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Carbon–biodiversity relationships in a highly diverse subtropical forest

Andreas Schuldt[1] | Xiaojuan Liu[2] | François Buscot[3,4] | Helge Bruelheide[4,5] | Alexandra Erfmeier[6] | Jin-Sheng He[7] | Alexandra-Maria Klein[8] | Keping Ma[2,9] | Michael Scherer-Lorenzen[10] | Bernhard Schmid[11] | Thomas Scholten[12] | Zhiyao Tang[7] | Stefan Trogisch[4,5] | Christian Wirth[4,13] | Tesfaye Wubet[4,14] | Michael Staab[15]

[1]Forest Nature Conservation, University of Göttingen, 37077, Göttingen, Germany

[2]State Key Laboratory of Vegetation and Environmental Change, Chinese Academy of Sciences, Institute of Botany, 100093, Beijing, China

[3]Department of Soil Ecology, UFZ-Helmholtz Centre for Environmental Research, 06120, Halle (Saale), Germany

[4]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, 04103, Leipzig, Germany

[5]Institute of Biology/Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, 06108, Halle (Saale), Germany

[6]Institute for Ecosystem Research, Kiel University, 24118, Kiel, Germany

[7]Institute of Ecology, College of Urban and Environmental Sciences and Key Laboratory for Earth Surface Processes, Peking University, Beijing, 100871, China

[8]Nature Conservation and Landscape Ecology, University of Freiburg, 79106, Freiburg, Germany

[9]College of Resources and Environment, University of Chinese Academy of Sciences, Beijing, China

[10]Faculty of Biology, Geobotany, University of Freiburg, 79104, Freiburg, Germany

[11]Department of Geography, Remote Sensing Laboratories, University of Zurich, 8057, Zurich, Switzerland

[12]Department of Geosciences, Soil Science and Geomorphology, University of Tübingen, 72070, Tübingen, Germany

[13]Systematic Botany and Functional Biodiversity, University of Leipzig, 04103, Leipzig, Germany

[14]Department of Community Ecology, UFZ-Helmholtz Centre for Environmental Research, 06120, Halle (Saale), Germany

[15]Ecological Networks, Technical University Darmstadt, 64287, Darmstadt, Germany

Correspondence

Andreas Schuldt, Forest Nature Conservation, University of Göttingen, 37077 Göttingen, Germany.
Email: andreas.schuldt@forst.uni-goettingen.de

Abstract

Carbon-focused climate mitigation strategies are becoming increasingly important in forests. However, with ongoing biodiversity declines we require better knowledge of how much such strategies account for biodiversity. We particularly lack information across multiple trophic levels and on established forests, where the interplay between carbon stocks, stand age, and tree diversity might influence carbon–biodiversity relationships. Using a large dataset (>4600 heterotrophic species of 23 taxonomic groups) from secondary, subtropical forests, we tested how multitrophic diversity and diversity within trophic groups relate to aboveground, belowground, and total carbon stocks at different levels of tree species richness and stand age. Our study revealed that aboveground carbon, the key component of climate-based management, was largely unrelated to multitrophic diversity. By contrast, total carbon stocks—that is, including belowground carbon—emerged as a significant predictor of multitrophic

diversity. Relationships were nonlinear and strongest for lower trophic levels, but nonsignificant for higher trophic level diversity. Tree species richness and stand age moderated these relationships, suggesting long-term regeneration of forests may be particularly effective in reconciling carbon and biodiversity targets. Our findings highlight that biodiversity benefits of climate-oriented management need to be evaluated carefully, and only maximizing aboveground carbon may fail to account for biodiversity conservation requirements.

KEYWORDS
BEF-China, carbon sequestration, climate mitigation, forest restoration, species richness, trophic levels

1 | INTRODUCTION

Promoting carbon sequestration and storage in forests plays a crucial role in global efforts to decelerate and mitigate detrimental effects of climate change (Bastin et al., 2019; Waring et al., 2020). While such strategies have gained international scientific and political attention since the adoption of the Kyoto Protocol (IGP Terrestrial Carbon Working Group et al., 1998), their co-benefits for other essential ecosystem properties and services are often not well established (Lewis et al., 2019). In particular, it remains disputed whether carbon-focused management approaches can also support biodiversity conservation (Di Marco et al., 2018).

A key objective for both carbon-mitigation strategies and biodiversity conservation should be the protection of undisturbed primeval and old-growth forests (Watson et al., 2018; Wirth, 2009), but on its own this may not be sufficient due to the limited area covered by these forests (Watson et al., 2018). Afforestation and reforestation measures are therefore at the heart of many current large-scale, carbon-focused policy approaches, but are often based on monoculture plantations (Hua et al., 2022; Lewis et al., 2019). A focus on monoculture plantations may turn out as misdirected when considering their comparatively low potential to safeguard and restore overall biodiversity (Holl & Brancalion, 2020; Hua et al., 2022; Lewis et al., 2019).

Alternative options, such as natural regeneration of secondary forests, may be more effective for both on-site carbon storage (Chazdon et al., 2016; Feng et al., 2022) and biodiversity conservation (Edwards et al., 2014). However, previous studies found mixed support for positive relationships between carbon storage and biodiversity (e.g., Buotte et al., 2020; Ferreira et al., 2018; Jung et al., 2021; Lecina-Diaz et al., 2018; Lennox et al., 2018; Matos et al., 2020; Sabatini et al., 2019; Soto-Navarro et al., 2020). General conclusions are difficult in particular because biodiversity assessments in most studies relied on only one or few selected taxa (often plants or selected vertebrates; Di Marco et al., 2018; Ferreira et al., 2018; Lecina-Diaz et al., 2018; Matos et al., 2020). Recent research has especially emphasized the important role of tree species richness as a driver of carbon sequestration and storage (Feng et al., 2022; Huang et al., 2018; Liu et al., 2018; Poorter et al., 2015), but whether overall

biodiversity—and especially the enormous diversity of heterotrophic organisms (such as arthropods) associated with trees—responds positively to increased carbon storage of forests is less clear (Di Marco et al., 2018). This question is highly relevant in light of the increasing loss of biodiversity in forests (Dirzo et al., 2014; Seibold et al., 2019) and the dependence of human well-being on biodiversity (Cardinale et al., 2012). Diversity patterns across organism groups can be highly variable and overall biodiversity may not be adequately represented by individual taxa (Schuldt et al., 2015), but biodiversity across multiple trophic levels may be decisive in regulating ecosystem functionality (Albert et al., 2022; Lefcheck et al., 2015; Schuldt et al., 2018; Yuan et al., 2020).

