Tree diversity increases carbon stocks and fluxes above- but not belowground in a tropical forest experiment

Running title: Tree diversity increases carbon sequestration

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Keywords: carbon storage, carbon flux, forest biodiversity, ecosystem functioning, tropical planted forest, reforestation, Sardinilla experiment, TreeDivNet

Abstract

International commitments advocate large-scale forest restoration as a nature-based solution to climate change mitigation through carbon (C) sequestration. Mounting evidence suggests that mixed compared to monospecific planted forests may store more C, exhibit lower susceptibility to climate extremes and offer a broader range of ecosystem services. However, experimental studies comprehensively examining the control of tree diversity on multiple C stocks and fluxes above- and belowground are lacking. To address this gap, we leverage data from the Sardinilla experiment in Panama, the oldest tropical tree diversity experiment which features a gradient of one-, two-, three- and five-species mixtures. Over 16 years, we measured multiple above- and belowground C stocks and fluxes, ranging from tree aboveground C, over leaf litter C production, to soil organic carbon (SOC). We show that tree diversity significantly increased aboveground C stocks and fluxes, with a 57% higher gain in aboveground tree C in five-species mixtures compared to monocultures (35.7±1.8 *vs* 22.8±3.4 Mg C ha^{-1}) 16 years after planting. In contrast, we observed a net reduction in SOC (on average -11.2±1.1 Mg C ha^{-1}) and no significant difference in SOC_3 stocks (the tree-derived SOC fraction) between five-species mixtures and monocultures (13.0±0.9 *vs* 15.1±1.3 Mg C ha^{-1}). Positive tree diversity effects persisted despite repeated climate extremes and strengthened over time for aboveground tree growth. Higher tree growth in mixtures enhanced leaf litter and coarse woody debris C fluxes to the soil, resulting in a tightly linked C cycle aboveground. However, the only link between above- and belowground C stocks and fluxes was between leaf litter C inputs and SOC_3 which was positively affected by diversity. Our study elucidates the mechanisms through which higher tree diversity bolsters the climate mitigation potential of tropical forest restoration. Restoration schemes should prioritize mixed over monospecific planted forests.

Introduction

Forest restoration is promoted as a key strategy for mitigating climate change through carbon (C) sequestration. Several global initiatives, such as the Bonn Challenge and the New York Declaration on forests, aim to restore 350 Mha of forests by 2030. Forest restoration, in particular in the tropics, has the most significant climate mitigation potential of 20 proposed nature-based solutions, potentially sequestering up to 10.1 $PgCO_2$ equivalents per year (Griscom et al., 2017). However, massive reforestation efforts should ensure the protection of land for agriculture (Dooley et al., 2022) and avoid the replacement of other ecosystems, such as natural grasslands (Parr et al., 2024; Seddon, 2022). A solution is to target the vast areas of degraded land suited for forest growth (Bauhus et al., 2010). Current reforestation pledges largely focus on monospecific planted forests (Lewis et al., 2019) despite the mounting evidence that tree species-diverse planted forests (hereafter mixed planted forests or mixtures) can exhibit lower susceptibility to stress and disturbances such as droughts and storms while simultaneously providing a broader range of ecosystem services such as C sequestration, biodiversity conservation and cultural services at higher levels than monospecific plantations (Messier et al., 2021). Consequently, mixed planted forests better fulfil current international targets such as the Kunming-Montréal Global Biodiversity Framework (CBD, 2022).

Biodiversity-ecosystem function theory suggests that mixed planted forests may outperform monocultures in terms of productivity, through complementary resource partitioning across species, abiotic facilitation or biotic feedbacks (Barry et al., 2019). Thus, mixed planted forests may also outperform monocultures with respect to their role in climate regulation. Indeed, there is accumulating evidence that mixed planted forests can store more C than their monoculture counterparts (Chen et al., 2023; Lecina-Diaz et al., 2018; Messier et al., 2021; van der Sande et al., 2017; Warner et al., 2023; Xu et al., 2020). More importantly, mixtures may also be more stable than monocultures in the face of climate extremes or climate variability in general (Isbell et al., 2018), as some species may ‘insure’ the community against the reduced functioning of other species (Yachi and Loreau, 1999). Mixed planted forests indeed feature higher temporal stability of biomass

production than monocultures during periods with variable climatic conditions, including particularly wet and dry years (Jucker et al., 2014; Schnabel et al., 2021). However, most existing studies assessed (or indirectly inferred) tree diversity effects on C stocks, fluxes, and stability in terms of aboveground tree C (AGC), with fewer studies examining root C or soil organic C (SOC) (e.g. Xu et al., 2020) and even fewer ones the multiple C fluxes above- and belowground, connecting these C pools.

