs of species in a community (Webb et al. 2002); and abundance-weighted mean nearest taxon distance (MNTD), which is the abundance-weighted phylogenetic distance separating a species with its closest relative in a community (Webb et al. 2002). The values of those phylogenetic diversity measures were calculated using the function "pd," "mpd," and "mntd" in the R package Picante (Kembel et al. 2010).

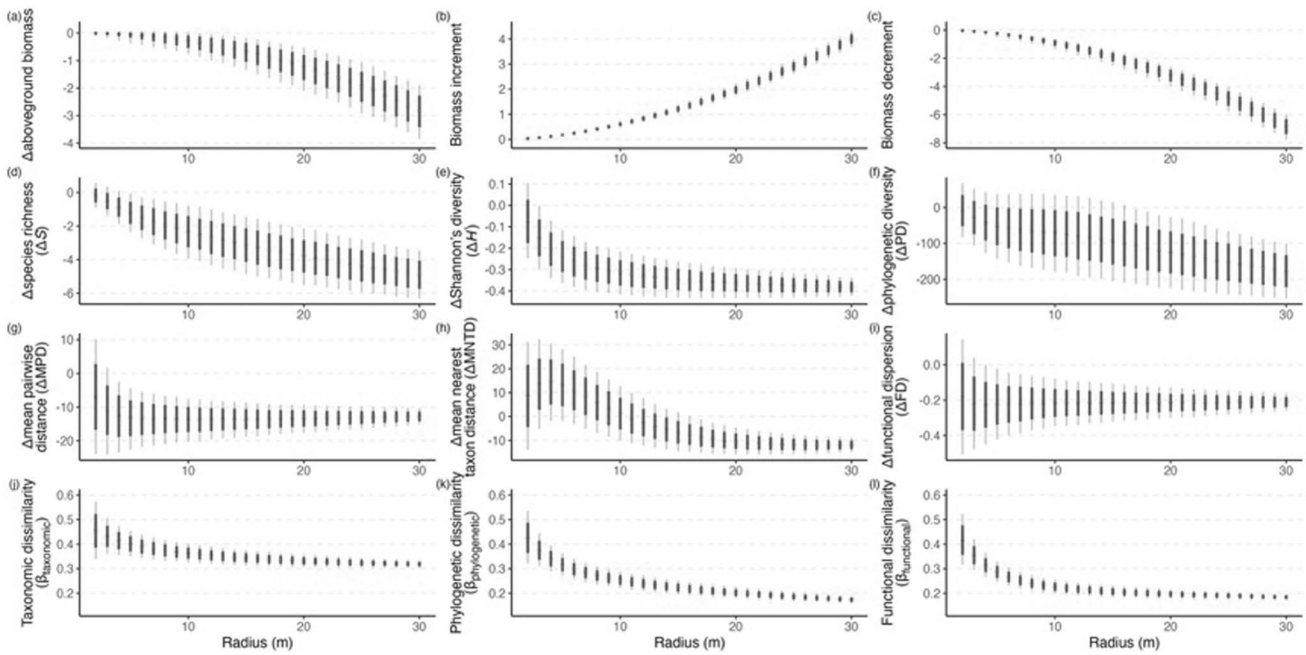
For a replicate of the sampling quadrat, we also estimated the multiple dimensions of community compositional change between the two surveys (i.e.,  $\beta$ -diversity), including taxonomic, functional, and phylogenetic. Taxonomic  $\beta$ -diversity was calculated using the Bray–Curtis dissimilarity index (Bray and Curtis 1957) following

$$D_{2005,2015} = \frac{\sum_{i=1}^S |x_{i,2005} - x_{i,2015}|}{\sum_{i=1}^S (x_{i,2005} + x_{i,2015})} \quad (5)$$

where  $x_{i,2005}$  and  $x_{i,2015}$  is the abundance of species  $i$  in 2005 and 2015, respectively, and  $S$  is the total number of species in the two surveys. For both functional and phylogenetic  $\beta$ -diversity, we used an abundance-weighted dissimilarity index, i.e.,

$$W - \text{UniFrac} = \frac{\sum_i^n b_i \times \left| \frac{2005_i}{2005_T} - \frac{2015_i}{2015_T} \right|}{\sum_j^{n'} d_j \times \left| \frac{2005_j}{2005_T} + \frac{2015_j}{2015_T} \right|} \quad (6)$$

where  $n$  is the number of branches in a dendrogram,  $b_i$  is the length of branch  $i$ ,  $2005_i$  and  $2015_i$  are the number of individuals that descend from branch  $i$  in 2005 and 2015, respectively,  $2005_T$  and  $2015_T$  are the total numbers of individuals in 2005 and 2015, respectively.  $n'$  is the number of different individuals in the two surveys,  $d_j$  is the distance from the root to individual  $j$ , while  $2005_j$  and  $2015_j$  are the number of times the individual  $j$  observed in 2005 and 2015, respectively (Lozupone et al. 2007). For functional  $\beta$ -diversity, the dendrogram was constructed using hierarchical clustering



**Fig. 3** Ten-year changes in aboveground biomass and its components (i.e.,  $\Delta$ biomass, increment, and decrement; **a–c**), the multiple dimensions of biodiversity loss (i.e.,  $\Delta$ biodiversity; **d–i**), and community compositional change (i.e.,  $\beta$ -diversity; **j–l**) along a spatial gradient within a natural subtropical forest plot. The red points, blue, and gray bars represent the median values, 75%, and 95% CIs of the variables randomly sampled 10,000 times, respectively. The different dimen-

sions of  $\Delta$ biodiversity include changes in species richness ( $\Delta S$ ), Shannon’s diversity ( $\Delta H'$ ), mean pairwise distance ( $\Delta MPD$ ), mean nearest taxon distance ( $\Delta MNTD$ ), functional dispersion ( $\Delta FD$ ). Those of  $\beta$ -diversity include taxonomic ( $\beta_{\text{taxonomic}}$ ), phylogenetic ( $\beta_{\text{phylogenetic}}$ ), and functional  $\beta$ -diversity ( $\beta_{\text{functional}}$ ). (Color figure online)