Another potential shortcoming of carbon–biodiversity analyses is that they have often only considered carbon stored in aboveground biomass (Keith et al., 2021). However, belowground carbon stocks in roots and soil can be large (Liu et al., 2018; Scholten et al., 2017) and provide an important resource for belowground organisms, showing dynamics that are not necessarily reflected by aboveground carbon stocks (Mayer et al., 2020). Furthermore, many other forest organisms are strongly associated with deadwood (Stokland et al., 2012; Ulyshen, 2018). This means that although carbon in such necromass often makes up a smaller fraction of the total carbon stored in forests (Liu et al., 2018), it still may have a disproportionate effect on biodiversity. Taking into account carbon from multiple forest compartments and total carbon stocks may therefore enable a better understanding of whether and how management strategies focused on rebuilding carbon stocks benefit biodiversity conservation.

When expanding the scope to total forest carbon, restoration and preservation of established forests become particularly important. This is because these forests have accumulated and maintained substantial belowground and forest-floor carbon stocks that may be depleted in afforestation and plantations (Mayer et al., 2020; Waring et al., 2020; Wirth, 2009). Relationships between carbon and overall biodiversity in such forests may strongly depend on tree species richness and time since restoration (as reflected in stand age). Tree species richness generally increases carbon storage (Feng et al., 2022; Huang et al., 2018; Liu et al., 2018; Poorter et al., 2015) and provides complementary resources that increase the diversity of associated, heterotrophic forest biota (Cardinale et al., 2012;

Schuldt et al., 2019). At the same time, carbon accumulation and biodiversity can also increase with forest age (Heinrich et al., 2023; Poorter et al., 2021). Therefore, tree species richness and stand age may be key drivers of the relationships between carbon and overall biodiversity, but these interdependencies have not been studied in detail so far.

Here, we use a large dataset from a secondary, subtropical forest to analyze how biodiversity across a wide range of aboveground and belowground animal and microbial taxa relates to major carbon stocks across combined gradients of tree species richness and stand age. Specifically, we aimed at identifying the influence of forest carbon stocks, tree species richness, and stand age on the biodiversity of heterotrophs (i.e., heterotrophic diversity), and particularly on the diversity across multiple trophic groups (i.e., multidiversity) from bacteria, mycorrhiza, and other fungi to decomposers, herbivores, and predators. Our analyses are based on the assessment of 23 taxonomic groups with more than 4600 species, combined with extensive quantification of aboveground, forest-floor, and belowground carbon stocks, studied in 25 study plots in southeast China. Plot selection follows a comparative study design, that is, these plots were deliberately selected to represent large gradients in tree species richness and stand age (Baruffol et al., 2013; Bruelheide et al., 2011; Imbens & Rubin, 2015; Liu et al., 2018). Insights from low-latitudinal forests are particularly relevant in this context because these forests are hotspots of biodiversity and at the same time feature a high carbon sequestration and storage potential (Feng et al., 2022; Zhu et al., 2021).

We addressed the following hypotheses: (i) Relationships between carbon stocks and heterotrophic diversity are stronger when not exclusively considering tree aboveground carbon, but also the contribution of deadwood and belowground root and soil organic carbon to overall carbon stocks. (ii) Such carbon–biodiversity relationships are strongly determined by the effects of tree species richness and stand age on both carbon and the diversity of heterotrophic organisms. (iii) Carbon–biodiversity relationships depend on the trophic groups examined: primary consumers or mycorrhizal fungi with direct trophic links to plants and plant biomass show stronger associations with tree and soil carbon stocks than higher trophic levels such as predators and parasitoids. Our results help to better evaluate the role of carbon storage optimization for biodiversity conservation in forest restoration.

2 | MATERIALS AND METHODS

2.1 | Study site

Our study was conducted in the Gutianshan National Nature Reserve (29°140′ N; 118°070′ E) in Zhejiang Province, southeast China. The climate is subtropical with a mean annual temperature of 15.3°C and a mean annual precipitation of 2000mm (Hu & Yu, 2008). The reserve is located in a mountainous area, has a size of around 80km², and is representative of Chinese mixed broadleaved forest with a

strong dominance of evergreen species (such as *Schima superba* and *Castanopsis eyrei*; Bruelheide et al., 2011). More than 1400 vascular plant species, of which around 260 are woody, have been recorded in the reserve (Lou & Jin, 2000). The reserve was initially protected in 1975 as a National Forest Reserve and was designated a National Nature Reserve in 2001 (Bruelheide et al., 2011). Forests are largely secondary, resulting from extensive deforestation in the 1950s. No forest management took place in the selected plots since the beginning of the 1990s (Bruelheide et al., 2011).

We initially established 27 study plots (30×30m) in 2008 (see map in Figure S1), of which two had to be excluded from our analyses due to the unintended harvesting of some trees, which precluded a comparison of carbon stocks with all other plots. Plots were selected randomly from suitable areas (excluding slopes >60° and inaccessible terrain) of the nature reserve, but under the constraint that the selected plots captured the gradients in tree species richness (3–20 species >10cm diameter at breast height (dbh)) and stand age (22–116years; mean age determined as the age of the fifth-largest tree in a plot (see Bruelheide et al., 2011) was 70.3years±24.7 SD) typical of the reserve. That is, we adopted a comparative study design based on stratified randomization that deliberately selected plots along predefined gradients and therefore allows for better detection of causal relationships than completely randomized sample surveys (Baruffol et al., 2013; Bruelheide et al., 2011; Imbens & Rubin, 2015; Liu et al., 2018). Previous studies at our study site have shed light on biodiversity patterns among taxa and on tree species richness–carbon relationships, showing the general importance but also nonlinearities in the effects of tree diversity on both carbon and the diversity of forest biota (Liu et al., 2018; Schuldt et al., 2015). However, relationships between carbon and overall biodiversity and their dependence on tree species richness and stand age remain unresolved.