We posit that tree species richness (hereafter tree diversity) may affect C stocks and fluxes both above- and belowground. C stocks refer to the C stored in reservoirs such as AGC or SOC, whereas C fluxes are the flow of C between these reservoirs over time. We anticipate comparable diversity effects above- and belowground as has been shown in grassland experiments (Ravenek et al., 2014; Weisser et al., 2017). Indeed, there is evidence for significant tree diversity effects on various C fluxes, ranging from enhanced leaf litter (Huang et al., 2017) and coarse woody debris (CWD) production (Liu et al., 2018) to enhanced microbial respiration and thus decomposition (Chen et al., 2020). Ultimately, the balance of these different C fluxes determines net tree diversity effects on C sequestration in forests (Liu et al., 2018). For example, tree diversity is often reported to increase tree biomass production (hence C gain, Potvin et al., 2008) but may, in some cases, also increase tree mortality (hence C loss, Searle et al., 2022). Similarly, tree diversity may increase SOC through diversity-induced enhancements of C inputs into the soil via plant litter or root exudate production, but changes in soil community and functioning may also enhance C losses due to decomposition (Chen et al., 2020; Handa et al., 2014; Lange et al., 2015). As a result no or no coherent effect of tree diversity was also reported (e.g. Martin-Guay et al., 2022; Scherer-Lorenzen et al., 2007).

Comprehensive assessments of the multiple C stocks and fluxes in forests and their intricate relationships are scarce (Xu et al., 2020). A notable exception is Liu et al. (2018), who studied naturally established subtropical forests in China, revealing significant positive effects of tree diversity on AGC, root C, CWD, and SOC, and significant correlations between tree diversity and AGC, CWD, and leaf litter production. However, in complex natural environments like forests, environmental variation and tree diversity

interactively influence carbon stocks and fluxes (van der Sande et al., 2017). Despite attempts using structural equation models (SEMs) to identify direct and indirect relationships (Chen et al., 2018; Chen et al., 2023; Li et al., 2020), mechanistically disentangling these drivers remains challenging in observational studies. Planted tree diversity experiments, which were specifically designed to compare monocultures and mixtures of increasing diversity while controlling for environmental variation (Depauw et al., 2024; Scherer-Lorenzen et al., 2005), offer an ideal setting for elucidating linkages among C stocks and fluxes. Until recently, the young age of most tree diversity experiments, the slow development of trees in boreal and temperate experiments and the different response times and dynamics of C compartments over the course of stand development (e.g. faster responses of aboveground compared to belowground C; Ravenek et al., 2014) prevented analysing the temporal dynamics of tree diversity effects on C stocks and fluxes. Moreover, a temporal perspective on C residence time, i.e. the time C is stored within a reservoir, is a prerequisite for assessing the stability of C storage under climate variability and investigating whether tree diversity's control on C stocks and fluxes increases as forest stands develop. Increases in ecosystem functioning over time in more diverse tree communities have been demonstrated for aboveground tree productivity (Guerrero-Ramírez et al., 2017; Jucker et al., 2020) but not for multiple C stocks and fluxes and their relationships.