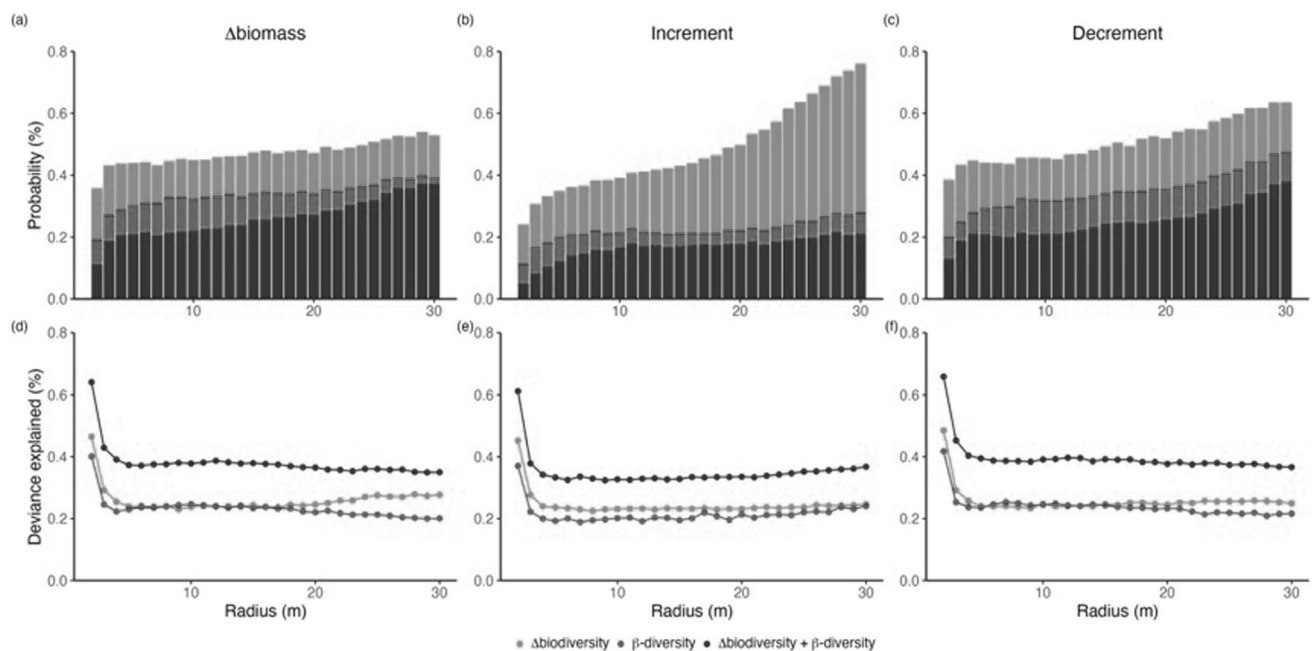
with the Euclidean distance matrix of the standardized functional traits considered (Petchey and Gaston 2007). For phylogenetic  $\beta$ -diversity, the dendrogram was the molecular phylogeny constructed. The dimensions selected were majorly weighted by abundance because we assumed that the abundance-weighted dimensions would have stronger relationships with biomass than their non-weighted versions in natural ecosystems. Some widely used but non-weighted dimensions, such as species richness and Faith’s PD, were also included to compare the current study with previous findings (Flynn et al. 2011).

**Statistical analysis**

For each size of the sampling quadrat, we determined the most parsimonious relationships of  $\Delta$ biomass and its components (i.e., increment and decrement) as a function of both  $\Delta$ biodiversity and  $\beta$ -diversity. To do this, we first constructed a series of linear regression models to include all the combinations of the different dimensions calculated for both  $\Delta$ biodiversity and  $\beta$ -diversity. That is,

$$\Delta \text{biomass}_{i,l} \sim \sum_{j=1}^6 a_j \times \Delta \text{biodiversity}_{j,l} + \sum_{k=1}^3 b_k \times \beta \text{-diversity}_{k,l} \tag{7}$$

where  $\Delta \text{biomass}_{i,l}$  represents the net change of aboveground biomass or its components in a replicate  $l$ ,  $\Delta \text{biodiversity}_{j,l}$  and  $\beta$ -diversity $_{k,l}$  represent a measure of  $\Delta$ biodiversity and  $\beta$ -diversity in a replicate  $l$ , respectively,  $a_j$  and  $b_k$  represent the regression coefficients of  $\Delta$ biodiversity and  $\beta$ -diversity, respectively. For those dimensions not included,  $a_j$  and  $b_k$  were set to zero. Because of the high correlations among those dimensions (Appendix: Fig. 7; |Spearman’s  $\rho$ | > 0.3), any multiple regression model with the variance inflation factor (VIF) of any parameter being greater than three was excluded to avoid biases in coefficient estimates (Cade 2015). At the same time, a null model, i.e., an intercept-only model (e.g.,  $\Delta \text{biomass}_i \sim 1$ ), was constructed. Akaike’s information criterion corrected for small sample sizes ( $AIC_c$ ; Burnham and Anderson 2002, 2004) was calculated for each model that remained, and relatively better-ranked models were selected (i.e.,  $AIC_{\text{cmodel}_i} - AIC_{\text{cnull}} < -2$ ). If the selected models were not empty, the top-ranked model



**Fig. 4** Model probability of net biomass change (i.e.,  $\Delta$ biomass; **a**) and its components (increment and decrement; **b**, **c**) as a function of biodiversity loss (i.e.,  $\Delta$ biodiversity) or community compositional change (i.e.,  $\beta$ -diversity) and the associated percentage of deviance explained (i.e.,  $De$ ) in the dependent variable (**d–f**) along a spatial gradient within a natural subtropical forest plot.  $\Delta$ biomass and its components were calculated as 10-year changes in aboveground biomass, the amounts of increased, and decreased biomass, respectively.

with the lowest  $AIC_c$  was used as the most parsimonious model, and then the standardized coefficient ( $\beta_n/SE_n$ ) of each term was calculated. Meanwhile, the percentage of deviance explained in the response variable ( $De$ ) was used to measure the model's goodness of fit. Before model fitting, all variables were standardized (i.e., mean/standard deviation). Because our models did not include spatial and environmental factors (e.g., soil nutrients), which might bias the results of the multi-model inference and the estimation of standardized coefficients (Liang 2012), to minimize their confounding effects, we repeated above random sampling, the associated calculation of  $\Delta$ biomass,  $\Delta$ biodiversity, and  $\beta$ -diversity, and statistical analyses 10,000 times. The number of times the most parsimonious model identified was not the null model was counted and then divided by 10,000 as the model probability of  $\Delta$ biodiversity and  $\beta$ -diversity. Then, for a measure of  $\Delta$ biodiversity or  $\beta$ -diversity, the median and the confidence interval (95% CI) of its estimated standardized coefficients were calculated. The median coefficient was considered significant when its 95% CI did not contain

zero. All data analyses were performed in R 3.5.3 (R Core Team 2015).