2.2 | Biodiversity data

We used tree species richness and woody plant diversity as key predictors of heterotrophic biodiversity and carbon stocks (Schuldt et al., 2023). Woody plant diversity was completely inventoried in 2008 and quantified as the number of tree and shrub species >1m height per plot. Note that this is different from the design variable tree species richness in our comparative study, because stratification of plots along the richness gradient was based on the richness of only canopy trees (all trees ≥10cm dbh). We assumed that ecosystem functions including productivity and carbon stocks are primarily affected by canopy trees (which was indeed the case; see Baruffol et al., 2013; Liu et al., 2018), while biodiversity of heterotrophs might additionally be influenced by the resource diversity provided by woody plant diversity (i.e., including shrub species; Schuldt et al., 2015). Woody plant diversity and tree species richness were only weakly correlated with each other (despite the fact that woody plant diversity also included all canopy trees ≥10cm dbh; Pearson's $r = .39$, $p = .055$; Table S1).

We assessed heterotrophic biodiversity for seven groups of organisms that aggregated data for a total of 23 higher-level taxa of aboveground arthropods, soil fungi, and bacteria. We defined taxa by the lowest taxonomic rank or group level that consistently reflected a common trophic level of the constituent species, that is, order level for most arthropods, and functional group (mycorrhiza, saprotrophic, and pathogenic) for fungi. Bacteria could only be analyzed at the phylum level. The 23 taxa were then grouped into (1) arthropod parasitoids (parasitic wasps) and predators (spiders, ants, predatory wasps, and centipedes), (2) herbivores (lepidopteran larvae, weevils, longhorn beetles, and bark beetles), and (3) decomposers (isopods and diplopods), as well as (4) mycorrhizal fungi (arbuscular and ectomycorrhizae), (5) saprotrophic fungi, (6) pathogenic fungi, and (7) bacteria (eight phyla: Acidobacteria, Actinobacteria, Alphaproteobacteria, Bacteroidetes, Betaproteobacteria, Chloroflexi, Deltaproteobacteria, and Gammaproteobacteria).

Sampling of heterotrophs was conducted between 2008 and 2012 with a set of methods that cover the wide range of habitat use and activity patterns of arthropods and microorganisms and that were best suited to assess the focal taxa. Specifically, we used flight interception traps to sample herbivorous longhorn and bark beetles as well as canopy ants (four traps per plot with crossed Plexiglas panels of 50×30 cm, in the corners of the central 10×10 m of each plot, active and emptied monthly between May and August 2010; Schuldt et al., 2015), branch beating to collect predatory spiders and ants as well as herbivorous lepidopteran larvae (25 saplings per plot (mean height 1.77 m ± 0.48 SD) sampled every 2 m along a transect running diagonally through each plot, using a 70 cm diameter beating tray, in September 2011, April 2012, and June 2012; Schuldt et al., 2014), pitfall traps for predatory epigeic spiders, ants, centipedes, herbivorous weevils, and macrofaunal decomposers (isopods and diplopods; four plastic cups of 550 mL and an opening diameter of 8.5 cm in the corners of the central 10 m x 10 m of each plot emptied bi-monthly between March and September 2009; Schuldt et al., 2011), and reed-filled trap nests to sample cavity-nesting predatory wasps and their parasitic wasps (two traps per plot each consisting of four reed-filled plastic tubes of 22×12.5 cm, fixed to a wooden pole of 1.5 m height, running from September 2011 to October 2012, where internodes containing nests were exchanged monthly and reared in glass test tubes until eclosion; Staab et al., 2016). Ants were additionally sampled with bait traps (36 bait platforms per plot consisting of plastic dishes of 5 cm diameter and 1 cm height, fixed both at ground level and at breast height on small trees and baited with both honey water and canned fish, with ants sampled after 180 min in May 2012; Schuldt & Staab, 2015). We included the parasitoids in the predator category for our analyses (termed "arthropod predators" in the following for simplicity), because the parasitoids sampled can only be considered to be a relatively specialized subset of overall parasitoid diversity in the study plots (Staab et al., 2016). All arthropods were identified to species or morphospecies. Further information is provided in Schuldt et al. (2015, 2018).

Soil fungi and bacteria were identified from sieved and freeze-dried soil cores (eight cores of 10 cm diameter from the upper 10 cm of soil per plot, taken in September 2012 and pooled per plot as a composite sample; see Schuldt et al., 2015). After extraction of fungal and bacterial DNA (MoBio soil DNA extraction kit) from 1 g of each composite sample, we used the primer pairs ITS1F48 (5′-CTTGGTCATTTAGAGGAAGTAA-3′) and ITS4 (5′-TCCTCCGC TTATTGATATGC-3′) to amplify the fungal internal transcribed spacer (ITS) rRNA region, and the primer pairs BAC341F (5′-CCTACGGGAGGCAGCAG-3′) and BAC 907R (5′-CCGTCAATTCM TTTGAGTTT-3′) to amplify the V3–V5 region of the bacterial 16S rRNA gene. Pyrotag amplicon sequencing of fungal ITS and bacterial 16S rRNA genes was conducted using custom fusion primers. An equimolar mixture of each library was subjected to unidirectional pyrosequencing from the 907R and ITS4 ends of the amplicons, using a 454 Titanium amplicon sequencing kit and a Genome Sequencer FLXþ 454 System (454 Life Sciences/Roche Applied Biosystems). Sequences were quality-filtered and normalized to 10,000 fungal ITS and 20,000 bacterial 16S rDNA reads per plot using MOTHUR (Schloss et al., 2009). Sequences were clustered into species-level operational taxonomic units (OTUs) with CD-HIT-EST using a 97% pairwise similarity threshold (Wubet et al., 2012). Bacterial 16S OTU sequences were assigned taxonomy against the Silva SSU reference database and fungal ITS OTU sequences against the UNITE database (Tedersoo et al., 2014). Further information is provided in Schuldt et al. (2015). Fungal reference sequences were assigned to functional groups (arbuscular and ectomycorrhizae, saprophytes, and pathogens) on the basis of sequence similarity using the default parameters of the GAST algorithm against the functional reference dataset (Huse et al., 2008; Tedersoo et al., 2014).