Here, we use data on temporal changes in ten C-related stocks and fluxes measured in the oldest tropical tree diversity experiment, the Sardinilla experiment established in 2001 in Panama, which is part of the global network of tree diversity experiments (TreeDivNet). After two decades of C-related research (Cesarz et al., 2022; Coll et al., 2008; Guerrero-Ramírez et al., 2016; Guillemot et al., 2020; Hutchison et al., 2018; Kunert et al., 2019; Kunert et al., 2022; Madsen et al., 2020; Moore et al., 2018; Murphy et al., 2008; Potvin et al., 2011; Ruiz-Jaen and Potvin, 2011; Sapijanskas et al., 2013; Sapijanskas et al., 2014; Scherer-Lorenzen et al., 2007; Schnabel et al., 2019; Wolf et al., 2011) and due to the comparably fast tree growth in the tropics, the Sardinilla experiment features a wealth of C-related variables above- and belowground for planted forests with 1–5 tree species and considerably large-sized trees (with the tallest trees over 25

m), which we leverage here to explore tree diversity effects on C stocks and fluxes across 16 years (2001–2017). Since planting, the experiment experienced repeated climate extremes including a severe El Niño-driven drought and a Hurricane (see methods). Although it is not possible to disentangle the intertwined impacts of stand development and these climate extremes, their occurrence has provided us with the unique opportunity to evaluate the role of tree diversity for C stocks and fluxes in the face of severe climate events. We anticipate a stronger positive tree diversity effect at later stages of stand development, due to enhanced ecosystem functioning in more diverse tree communities over time (Guerrero-Ramírez et al., 2017) and a higher stability of diverse communities to climatic extremes (Schnabel et al., 2021). Specifically, we tested the following hypotheses: (H1) C stocks and fluxes increase with increasing tree diversity. (H2) Positive tree diversity effects on C stocks and fluxes increase with stand development despite repeated climate extremes. Finally, we use SEMs to test how C stocks, fluxes, and their control through tree diversity are connected through direct and indirect relationships above- and belowground using ten explicit hypotheses (Supplementary Table S1).

Methods

Description of the study site

This study is based on data collected over 16 years in the Sardinilla planted forest. Established in 2001 (Scherer-Lorenzen et al., 2005) Sardinilla is the oldest experiment of the International Network of Tree Diversity Experiments (TreeDivNet; https://treedivnet.ugent.be/). The site was originally planted with six native tree species, namely *Luehea seemannii* Triana & Planch (Ls), *Cordia alliodora* (Ruiz & Pavon) Oken (Ca), *Anacardium excelsum* (Bert. & Balb. Ex Kunth) Skeels (Ae), *Hura crepitans* L. (Hc), *Tabebuia rosea* (Bertol.) DC. (Tr) and *Cedrela odorata* L. (Co). A total of 24 plots ranging from 0.2025 to 0.2304 ha (approximately 45 x 45 m) were established following a randomized complete block design. Of these, 12 plots were monocultures (2 plots per species), six plots contained a three-species mix with each species

present in two plots, and six plots contained all tree species. Due to high mortality experienced by Ca in the two years after planting, only 22 plots were maintained over the 16 years of the experiment. This paper thus considers the effect of three diversity levels, grouped as 1, 2-3, and 5 species. Elevation across the site ranges from a ridge at 79 m ASL to low areas at 67 m ASL (Healy et al., 2008) resulting in a gradient of soil types ranging from Vertic Luvisol on the ridge to Gleyic Luvisol in the low part of the plantation (Oelmann et al., 2010). Despite the low pH, soils of the Sardinilla plantation are characterized by high nutrient availability because of the carbonate-rich parent material (Oelmann et al., 2010). In the first 10 years of plantation establishment, soil organic matter decreased by 18% in the plantation (Moore et al., 2018). Further details on the Sardinilla tree diversity experiment can be found in Scherer-Lorenzen et al. (2005) and Potvin and Dutilleul (2009).

We examined three periods: an early (p1), a mid (p2), and a late period (p3) of plantation development (Fig. S1). These periods were characterized by repeated climate extremes, with the mid-period featuring an extremely wet year (2010) and the late period a severe El Niño-driven hotter drought (2015) triggering growth reductions and elevated tree mortality (Browne et al., 2021; Detto et al., 2018; Hutchison et al., 2018; Schnabel et al., 2019). Subsequently, in November 2016, the experiment was hit by Hurricane Otto, a tropical storm that formed off the coast of Panama in the Caribbean Sea inducing stem breakages in the experiment. Climatic conditions at the Sardinilla experiment were characterized in terms of annual mean temperature, precipitation sum, and drought index (Standardized Precipitation Evapotranspiration Index (SPEI; Vicente-Serrano et al., 2010)), with all climate variables illustrating the climate extremes described above in terms of temperature and precipitation extremes and drought conditions (Supplementary Fig. S2).