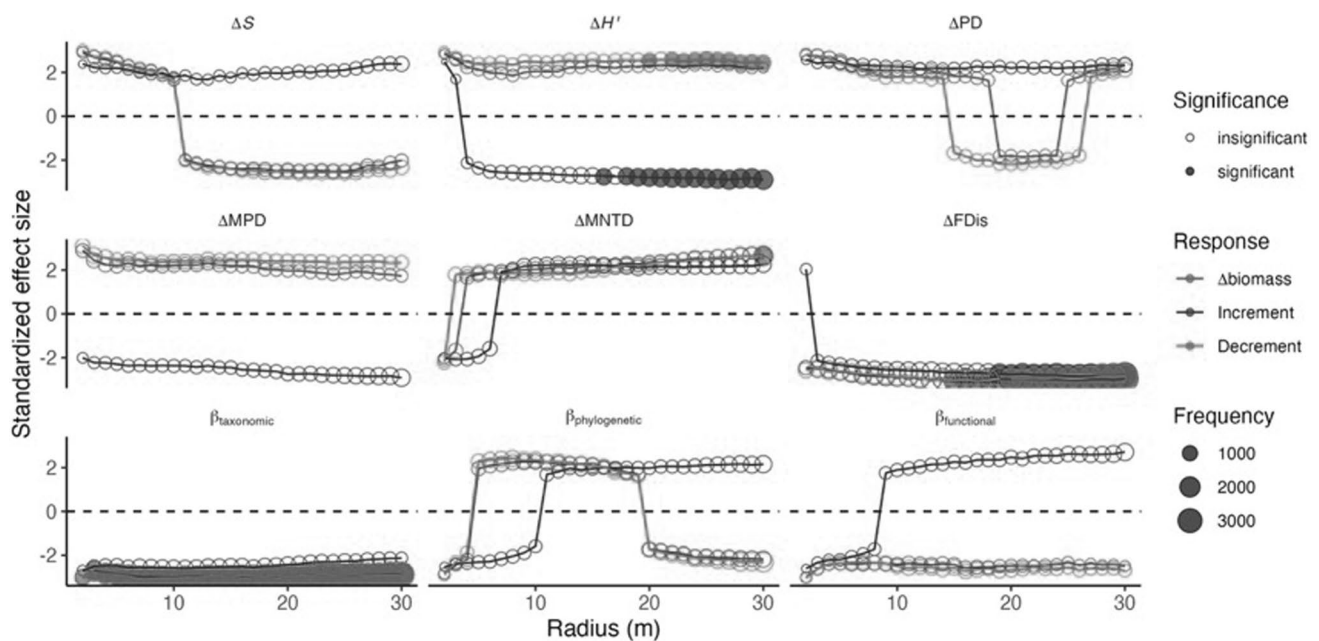
Model probability was calculated as the proportion of the most parsimonious model identified for  $\Delta$ biomass and its components including  $\Delta$ biodiversity or  $\beta$ -diversity or both over 10,000 random samples. The points in plots d–f represent the median values of the  $De$  values of the most parsimonious models identified for  $\Delta$ biomass and its components including  $\Delta$ biodiversity or  $\beta$ -diversity or both over 10,000 random samples

zero. All data analyses were performed in R 3.5.3 (R Core Team 2015).

## Results

With the increase of quadrat radius in the surveys, aboveground community biomass increased at an accelerating rate, while MNTD decreased and other measures of biodiversity increased at decelerating rates (Appendix: Figs. 8, 9). Consistently,  $\Delta$ biomass and biomass decrement decreased, whereas biomass increment increased at accelerating rates (Fig. 3a–c).  $\Delta$ biodiversity and  $\beta$ -diversity decreased at decelerating rates with quadrat radius; however,  $\Delta$ FDi seemed to be invariant, and  $\Delta$ MNTD tended to be positive and increase with quadrat radius at small spatial scales (Fig. 3d–l). Notably, only at large spatial scales,  $\Delta$ biomass, its components, and  $\Delta$ biodiversity were significantly negative.

For  $\Delta$ biomass and its components, the model probabilities of  $\Delta$ biodiversity and  $\beta$ -diversity were generally low, but all tended to increase with quadrat radius (Fig. 4a–c).  $\Delta$ biomass



**Fig. 5** Standardized coefficients of biodiversity loss (i.e.,  $\Delta$ biodiversity) and community compositional change (i.e.,  $\beta$ -diversity) on net biomass change (i.e.,  $\Delta$ biomass) and its components (i.e., increment and decrement) along a spatial gradient within a natural subtropical forest plot. The different dimensions of  $\Delta$ biodiversity include changes in species richness ( $\Delta S$ ), Shannon's diversity ( $\Delta H'$ ), mean pairwise distance ( $\Delta$ MPPD), mean nearest taxon distance ( $\Delta$ MNTD), functional dispersion ( $\Delta$ FDis). Those of  $\beta$ -diversity include taxonomic ( $\beta_{\text{taxonomic}}$ ), phylogenetic ( $\beta_{\text{phylogenetic}}$ ), and functional  $\beta$ -diversity ( $\beta_{\text{functional}}$ ).  $\Delta$ biomass and its components were calculated as 10-year changes in aboveground biomass,

and decrement had similar distributions of model probability across the spatial gradient, of which the models including both  $\Delta$ biodiversity and  $\beta$ -diversity accounted for the major occurrences and increasing tendencies. In contrast, the biomass increment had an increasing trend mainly from models including only  $\Delta$ biodiversity measures. Nevertheless, deviance explained (i.e.,  $De$  value) of the  $\Delta$ biodiversity and  $\beta$ -diversity models identified for  $\Delta$ biomass and its components all declined and then generally stabilized with quadrat radius (Fig. 4d–f). Notably, the models including both  $\Delta$ biodiversity and  $\beta$ -diversity measures tended to obtain the highest  $De$  values.