2.3 | Carbon stocks and abiotic plot conditions

Carbon stocks were quantified for aboveground, forest-floor, and belowground carbon in Mg C ha^{-1}. Total carbon was quantified as the sum of these three components. Aboveground carbon comprised carbon in the live biomass of trees (estimated based on stem diameters and allometric equations for all trees >3 cm diameter at breast height) and herbs (based on harvested herb-layer biomass in four 1 m^2 quadrats at the corners of the central 10×10 m subplot per plot in 2008). Forest-floor carbon included deadwood (lying and standing coarse woody debris >10 cm diameter and fine woody debris from 3 to 10 cm diameter, inventoried across the full area of all plots in 2009) and leaf litter (based on four 19 cm diameter sample cores from undisturbed litter patches per plot taken in 2009 and 2010). Belowground carbon included soil organic C (measured with a Vario EL III Elemental Analyzer from nine soil cores (with a diameter of 3 cm and a depth of 50 cm) per plot taken in 2008) and roots biomass C (calculated with allometric equations for coarse roots ≥2 mm diameter, fine roots <2 mm, and herb roots). Carbon stocks were converted from biomass assuming a 46% C fraction in aboveground biomass, 45%

in deadwood, and 44% in roots (Wu et al., 2017; Zeng et al., 2013; Zhang et al., 2010). Full details on measurements and estimation methods for all carbon components are provided in Liu et al. (2018).

To characterize the abiotic conditions of the study plots, we used elevation, slope, northness, soil pH, and annual temperature of each plot. Elevation (m above sea level), slope (°), and northness (exposure of the plots as the cosine of geographic aspect) were measured during plot establishment. Soil pH was measured potentiometrically in H_2O suspension from nine pooled soil cores (0–10 cm) per plot in summer 2009. Mean annual temperature data were obtained from continuous HOBO data logger measurements (30-minute time interval) between June 2011 and June 2012.

2.4 | Statistical analyses

To be able to aggregate species richness in an unbiased way within and across trophic groups, we standardized the data per taxon and calculated multidiversity indices (Allan et al., 2014; Schuldt et al., 2018). This was done because raw species richness differed widely in magnitude across taxa, depending on the sampling method and overall diversity per taxon. Standardization was achieved by scaling observed values per plot to the maximum observed value across all plots per taxon. We then used average values across taxa to aggregate data to seven trophic groups (arthropod predators, arthropod herbivores, macrofaunal decomposers, mycorrhizae, saprotrophic fungi, pathogenic fungi, and bacteria) and to aboveground (averaged across the three aboveground trophic groups), belowground (averaged across the four belowground trophic groups), and total (averaged across all seven trophic groups) multidiversity. Forest-floor, belowground, and total carbon stocks were log-transformed in all analyses to meet assumptions of normality and homoscedasticity (as inferred from residual regression plots). Using untransformed data qualitatively yielded the same results (i.e., consistent positive, neutral, or negative effects with both untransformed and transformed values).

We tested carbon–biodiversity relationships by first checking for correlations between heterotrophic diversity and carbon stocks. For this purpose, we fitted linear regressions of the diversity of each trophic group and of aggregated multidiversity across trophic groups with each carbon stock component. We extracted standardized regression coefficients and their 95% confidence intervals as measures of effect sizes. We adjusted p-values for multiple testing using the Benjamini–Hochberg method to control for false discovery rate. We also ran alternative models for overall and belowground multidiversity that excluded bacteria from the multidiversity index, to test whether our inability to classify bacterial phyla into functional groups affected the correlation strength.

Moreover, we used path modeling to disentangle the pathways via which these predictors influence multidiversity, because carbon stocks, tree species richness, and stand age were correlated to some extent and we were interested in the role that the latter two play in mediating the relationships between carbon and the diversity of

heterotrophs (Table S1). We ran one path model each for overall multidiversity, aboveground multidiversity, and belowground multidiversity. The initial models included total carbon stocks, tree species richness, stand age, and woody plant diversity (as an additional plant diversity metric that might have a strong influence on the diversity of heterotrophs) as predictors (Figure S2). We additionally ran alternative models for overall multidiversity where total carbon was replaced by either aboveground carbon (as the most commonly used carbon stock in carbon–biodiversity studies) or belowground carbon. To control for potential effects of abiotic conditions of the study plots on carbon–biodiversity relationships, we added the abiotic plot conditions as further moderators of carbon stocks in all models. As predictors, we used the first two principal components from a principal components analysis (PCA) on elevation, slope, northness, soil pH, and annual temperature. These two principal components explained 65% in the variation of the abiotic variables (Table S2).

For all path models, we expected carbon stocks to be affected by tree species richness (as shown by Liu et al., 2018) and stand age (increasing plant biomass with succession: stand age was strongly correlated with tree basal area of the study plots (see Baruffol et al., 2013 for details on basal area measurements; Pearson correlation $r = .87$; $p < .001$), and multidiversity to be influenced by tree species richness, stand age (Poorter et al., 2021), woody plant diversity (Schuldt et al., 2015), and carbon stocks (Srivastava & Lawton, 1998). We additionally included the covariances between the two design variables of the comparative study design, tree species richness, and stand age, and between tree species richness and woody plant diversity. We also tested alternative models in which the path from carbon to multidiversity was replaced by a covariance structure (testing whether carbon–biodiversity relationships were better modeled by a causal path from carbon to multidiversity or as a nondirectional covariance).

All predictors were scaled to mean = 0 and standard deviation = 1 to allow for a direct comparison of path coefficients. We sequentially dropped noninformative pathways based on the resulting reduction in AICc of the path models. The final models were those with the lowest AICc and needed to include 0 in the 95% confidence interval of the root mean square error approximation. Robustness of the results was assessed by calculating bootstrapped p-values (1000 bootstrap draws). We calculated absolute effect sizes of the predictors in the path models as the product of standardized path coefficients connecting each predictor with multidiversity.