Data collection

We measured ten compartments of the forest C cycle, namely aboveground tree C (AGC), tree coarse root C (CRC), coarse woody debris C (CWDC), C in herbaceous biomass (herbaceousC), leaf litter C production

(litterC), soil organic C (SOC), leaf litter decomposition, root decomposition, soil microbial biomass C (C_{mic}), and soil respiration. In addition, we included canopy opening as a co-variable, with potentially important influences on C stocks and fluxes. Each variable was measured during three periods of plantation development: an early (2001 for SOC and 2005, 2006 & 2007 for the other variables), a mid (2011, 2012 & 2013), and a late period (2016 & 2017) (see Supplementary Fig. S1 for a timeline). Three variables were only measured in some periods: C_{mic} in the mid (2013) and late (2017), root decomposition in the mid (2012), and soil respiration in the late (2017) period. If not stated otherwise, the sample size for all variables was n = 22 plots. We aggregated variables to periods in our analysis as not all variables were measured in all years. To scale individual tree measurements up to community measures, we used diameter and height inventories of all trees in the plantation conducted at the end of each growing season (December-January) in 2005, 2012, and 2016. The measurement of individual variables is described briefly below, with details provided in the Supplementary Methods.

Aboveground tree carbon

Aboveground tree biomass (AGB) estimates were based on species- and diversity-specific allometric equations developed after harvesting and measuring 150 and 167 trees in the experiment in 2005 and 2017. AGB was calculated as the sum of trunk and branch biomass (excluding leaves to focus on the more permanent C-components of the trees). Allometric models are provided in Supplementary Material. The best-fitting models were then combined with annual diameter and height inventories of all trees in the experiment conducted at the end of each growing season (December-January) to estimate the AGB of each tree in each period. Allometric models calibrated in 2017 were used for the mid and late period. AGB was converted to aboveground tree C (AGC) using species-specific trunk C concentrations (Elias and Potvin, 2003).

Coarse root carbon

To estimate coarse root C (CRC) we relied on root:shoot ratios from the Sardinilla site based on two different root excavation campaigns. For CRC in the early period, we relied on root:shoot ratios developed in 2004 from excavating of three-year-old trees (Coll et al., 2008). For CRC values in the mid and late period, we used species-specific root:shoot ratios developed in 2017 (Guillemot et al., 2020). The species-specific root:shoot ratios were then multiplied with AGC to obtain CRC estimates of all trees in the experiment.

Coarse woody debris carbon

All visible branches and stems fallen on the ground were collected annually in each plot and weighted to obtain a measure of coarse woody debris (CWD) biomass. We used samples collected at the end of the dry season (around March), except for the early period, where the collection lasted from July to August. CWD was put back after weighing. CWD biomass was converted to C (hereafter CWDC) using the species-specific trunk C concentration detailed above.

Herbaceous carbon

Herbaceous vegetation was cut, dried, and weighed in four quadrats (0.5 m^2) per plot, see Potvin et al. (2011). C concentration was determined using an elemental analyser, and herbaceous biomass was converted to herbaceous C using the average C concentration (42.72%) of legumes and grasses/non-leguminous herbs.

Leaf litter carbon

Leaf litter was collected bi-weekly in 3–6 litter traps of 1 m^2 per plot, with trap numbers varying with the number of tree species per plot. Each trap was positioned 1 m away from a tree of each species present in each plot, see Scherer-Lorenzen et al. (2005). The litter was dried at a constant temperature of 70°C. Leaf

litter production was calculated by dividing total dry biomass in grams from each trap by the number of days between two litter collection dates to determine the rate of litter fall per day per m^2. Litter biomass production was converted to litter C production (hereafter 'litter C') using plot- and species-specific carbon concentrations from dry season litter (Scherer-Lorenzen et al., 2007).