Of the measures of  $\Delta$ biodiversity and  $\beta$ -diversity,  $\Delta$ MNTD,  $\Delta$ FDis, and taxonomic  $\beta$ -diversity showed significant effects on  $\Delta$ biomass, however, only at large spatial scales (Fig. 5). Correspondingly, the effects of  $\Delta$ FDis were consistently negative for both biomass increment and decrement, whereas that of taxonomic  $\beta$ -diversity was only significantly negative for biomass decrement. At the same time,  $\Delta H'$  showed significant

the amounts of increased, and decreased biomass, respectively. The points represent the median values of the standardized coefficient estimated for each predictor included in the most parsimonious models identified for  $\Delta$ biomass and its components over 10,000 random samples. A solid point represents the 95% CI of the standardized coefficient estimated for a predictor in 10,000 random samples excludes zero (i.e., significant effect). The size of a point represents the number of occurrences of a predictor present in the most parsimonious models identified for  $\Delta$ biomass and its components in 10,000 random samples

but opposite effects on biomass increment and decrement at large spatial scales, which aligns with its neutral effects on  $\Delta$ biomass over the whole spatial gradient.

## Discussion

Biodiversity loss and community compositional change driven by global environmental change are suspected to impact the biomass production of natural communities differently over a continuum of spatial scales (Mori et al. 2018; Gonzalez et al. 2020; Qiu and Cardinale 2020), although hitherto empirical evidence is lacking. Previous studies are mainly conducted at one or few discrete spatial scales using relatively small-scale experiments (Bond and Chase 2002; Li et al. 2019b; Luo et al. 2019a) and are often focused on one dimension of biodiversity and community structure primarily on the taxonomic level (Chisholm et al. 2013; Barry et al. 2021). Our study investigates the influences of both  $\Delta$ biodiversity and  $\beta$ -diversity on  $\Delta$ biomass



and its components over a continuous gradient of spatial scales and disentangles the relative importance of multiple dimensions of biodiversity and community structure in a natural forest ecosystem. Our results showed that (1) over a 10-year study period, which included dramatic environmental changes,  $\Delta$ biomass,  $\Delta$ biodiversity, and  $\beta$ -diversity declined with decreasing spatial scale; (2) significant effects of  $\Delta$ biodiversity and  $\beta$ -diversity on  $\Delta$ biomass occurred at larger spatial scales; and (3)  $\Delta$ MNTD,  $\Delta$ FDis, and taxonomic  $\beta$ -diversity were shown to be relatively better predictors (as compared to other dimensions considered here) for  $\Delta$ biomass at larger spatial scales. Below, we discuss these findings and their relative importance for assessing biomass production in natural ecosystems.

Within our forest system,  $\Delta$ biodiversity tended to be negative and generally decreased with quadrat radius, suggesting the scale dependency of plant biodiversity responses to environmental changes (Lan et al. 2015; Li et al. 2015b). At small spatial scales, all  $\Delta$ biodiversity measures were insignificant, which agrees with previous studies (Vellend et al. 2013; Dornelas et al. 2014). Particularly,  $\Delta$ MNTD tended to be positive and increase with quadrat radius, indicating strong interspecific competition at small spatial scales (Webb et al. 2002), where the colonization of species dissimilar to the dominant species in a community may help maintain biodiversity at small spatial scales (Chesson 2000). At larger spatial scales, all  $\Delta$ biodiversity measures were significantly negative (Gonzalez et al. 2016), indicating that species immigration cannot offset species loss, probably because the lost species were rare (LaManna et al. 2016; Obst et al. 2018). Compared with common species, rare species could be more difficult to replenish since they might have also been lost at larger spatial scales. On the other hand,  $\Delta$ FDis did not change across spatial scales, indicating that functional diversity is not scale-dependent (Niu et al. 2020).

Our results also showed that comparing across different dimensions of biodiversity,  $H'$ , MPD, MNTD, and FDis were more stable than  $S$  and PD at larger spatial scales. These results suggest that at larger spatial scales, new species added to or removed from a community contribute little to the change in its overall biodiversity, particularly when considering Shannon diversity, functional, and phylogenetic diversity. Consistent with  $\Delta$ biodiversity, we also found that  $\beta$ -diversity generally decreased with decreasing spatial scale; community composition was more similar and more stable at larger spatial scales (also see Zhou et al. 2018). These results can draw several implications: First, similar species can coexist at larger spatial scales, probably due to high environmental heterogeneity (e.g., soil nutrients, symbionts,

pathogens; Yackulic 2017). Second, species redundancy can be high at large spatial scales (Kondratyeva et al. 2020). Redundant species are likely to be removed by disturbances (e.g., drought) because they are often rare in terms of mean abundance (Jain et al. 2014) and can be removed by both abiotic conditions and biotic interactions (e.g., competition; McLean et al. 2019).

In contrast with  $\Delta$ biodiversity and  $\beta$ -diversity,  $\Delta$ biomass decreased with quadrat radius at an accelerating rate. Aboveground community biomass might remain unchanged at small spatial scales with considerable biodiversity loss and community compositional shift. In contrast, similar biodiversity loss and community compositional change might occur at larger scales with substantially greater declines in aboveground community biomass. These contrasting results may imply that overall  $\Delta$ biomass might have weak relationships with both  $\Delta$ biodiversity and  $\beta$ -diversity across the whole spatial scale gradient, which is supported by their generally low model probabilities, alluding to the need for further partitioning of  $\Delta$ biomass into different components to infer their mechanistic responses better. Thus, for  $\Delta$ biodiversity and  $\beta$ -diversity, their weak relationships with  $\Delta$ biomass may be attributed to the following mechanisms, which should be more fully explored in future studies: (I) they have no or a weak relationship with all the components of biomass (i.e., increment and decrement); (II) they have a strong relationship with all the components of biomass, but with little contribution to overall  $\Delta$ biomass; (III) they have strong but opposite relationship with different biomass components that are cancelled out at the community level.