All analyses were conducted in R version 4.0.3 (www.r-project.org), and path models were calculated with the R package *lavaan* (Rosseel, 2012).

3 | RESULTS

Biodiversity data were based on 715 (mean 139 ± 12 SD per plot) species of aboveground arthropods, 1658 (mean 335 ± 33 SD per plot) fungal OTUs, and 3067 (mean 1468 ± 86 SD per plot) bacterial OTUs. The mean total carbon stock across the 25 study plots was 149.2

(±60.6 SD) Mg C ha^{-1}, of which aboveground carbon (tree biomass) accounted for 38.5% (57.5±27.6 Mg C ha^{-1}), forest-floor carbon (dead wood and leaf litter) for 7.4% (11.1±7.4 Mg C ha^{-1}), and belowground carbon for 54% (80.7±39.3 Mg C ha^{-1}). Tree species richness varied from 3 to 20 and woody plant diversity from 25 to 69 species per plot.

The biodiversity of heterotrophic organisms showed variable relationships with forest carbon stocks, but when statistically significant, these relationships were always positive (Figure 1; Table S1). In general, biodiversity of only few of the examined trophic groups (arthropod herbivores, saprotrophic fungi, and mycorrhizal fungi) showed a strong association with aboveground and forest-floor carbon, of which only the relationship between saprotrophic fungi and aboveground carbon remained significant after adjusting for multiple testing (Figure 1a,b). Carbon–biodiversity associations were stronger for (log-transformed) belowground carbon, with particularly strong relationships in macrofaunal decomposers, mycorrhizal fungi, and saprotrophic fungi (Figure 1c). Heterotrophic diversity—again particularly the diversity of lower trophic levels such as arthropod herbivores, macrofaunal decomposers, as well as saprotrophic and mycorrhizal fungi—showed the strongest relationships with (log-transformed) carbon stocks pooled across all forest compartments (Figure 1d). By contrast, bacteria, pathogenic fungi, and aboveground arthropod predators generally showed weak associations with carbon stocks, irrespective of whether carbon from individual forest compartments or overall carbon was considered. This lack of effect also applied when the eight bacterial phyla were tested individually (Table S3). When heterotrophic diversity was averaged across trophic groups (i.e., multidiversity), belowground multidiversity showed positive relationships with carbon stocks from all compartments, with particularly strong relationships to belowground and total carbon (Figure 1). Multidiversity averaged over aboveground trophic groups and over all examined taxa was

particularly related to (log-transformed) belowground and total carbon, but not to aboveground or forest-floor carbon. Relationships between carbon stocks and belowground or overall multidiversity were very similar and remained qualitatively unchanged when bacteria were excluded from the multidiversity indices (Table S3).

Path models revealed the ways in which carbon stocks were associated with different components of biodiversity. Total carbon increased multidiversity in similar ways for overall, above- and belowground biodiversity (Figure 2a; Figure S3). Total carbon stocks, in turn, were strongly driven by tree species richness and stand age, both of which affected multidiversity only indirectly via total carbon. In addition, multidiversity was directly related to woody plant diversity (comprising all trees and shrubs ≥1 m height), independent of tree species richness and stand age. Results for the path model using belowground carbon stocks were similar, with the exception that stand age acted directly, rather than via carbon stocks, on multidiversity (Figure 2c). By contrast, carbon stocks were unrelated to multidiversity when only aboveground carbon stocks were taken into account (Figures 1 and 2b). Rather, stand age and woody plant diversity directly increased multidiversity, with a particularly strong effect size for stand age (inset diagram Figure 2b). Abiotic plots conditions did not affect the carbon–biodiversity relationships and were not retained in any of the path models. Path models fitting the relationship between multidiversity and carbon stocks as a covariance rather than a direct path were statistically inferior in all cases (Tables S4–S8).

4 | DISCUSSION

Our study demonstrates that while the biodiversity of heterotrophic organisms can show strong positive associations with tree and soil organic carbon stocks in species-rich subtropical,
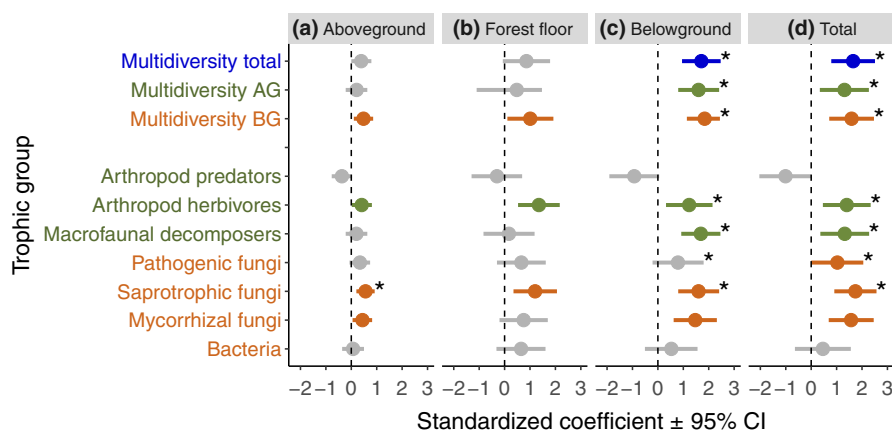