Soil organic carbon

Four soil cores were collected from each plot during plantation establishment (2001) and in the mid and late periods, dried, and analysed for bulk density, SOC concentration (%), and $\delta^{13}C$ values. SOC (kg m^{-2}) stock was calculated from bulk density and C concentration. We examined not only SOC but also its C_3- and C_4-derived fractions since the latter is associated with the C_4 grasses within the herbaceous vegetation and in the pasture that existed prior to the plantation establishment, while the former is associated with the C_3 inputs via litter of the trees and C_3 herbaceous plants (Moore et al., 2018). Assuming a C_3 plant $\delta^{13}C$ input of -28 ‰ and a residual C_4 plant $\delta^{13}C$ of -13 ‰, estimates of the percentage and mass of C_3-plant derived SOC (SOC_3) and C_4-plant derived SOC (SOC_4) were made (Moore et al., 2018), where SOC_3 and SOC_4 are percentages of total SOC that add up to one hundred percent. This approach allowed us to determine the temporal changes in SOC derived predominately from trees (SOC_3) and C_4 grasses in the former pasture (SOC_4).

Leaf litter decomposition

Leaf litter decomposition, hereafter litter decomposition, was measured using nylon bags filled with dry litter from litter traps in the center of the plots. For species mixtures, equal proportions of litter from each species were used, see Scherer-Lorenzen et al. (2007). Litter decomposition was measured in n = 17 plots in the early and mid and n = 11 plots in the late period. Mass loss was determined by drying and weighing the remaining litter. The percent mass remaining was divided by the number of days of decomposition for standardization and averaged per plot.

Root decomposition

Root decomposition was measured using the root material of the five tree species using nylon mesh bags filled with dry roots of 4th and 5th orders (Guerrero-Ramírez et al., 2016). Decomposition bags were installed in the ten monocultures and three five-species mixture plots (n = 13). Mass loss was determined by washing and drying the roots and, as for litter decomposition, the percent mass remaining was divided by the number of days of decomposition.

Soil microbial biomass

C_{mic} was measured as substrate-induced respiration, that is, the respiratory response of microorganisms to glucose addition (Anderson and Domsch, 1978). C_{mic} was calculated according to Beck et al. (1997) using the same analytical devices (RMS Schuller, Darmstadt, Germany) for all measurements, see Cesarz et al. (2022).

Soil respiration

Soil respiration was measured with a portable infrared gas analyser equipped with a soil respiration chamber at six to eight randomly chosen locations per plot in the wet season (late July and early August). Changes in CO_2 concentration over time were recorded every 5 sec over 90–120 sec when pressing the chamber gently on the forest.

Canopy opening

Canopy opening was measured using four hemispheric photos per plot in October or November when trees were fully leaved-out. Photos were analysed by the Gap Light Analyser (GLA) program (Frazer et al., 1999) to extract canopy structure from hemispheric photos, see Sapijanskas et al. (2014). Canopy opening (a gap

fraction in %) can be considered a measure of canopy space-filling, which may mediate tree diversity effects on C stocks and fluxes (see Supplementary Table S1).

Data Analysis

We expressed the stock and flux variables in a common unit of 1 m^2 to avoid extrapolating variables that were measured only in small areas. We considered AGC, CRC, SOC and C_{mic} as stock variables. AGC and CRC (kg) of individual trees were summed per plot and then expressed at the scale of one m^2 to ensure comparability of all measurements and to account for slight variations in plot size (plots ranging from 0.2025 to 0.2304 ha). For SOC (initially measured as kg m^{-2}), the data were averaged at the plot level for each year. We also calculated changes in stocks between the three observation periods as:

$$\Delta stock = \frac{(stock_{t+1} - stock_t)}{time} \quad (1)$$

where *stock* is either AGC, CRC or SOC and its fractions SOC_3 and SOC_4 in period *t* and *time* is the number of years and months between two measurements (see Supplementary Fig. S1 for a timeline) resulting in Δstock estimates in kg C m^{-2} $year^{-1}$. We considered CWDC, herbaceousC, litterC, leaf litter decomposition, root decomposition, and soil respiration as annual flux variables. CWDC produced in one year was found to mostly decompose until the end of the wet season in each year of our observation period. Similarly, herbaceousC regrew each year and dead herbaceous material decomposed completely within a year. We therefore considered annual measurements of CWDC and herbaceousC in our tropical forest system as annual fluxes (kg C m^{-2} $year^{-1}$) rather than as stocks, as this attribution more closely reflected the reality in the examined tropical forest compared to calculating changes in these variables between several years. The C flux variables were analysed as follows. CWDC was estimated at the level of the plots and down-scaled to 1 m^2 accounting for plot size. HerbaceousC was averaged at the plot level for each year. LitterC (kg C m^2 day^{-1}) was averaged per plot and across the different collection dates and then scaled to an annual flux

(kg C m^2 $year^{-1}$). Litter and root decomposition was averaged across the different samples within one plot and expressed in % mass remaining; decomposition data was not analysed jointly with other variables as decomposition was not measured for all plots in all periods. Microbial biomass (µg C_{mic} g^{-1} dry weight soil) and soil respiration (µmol m^{-2} s^{-1}) were calculated as average values across measurement locations per plot. Canopy opening, our co-variable, was averaged across the different samples within one plot and expressed in %.

Multivariate Analyses of Variance

A snapshot of the compartments of the forest C cycle after 16 years of growth (2016-2017) was obtained by Multivariate Analyses of Variance (MANOVA) testing the effect of tree diversity for different compartments expected to be correlated. Two MANOVAs examined the tree biomass related variables (AGC, CRC and CWDC) and the soil related ones (SOC, SOC_4 and SOC_3). A third MANOVA analysed the effect of tree diversity on canopy opening and litterC considering that both variables might be correlated. The fourth MANOVA considered soil microbial biomass and soil respiration. The analyses were performed using Proc GLM of SAS version 9.4.

Understanding the build-up of the diversity effects across the examined periods proceeded using mixed-effects Analyses of Variance (mixed-effects ANOVAs). As we were interested in temporal dynamics, we focused on annual C fluxes and changes in stocks rather than on stocks per se to ensure a better comparability of the examined variables and to avoid legacy effects present in stock variables (see e.g. Chen et al. (2023)). The mixed-effects ANOVAs were performed for each Δstock and flux variable at the plot level, according to the following model:

$$R = \beta 0 + \beta 1 \times \text{diversity} + \beta 2 \times \text{time} + \beta 3 \times (\text{diversity} \times \text{time}) + b_i + \varepsilon_{ij} \quad (2)$$

where R is the respective response variable and *diversity* had four levels corresponding to the number of species planted per plot (1, 2, 3, and 5), and *time* had three levels (early, mid, and late period). $\beta 0$, $\beta 1$ and $\beta 3$ are the fixed effect coefficients, b_i is the random effect for experimental plot accounting for repeated measurements and ε_{ij} the error term. The model assumes the random effect b_i to be normally distributed with mean and variance of $N(0, \sigma^2)$. Our mixed-effects ANOVAs allow testing for the presence of a time by diversity effect, namely a differential build-up of C stocks and fluxes through time in response to tree diversity. ANOVAs were used to test for diversity effects on root decomposition and soil respiration which were only measured once. Extreme values and model assumptions, including normality and heteroscedasticity, were checked visually and with Shapiro-Wilk test (see also Supplementary Analysis 1). We decided to only remove two CWDC data points, as in all other cases, a plausible biological explanation existed. Mixed-effects ANOVAs were fit in R version 4.3.0 with the packages lme4 (Bates et al., 2015) and lmerTest (Kuznetsova et al., 2017). Least-squares means were estimated with the emmeans package (Lenth, 2020).