In our system, at small spatial scales, the low model probabilities of  $\Delta$ biodiversity and  $\beta$ -diversity occurred for both increment and decrement (i.e., mechanism I). This result is not surprising because, on the one hand, increment and decrement at small spatial scales might be mainly determined by one or several dominant species (Smith and Knapp 2003). On the other hand,  $\Delta$ biodiversity and  $\beta$ -diversity might have close connections with species immigration at small spatial scales (Liu and Zhou 2011); however, immigrated species could contribute little to increment due to intense competition, limited resources, and delayed responses (i.e., mechanism II) (Ratcliffe et al. 2015). With the increase of spatial scale, the model probabilities of  $\Delta$ biodiversity and  $\beta$ -diversity increased for both increment and decrement, especially the former. Nonetheless, in our system, the increment was generally lower than the decrement in absolute value, especially at large spatial scales. Moreover,  $\Delta$ biodiversity and  $\beta$ -diversity could have opposite effects on

increment and decrement at large spatial scales (e.g.,  $\Delta H'$ ; i.e., mechanism III).

In our system,  $\beta$ -diversity had a lower model probability than  $\Delta$ biodiversity, not only across the whole gradient but also across  $\Delta$ biomass and its components. Compared with  $\Delta$ biodiversity,  $\beta$ -diversity is often assumed to be of equal or even greater importance for  $\Delta$ biomass (Hector et al. 2011; Bowker et al. 2021), especially when dominant species mainly drive  $\beta$ -diversity (Dai et al. 2018). However, this is not the case in our study, especially at large spatial scales. In line with model probability, the percentage of deviance explained in the response variable ( $De$ ) was generally higher with  $\Delta$ biodiversity. Surprisingly, for both  $\Delta$ biodiversity and  $\beta$ -diversity,  $De$  generally decreased with quadrat radius. This trend might be associated with their decreasing variances with spatial scale because  $De$ , like the R-squared value (i.e.,  $R^2$ ), might increase with the range of continuous explanatory variables (Hector et al. 2011).

Nevertheless, our results found that the combination of  $\Delta$ biodiversity and  $\beta$ -diversity outperformed single  $\Delta$ biodiversity or  $\beta$ -diversity in terms of both model probability and  $De$ , especially at large spatial scales. This result is consistent with the significant effects of both  $\Delta$ biodiversity and  $\beta$ -diversity on  $\Delta$ biomass and its components at large spatial scales, which generally agrees with previous research (Gonzalez et al. 2020). Such results highlight that on the one hand, biodiversity and community structure tend to be more important for ecosystem functions and services at larger scales (e.g., landscape) than those reported from small-scale experiments (Birkhofer et al. 2018; Reu et al. 2022). On the other hand, explaining maximum variation in productivity requires both biodiversity and community structure (Hodapp et al. 2016). However, it should be noted that the relative importance of the different dimensions of  $\Delta$ biodiversity and  $\beta$ -diversity varied considerably for  $\Delta$ biomass and its components, especially at large spatial scales. Particularly, the phylogenetic and functional dimensions of  $\Delta$ biodiversity outperformed its taxonomic dimensions. By contrast, the taxonomic dimensions of  $\beta$ -diversity exceeded their phylogenetic and functional dimensions.

Regardless of the dimensions of  $\Delta$ biodiversity and  $\beta$ -diversity,  $\Delta$ biomass, and its components, the standardized coefficient converged around a similar absolute value (i.e., 2.5). Several reasons might account for the convergences. First, we standardized all the variables before analysis for direct comparison along the spatial gradient. Second, taxonomic  $\beta$ -diversity, which appeared to be the most influential