FIGURE 1 Effect sizes of the relationships of biodiversity of seven aboveground (green) and belowground (brown) trophic groups as well as average multidiversity measures across all trophic groups with carbon stocks in different forest compartments: (a) aboveground carbon (plant biomass), (b) forest-floor carbon (dead wood and leaf litter), (c) belowground carbon (soil organic and root carbon), and (d) overall carbon stocks (pooled across forest compartments) in 25 secondary forest plots selected to represent gradients of tree species richness and stand age. Data points (with 95% confidence intervals) are standardized coefficients from regressions of biodiversity over carbon. Grey colors indicate estimates and confidence intervals overlapping with zero (dashed lines), and colored data points and confidence intervals do not overlap with zero. Asterisks indicate significant relationships after adjusting p-values for multiple testing. See Table S3 for full data. Note that total C and belowground C were log-transformed to ensure normal and homoscedastic data distributions.
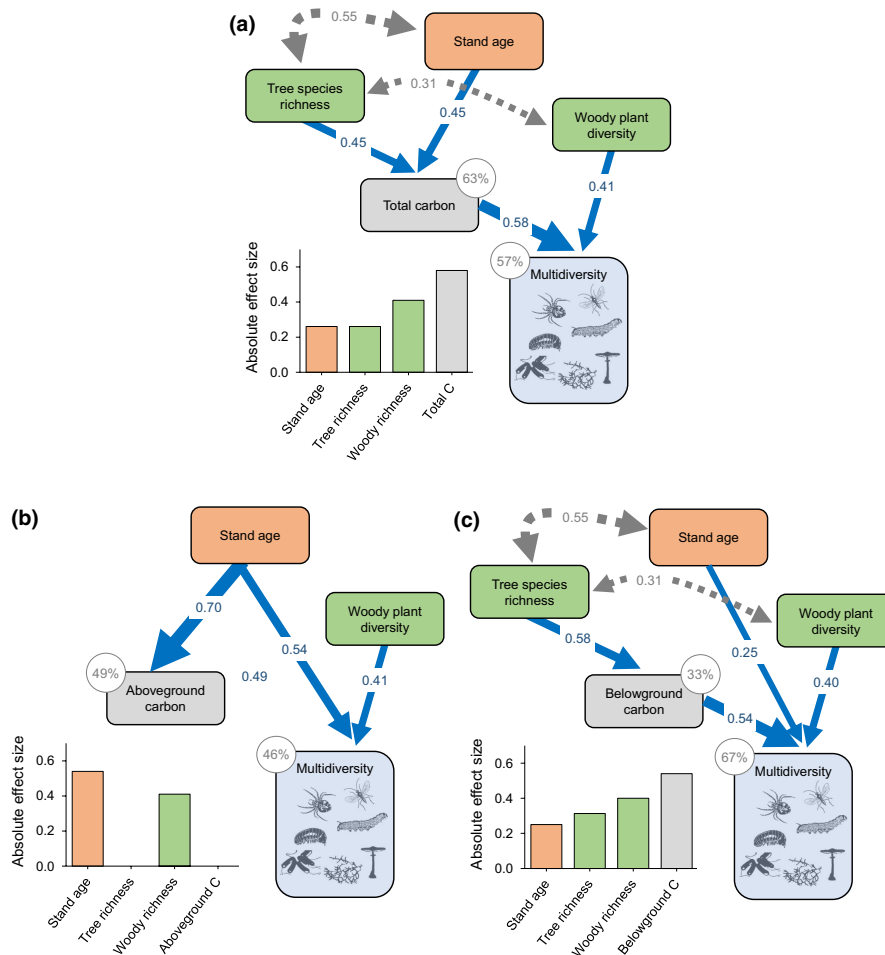
FIGURE 2 Path models showing the direct and indirect effects of tree species richness (green), stand age (orange), woody plant diversity (green; all trees and shrubs ≥1 m height), and carbon stocks (grey) on overall multidiversity for (a) total carbon stocks ($\chi^2 = 3.8$, df = 4, $p = .470$), (b) aboveground carbon stocks ($\chi^2 = 1.2$, df = 3, $p = .764$), and (c) belowground carbon stocks ($\chi^2 = 3.9$, df = 4, $p = .408$) in 25 secondary forest plots selected to represent gradients of tree species richness and stand age. Arrows show significant relationships ($p \leq .05$ based on 1000 bootstrap draws) and are scaled by their standardized effects (plotted on top of the arrows). Percentage values are explained variance of dependent variables. Blue arrows show expected causal relationships, and grey dashed lines are covariances. Full model results are shown in Tables S4–S8. Inset diagrams show the summed effects of the predictor variables based on the standardized path coefficients (absolute effect sizes calculated by summing up the product of standardized path coefficients for each pathway connecting a given predictor with multidiversity). Note that total C and belowground C were log-transformed to ensure normal and homoscedastic data distributions.

secondary forests, these relationships depend on the carbon stock components and trophic levels considered. Associations were strongest for total carbon stocks—that is, including the contribution of belowground carbon—whereas heterotrophic diversity was more weakly related to tree aboveground carbon stocks, the key carbon component in climate-based forest management strategies and in many previous analyses on carbon–biodiversity relationships (Keith et al., 2021; Vargas et al., 2014). Stand age and tree species richness emerged as important moderators of these relationships. Moreover, our findings for a wide range of above- and belowground trophic groups from multiple trophic levels indicate that studies of single trophic groups (single-taxon studies) might underestimate the complexity of carbon–biodiversity relationships. Our results thus highlight several important issues that need to be taken into account when aiming at biodiversity-friendly climate mitigation strategies in forests.

4.1 | Total carbon, not aboveground carbon, predicts biodiversity

Our findings suggest that the strong focus on aboveground carbon in many climate mitigation strategies (Giebink et al., 2022) might fail to adequately account for overall biodiversity in local-scale reforestation and restoration approaches in species-rich forests. Only few of the diversity metrics showed a notable relationship with aboveground carbon stocks. Such a lack of relationships has also been found in other established forest ecosystems at similar spatial scales, especially when looking at biodiversity across multiple taxa (Beaudrot et al., 2016; Sabatini et al., 2019; Sullivan et al., 2017). We note that our analyses deliberately included tree diversity as a predictor rather than as part of the response variables and that previous studies have found positive relationships between tree diversity and aboveground carbon stocks (Liu et al., 2018; Poorter et al., 2015). However, our study highlights

that these positive relationships do not necessarily apply to the enormous diversity of heterotrophic organisms, a discrepancy that can be explained by the fact that heterotrophic diversity does not always scale linearly with tree diversity (Schuldt et al., 2015). Aboveground carbon stocks might capture biodiversity patterns of heterotrophs more consistently in afforestation and regeneration after agricultural land use, where the rapid build-up of aboveground tree biomass in comparison with former land use can have a particularly strong impact on resource availability (Deere et al., 2018; Gilroy et al., 2014).

By contrast, belowground carbon emerged as a particularly important carbon source in capturing biodiversity patterns and in determining the overall relationship between total carbon stocks and heterotrophic diversity. Positive relationships were to be expected for belowground microorganisms given their essential dependence on belowground carbon inputs (Nielsen et al., 2011). However, also aboveground organisms and their diversity can show pronounced associations with belowground carbon. For example, brown food webs connect belowground microorganisms and decomposers—and therefore belowground carbon pools—to aboveground trophic groups (Bardgett & Wardle, 2010) and link aboveground biodiversity of heterotrophs to belowground nutrient cycling (Metcalfe et al., 2014; Schmitz & Leroux, 2020; Sobral et al., 2017).

Our results suggest that incorporating belowground carbon into the estimation of total carbon stocks may better capture the heterogeneity in quality and quantity of carbon resources for heterotrophic organisms, or the time and extent of undisturbed forest growth, as both above- and belowground carbon accumulate under such conditions (Mayer et al., 2020; Poorter et al., 2021). Forest biota have been shown to increase over decades in diversity in regenerating forests (Bruelheide et al., 2011; Poorter et al., 2021), with overall biodiversity thus following a similar trajectory with time as carbon stocks. Carbon stocks might reflect community recovery and lack of disturbance better than stand age because they may also be related to the severity of previous forest disturbances (Mayer et al., 2020), which is not taken into account when only time since disturbance is considered.

These findings highlight that accounting for belowground and total carbon stocks may help to improve both climate-focused forest management strategies (Vargas et al., 2014) and compatibility of such climate-focused strategies with biodiversity conservation. We note, however, that relationships of belowground and total carbon with biodiversity in our study were based on log-transformed carbon data. This means that the positive relationship with biodiversity becomes weaker at higher carbon stocks and that highly biodiverse forests are not necessarily characterized by highest total carbon stocks (Ferreira et al., 2018). Our findings caution against using carbon stocks as a simple proxy for overall biodiversity in such longer-established, species-rich forests.

4.2 | Carbon–biodiversity relationships moderated by stand age and tree diversity

Factors beyond the simple accumulation of tree biomass may play an important role in mediating carbon–biodiversity relationships in longer-established forests. The effects of tree diversity and stand age in the path models point to a key influence of the diversity of resources (Heidrich et al., 2020). In case of the aboveground path model, our results suggest independent co-variation between carbon and the biodiversity of heterotrophs due to the positive effects of stand age on both carbon and heterotrophic biodiversity (Liu et al., 2018; Poorter et al., 2015). In this context, the direct effect of woody plant diversity—a key driver of resource diversity and habitat heterogeneity for many heterotrophic organisms (Ampoorter et al., 2020)—on multitrophic diversity is important. This finding indicates that additional effects of resource diversity (via young trees and shrubs) that go beyond the resources provided by canopy trees (and that are therefore not captured by aboveground carbon stocks) may be a more important driver of aboveground biodiversity. Also when considering belowground and total carbon, the effects of tree species richness and stand age on both carbon stocks and heterotrophic diversity suggest that resource diversity and the extent of undisturbed forest growth—as represented by tree species richness and stand age—strongly determine the relationships between carbon and the biodiversity of heterotrophs. That is, changes in tree species richness and stand age can be expected to change carbon stocks and heterotrophic diversity, and therefore the strength of the relationship between the latter two.

These findings underline that combined carbon–biodiversity strategies ignoring tree species richness, stand age and woody plant diversity, and instead focusing on fast-growing monocultures to maximize carbon sequestration (Lewis et al., 2019), are poor options for forest restoration and afforestation in terms of biodiversity conservation.

In this context, it is interesting to note that forest-floor carbon, which is primarily composed of deadwood carbon, was only related to the biodiversity of few trophic groups. This was particularly the case for arthropod herbivore diversity (but note this relationship was not statistically significant after adjusting for multiple testing)—which included primary consumers that feed on constitutionally weakened or freshly dead trees, such as many bark beetles and longhorn beetles—whereas relationships with decomposers and microorganisms were weaker or lacking. Deadwood plays an important role as a resource for saproxylic forest organisms (Stokland et al., 2012), but the amount of deadwood reflected by forest-floor carbon stocks apparently only weakly influenced the overall patterns of heterotrophic diversity in our study system. Previous studies have shown that the composition and diversity (e.g., in terms of chemical composition and physical attributes) of deadwood are key drivers of deadwood-associated biodiversity (Stokland et al., 2012), but these deadwood diversity features have not been included here.

This shortcoming in the case of deadwood and our findings of tree species richness and stand age as key moderators point to a general and potentially problematic issue of carbon–biodiversity relationships: a simple quantification of carbon stocks ignores the qualitative characteristics of these stocks that might be important drivers of the biodiversity of heterotrophic organisms and that are based on the heterogeneity of abiotic and biotic ecosystem

characteristics (e.g., Aponte et al., 2020; Liu et al., 2018; Poorter et al., 2015). As outlined previously, an important role of resource diversity determining how carbon stocks relate to the biodiversity of heterotrophs is suggested in our study by the dependence of carbon stocks, and therefore indirectly of the biodiversity of heterotrophs, on tree species richness. Our results are in line with previous findings showing that high tree species richness is not just a side-effect, but an important driver of forest carbon stocks (Díaz et al., 2009; Liu et al., 2018; Poorter et al., 2015).

4.3 | Associations with forest carbon stocks depend on trophic level

Tree species richness has been used by many studies as a proxy for overall biodiversity in carbon–biodiversity studies (e.g., Ferreira et al., 2018; Matos et al., 2020; Poorter et al., 2015). However, tree species richness is not necessarily a consistent and linear predictor of overall biodiversity in such species-rich forests (Schuldt et al., 2015). Our results across a much wider range of organism groups than often examined in carbon–biodiversity studies show that the strength and direction of the relationships between carbon and biodiversity depend on the trophic groups considered (see also Di Marco et al., 2018). The most consistent and positive relationships were evident for primary consumers and other groups closely associated with woody plants via trophic interactions (e.g., arthropod herbivores and mycorrhizae). For these taxa, the above-discussed resource availability that can covary with carbon stocks may be particularly relevant.