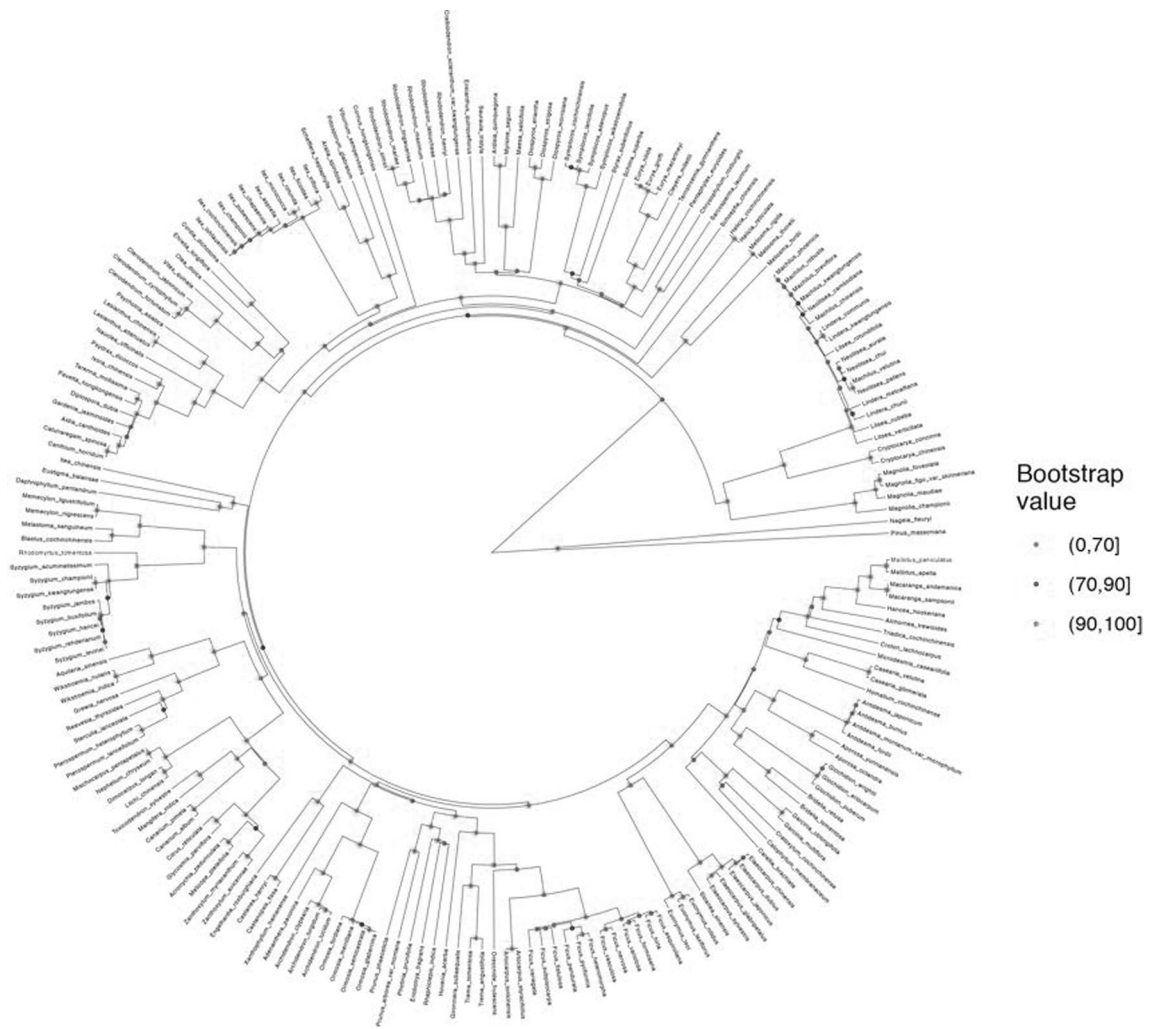
predictor here, had strong and significant correlations with the other measures of  $\Delta$ biodiversity and  $\beta$ -diversity at large spatial scales (Appendix: Fig. 7). Third, biotic homogenization in our system might somewhat drive the convergences (Van Der Plas et al. 2016). Fourth, the dimensions of  $\Delta$ biodiversity and  $\beta$ -diversity tend to not be included in the most parsimonious model if they have the standardized coefficients much above or below the converged values here. Although our results were generally in line with previous results (Lasky et al. 2014; Brun et al. 2019; Luo et al. 2019b; Abbasi et al. 2022), our study has the advantage of simultaneously considering all possible important dimensions of both  $\Delta$ biodiversity and  $\beta$ -diversity. Indeed, in our system, the results of unidimensional approaches additionally found that  $\Delta S$  and functional  $\beta$ -diversity also showed significant effects on  $\Delta$ biomass at large spatial scales (Appendix: Fig. 10).

## Conclusions

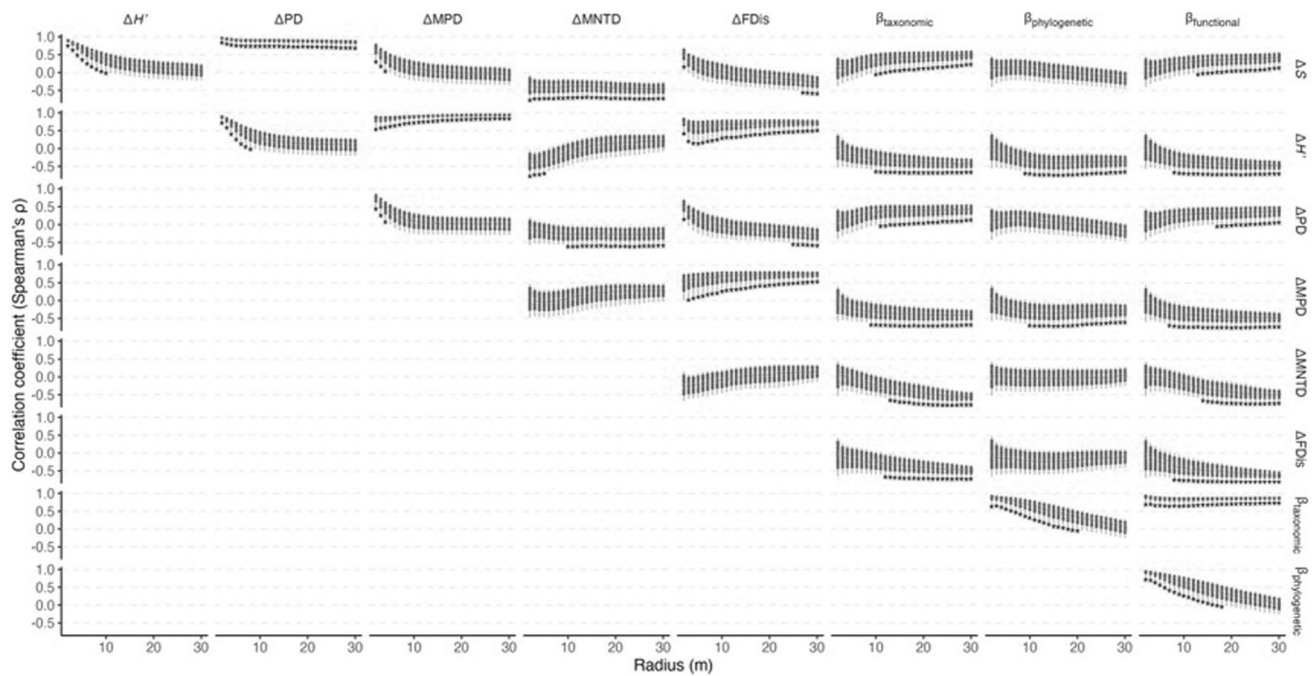
Although the relationships of  $\Delta$ biomass as a function of  $\Delta$ biodiversity and  $\beta$ -diversity were generally weak in our studied forest system, as also shown in previous studies (Liu et al. 2022), our results did support the scale-dependence of their relationships in natural forest ecosystems (Luo et al. 2019b). Here, we detected nonlinear responses in the effects of  $\Delta$ biodiversity and  $\beta$ -diversity on  $\Delta$ biomass and its components, benefitting from analyses across a continuous gradient of spatial scales. While these results generally agree with previous findings (Thompson et al. 2018; Qiu and Cardinale 2020; Barry et al. 2021), our results show that the responses of  $\Delta$ biomass and its components (i.e., increment vs decrement) to  $\Delta$ biodiversity and  $\beta$ -diversity varied considerably among their different dimensions, especially at larger spatial scales. These findings have important implications for forest conservation policy and management because optimizing the sustainability of ecosystem functions and services in the face of global environmental change requires a consideration of spatial scale, dimensions of biodiversity and community structure.