Higher trophic levels, such as arthropod predators/parasitoids and bacteria (the latter of which can play an important role in top-down control of multitrophic communities; Schuldt et al., 2017), showed weak or no relationships with carbon stocks. This finding probably reflects that plant-derived carbon resources are only of indirect relevance in the trophic ecology of higher trophic levels (Balvanera et al., 2006). For bacteria, the results might additionally indicate the difficulty of adequately capturing overall biodiversity at a specific spatial scale, as diversity patterns of these microorganisms vary particularly strongly at finer, subplot-level scales (Schuldt et al., 2015). A recent study showed that in grasslands fine-scale patterns of aboveground plant biomass can be related to microbial diversity, although the strength of the relationship depended on the ecosystems' primary productivity and was weak in more productive environments (Cavender-Bares et al., 2022). We were unable to classify bacteria into trophic groups, which further limits the interpretation of the bacterial results with respect to specific functional relationships. However, previous studies have emphasized the general importance of overall bacterial diversity in mediating ecosystem functions (Wagg et al., 2019), warranting the inclusion of bacterial phyla in our analyses. Importantly, inclusion or exclusion of bacteria in the calculation of multidiversity, and therefore the coarse resolution of the bacterial dataset, did not alter any of our results. The trophic group-dependent outcomes of our analyses indicate that

carbon–biodiversity relationships need to be interpreted with care—even if overall multidiversity is positively related to carbon stocks. Our measure of multidiversity averages diversity patterns across organism groups and therefore provides an estimate of the relationships that can typically be expected, whereas our analysis of individual organism groups and trophic levels shows the variability around this expectation. Our results suggest that the diversity of important groups of organisms, in our case particularly those at higher trophic levels, might not necessarily be captured in an adequate way by any form of carbon-focused management approaches.

We note that our large datasets on biodiversity and carbon stocks were assembled from measurements conducted over multiple years. However, we expect that this did not strongly influence our analyses and conclusions. For one, we considered stocks of carbon stored in tree biomass and soils, which should show little variation in consecutive years in longer-established forests (Yang et al., 2020). Moreover, while population sizes of individual species might vary across years, our biodiversity metrics are deliberately based on presence-absence data that are—especially in combination with the extensive sampling we conducted—less affected by population fluctuations and species turnover than metrics requiring more information than the pure number of species (Magurran & McGill, 2011).

5 | CONCLUSIONS

Our study—based on the assessment of biodiversity over multiple trophic groups and an extensive quantification of total carbon stocks—highlights that carbon–biodiversity relationships, and therefore the assumption that climate-oriented forest management strategies co-benefit overall biodiversity, need to be handled with care. The lack of strong associations between the biodiversity of heterotrophic organisms and aboveground carbon suggests that, at least for secondary forests and their consideration in carbon-focused policy approaches, maximizing aboveground carbon stocks can fail to adequately incorporate biodiversity conservation requirements.

Considering total carbon stocks, by accounting for belowground carbon and as a potential indicator of resource-diverse and undisturbed conditions, may help to achieve a more balanced perspective. However, the nonlinearity of the observed carbon–biodiversity relationships and their dependence on spatial scale and taxon groups suggest caution against unreflected usage of such findings. The dependence of these relationships on tree species richness and stand age suggests that restoring forest landscapes to mitigate climate change effects should utilize multispecies rather than monoculture plantations. When the aim is to simultaneously promote overall biodiversity, strategies might be even more effective by promoting long-term regeneration projects, rather than focusing on establishing new forests or short-term agroforestry approaches.

AUTHOR CONTRIBUTIONS

Andreas Schuldt conceived the idea for the manuscript; Andreas Schuldt, Xiaojuan Liu, François Buscot, Helge Bruelheide, Alexandra

Erfmeier, Jin-Sheng He, Alexandra-Maria Klein, Michael Scherer-Lorenzen, Keping Ma, Bernhard Schmid, Thomas Scholten, Zhiyao Tang, Stefan Trogisch, Christian Wirth, Tesfaye Wubet, and Michael Staab initiated and designed the research; Andreas Schuldt, Xiaojuan Liu, François Buscot, Helge Bruelheide, Alexandra Erfmeier, Jin-Sheng He, Alexandra-Maria Klein, Michael Scherer-Lorenzen, Keping Ma, Bernhard Schmid, Thomas Scholten, Zhiyao Tang, Stefan Trogisch, Christian Wirth, Tesfaye Wubet, and Michael Staab collected and/or contributed data; Andreas Schuldt conducted the statistical analyses and wrote the manuscript, with critical input from all coauthors.

CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the Dryad Digital Repository at https://doi.org/10.5061/dryad.83bk3 j9wg.

ORCID

Andreas Schuldt https://orcid.org/0000-0002-8761-0025
Xiaojuan Liu https://orcid.org/0000-0002-9292-4432
François Buscot https://orcid.org/0000-0002-2364-0006
Helge Bruelheide https://orcid.org/0000-0003-3135-0356
Alexandra Erfmeier https://orcid.org/0000-0002-1002-9216
Jin-Sheng He https://orcid.org/0000-0001-5081-3569
Alexandra-Maria Klein https://orcid.org/0000-0003-2139-8575
Keping Ma https://orcid.org/0000-0001-9112-5340
Michael Scherer-Lorenzen https://orcid.org/0000-0001-9566-590X
Bernhard Schmid https://orcid.org/0000-0002-8430-3214
Thomas Scholten https://orcid.org/0000-0002-4875-2602
Zhiyao Tang https://orcid.org/0000-0003-0154-6403
Stefan Trogisch https://orcid.org/0000-0002-1426-1012
Christian Wirth https://orcid.org/0000-0003-2604-8056
Tesfaye Wubet https://orcid.org/0000-0001-8572-4486
Michael Staab https://orcid.org/0000-0003-0894-7576

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SUPPORTING INFORMATION

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