## Appendix

See Figs. 6, 7, 8, 9, and 10.

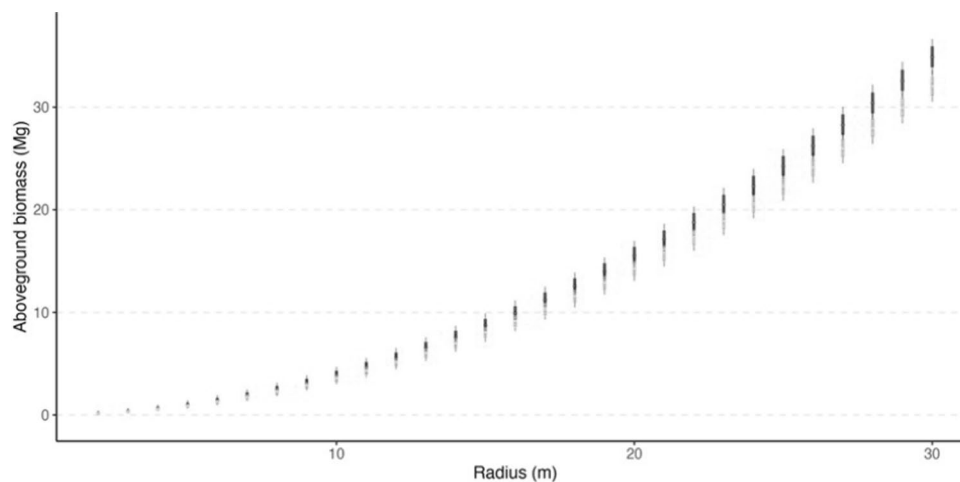


**Fig. 6** A molecular phylogeny constructed using three universal DNA barcodes including *rbcl*, *matK*, and ITS. 1000 bootstrap analysis was performed to evaluate the node support



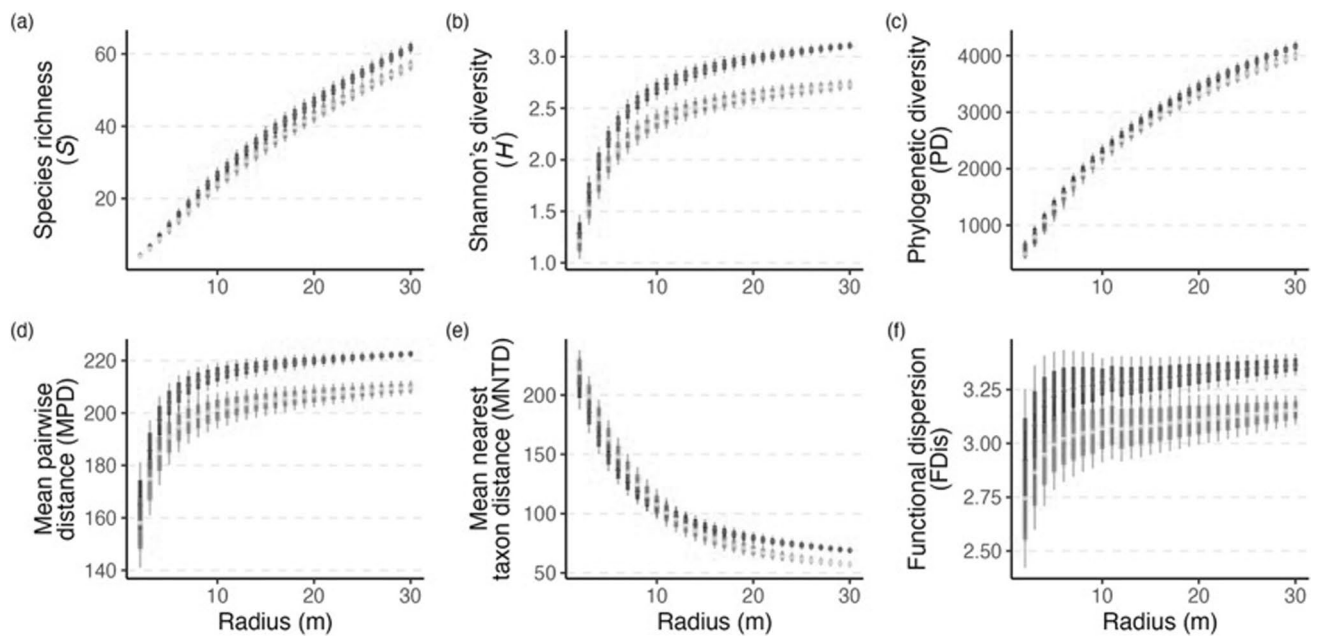
**Fig. 7** Pairwise correlations between the different dimensions of biodiversity loss (i.e.,  $\Delta$ biodiversity) and community compositional shift (i.e.,  $\beta$ -diversity) in 10 years along a spatial gradient within a natural subtropical forest plot. The red points, blue, and gray bars represent the median values, 75%, and 95% CIs of the correlations in 10,000 random samplings, respectively. The asterisks indicate significant correlations, i.e., the 95% CIs do not contain zero. The differ-

ent dimensions of  $\Delta$ biodiversity include changes in species richness ( $\Delta S$ ), Shannon's diversity ( $\Delta H'$ ), mean pairwise distance ( $\Delta MPD$ ), mean nearest taxon distance ( $\Delta MNTD$ ), functional dispersion ( $\Delta FDIs$ ). Those of  $\beta$ -diversity include taxonomic ( $\beta_{\text{taxonomic}}$ ), phylogenetic ( $\beta_{\text{phylogenetic}}$ ), and functional  $\beta$ -diversity ( $\beta_{\text{functional}}$ ). (Color figure online)



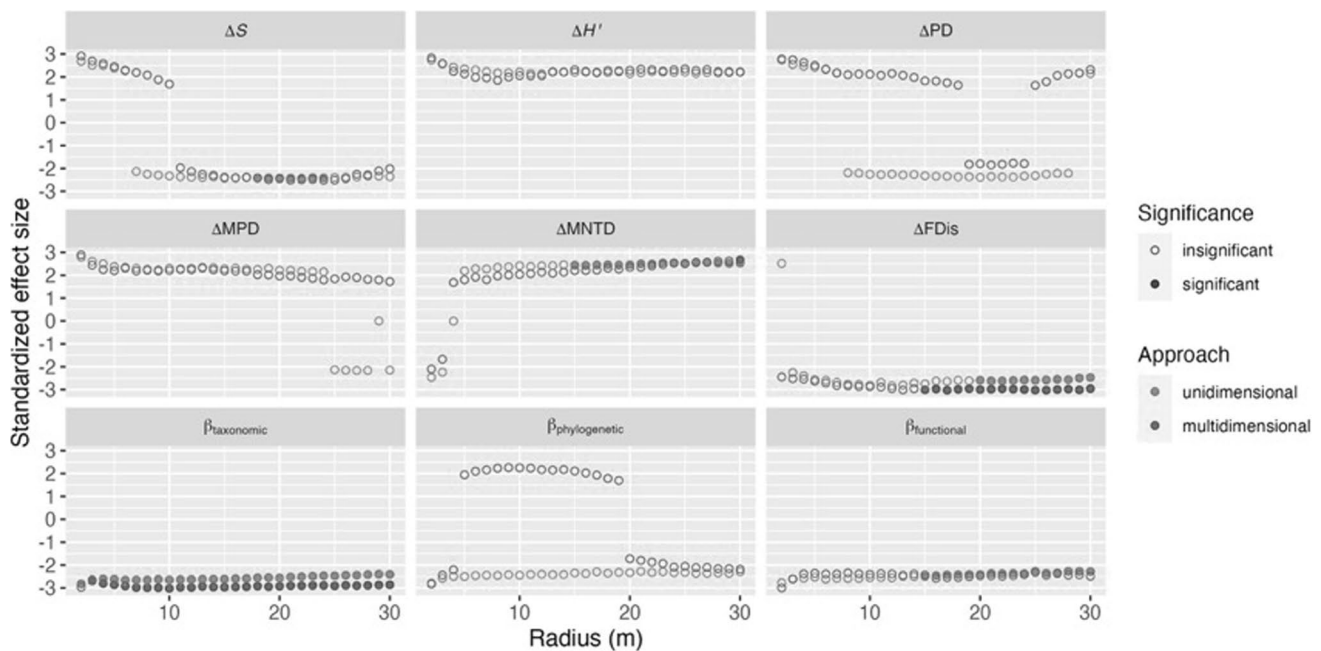
**Fig. 8** Distribution of aboveground biomass along a spatial gradient within a natural subtropical forest plot of Dinghushan Mountain. The red points, blue, and gray bars represent the median values, 75%, and 95% CIs of the biomass randomly sampled 10,000 times in the

first survey (i.e., 2005), respectively. The pink points and the green and gray bars represent the median values, 75%, and 95% CIs of the biomass randomly sampled 10,000 times in the second survey (i.e., 2015), respectively. (Color figure online)



**Fig. 9** Distribution of the different dimensions of biodiversity along a spatial gradient within a natural subtropical forest plot of Dinghushan Mountain. The red points, blue, and gray bars represent the median values, 75%, and 95% CIs of the variables randomly sampled 10,000 times in the first survey (i.e., 2005), respectively. The pink points, green, and gray bars represent the median values, 75%, and 95% CIs

of the variables randomly sampled 10,000 times in the second survey (i.e., 2015), respectively. The different dimensions for biodiversity included species richness ( $S$ ), Shannon's diversity ( $H'$ ), phylogenetic (PD, MPD, and MNTD), and functional diversity (FDIs). (Color figure online)



**Fig. 10** Standardized coefficients of biodiversity loss (i.e.,  $\Delta$ biodiversity) and community compositional change (i.e.,  $\beta$ -diversity) on net biomass change (i.e.,  $\Delta$ biomass) estimated by unidimensional and multidimensional approaches along a spatial gradient within a natural subtropical forest plot. Unidimensional approaches regressed  $\Delta$ biomass with every single dimension of  $\Delta$ biodiversity and  $\beta$ -diversity, whereas multidimensional approaches regressed  $\Delta$ biomass with the combinations of the different dimensions of both  $\Delta$ biodiversity and  $\beta$ -diversity. The different dimensions of  $\Delta$ biodiversity include changes in species richness ( $\Delta S$ ), Shan-

non's diversity ( $\Delta H'$ ), mean pairwise distance ( $\Delta$ MPD), mean nearest taxon distance ( $\Delta$ MNTD), functional dispersion ( $\Delta$ FDIs). Those of  $\beta$ -diversity include taxonomic ( $\beta_{\text{taxonomic}}$ ), phylogenetic ( $\beta_{\text{phylogenetic}}$ ), and functional  $\beta$ -diversity ( $\beta_{\text{functional}}$ ).  $\Delta$ biomass was calculated as the 10-year change in aboveground biomass. The points represent the median values of the standardized coefficient estimated for each predictor included in the most parsimonious models identified for  $\Delta$ biomass in 10,000 random samples. A solid point represents the 95% CI of the standardized coefficient estimated for a predictor in 10,000 random samples excludes zero (i.e., significant effect)

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**Author contributions** JJJ conceived the idea; JJJ designed the research; JJJ, YZ, LJ, WHY, JYL assembled the data and performed the experiments; JJJ analyzed the data; JJJ and JXQ wrote the initial manuscript with significant contributions from KSB.

**Data availability** The essential data and R script for reproducing the data analyses of this paper are available under reasonable request.

## Declarations

**Conflict of interest** None.

**Consent to participate** All authors included in this study gave written informed consent to participate in this research.

**Consent for publication** All authors included in this research gave written informed consent to publish the data and images contained within this case report.

**Ethics approval** Ethics approval was not required for this study according to local legislation.

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