Structural equation models

To understand the mechanisms underlying tree diversities control on C dynamics across time, we used structural equation models (SEMs). We developed a hypothesis-driven conceptual model based on *a priori* knowledge of mechanisms that may drive and relate C stocks and fluxes in forest ecosystems (Fig. S3; Table S1). This approach enabled us to test the direct and indirect relationships between C stocks, fluxes, and tree diversity. Indirect relationships are those that are mediated by other variables. We tested whether tree diversity affected C stocks and fluxes indirectly via diversity-induced decreases in canopy opening due to enhanced canopy space-filling or increases in tree growth through examining relationships between tree species richness, canopy opening, and tree growth (expressed as ΔAGC). Moreover, as we assumed canopy opening and ΔAGC to be correlated, we included a partial correlation between both. We subsequently expected canopy opening and tree growth to influence herbaceousC, litterC and CWDC in that (1)

decreased canopy at high diversity would correlate negatively with herbaceousC but positively with litterC while (2) enhanced tree growth at high diversity would correlate positively with litterC and CWDC. We did not include direct pathways between tree diversity and these variables as we expected tree diversity effects to be predominately mediated by canopy opening or tree growth. Finally, we expected herbaceousC, litterC, and CWDC to be the main aboveground C inputs to the soil, hypothesizing that they would positively influence and correlate with ΔSOC and ΔCRC. We used the summed belowground ΔC stock (ΔSOC_3 + ΔCRC) to test this assumption to avoid the need to fit too many pathways considering sample size (n = 22 plots). As we were interested in tree diversity effects, we focused on SOC_3, the tree-derived fraction of SOC, but also tested the same SEMs for SOC (sum of SOC_3 and SOC_4). Finally, we tested for potential direct effects of tree diversity on belowground ΔC stock not mediated by the tested relationships. To examine temporal trends, we fit separate SEMs for the three periods of plantation development. As information on ΔSOC, a crucial variable for our SEMs, was only available for the mid and late period (see Fig. S1) we fit SEMs only for these two periods.

All SEMs focussed on C fluxes and changes in stocks to ensure a better comparability between variables. Moreover, we only included variables available in kg C m^2 $year^{-1}$, except for canopy opening. We used piecewise SEMs (Lefcheck, 2016) to test the relative importance of and support for these hypothesized pathways. Global model fit was assessed via Fisher's C statistic ($P>0.05$). We assessed the independence of variables and included partial, non-directional correlations to improve model fit based on tests of directed separations ($P<0.05$ for violation of independence claims). For each SEM we calculated standardized path coefficients, scaled by the standard deviations of the variables, which allowed us to compare the strength of paths within and among models (Lefcheck et al., 2018). Individual pathways were fit as linear models considering the number of species planted per plot (1, 2, 3, and 5) as continuous and not as categorical variable as in the mixed-effects ANOVAs. SEMs were fit with the package piecewiseSEM (Lefcheck, 2016) and linear mixed-effects models with the packages lme4 (Bates et al., 2015) and lmerTest (Kuznetsova et al., 2017) in R version 4.3.0.

Results

C stocks and fluxes after 16 years of tree growth: a snapshot in time

Over a period of 16 years, the experimental tree plantation accumulated an average of 35.9±2.7 Mg C ha^{-1} in the trees (AGC + CRC), while SOC decreased on average by 11.2±1.1 Mg C ha^{-1}, resulting in a net gain of 24.7±2.9 Mg C ha^{-1} or 90.7±10.6 Mg CO_{2eq} ha^{-1}. MANOVA unveiled a significant effect of tree diversity on the C compartments directly related to trees: AGC, CRC and CWDC (Table 1, Fig. 1). The diversity effect was mainly driven by AGC (Fig. 1) with both CRC and CWDC being significantly correlated to AGC (0.708, p=0.0007 and 0.624, p=0.004, respectively). In 2017, according to Tukey Studentized range test, tree AGC in the 5-species plot, was, with 35.7±1.8 Mg C ha^{-1}, significantly higher than in monocultures (22.8±3.4 Mg C ha^{-1}), a 57% increase (Fig. 1). The MANOVA computed with the canopy-related variables (canopy opening and litterC) also showed a significant effect of diversity (Table 1) with a significant negative correlation between the two variables (-0.741, p=0.0004). This diversity effect was predominantly driven by litterC that was 64% higher in 5-species mixtures than in monocultures. At 1.1–1.4 Mg C ha^{-1} (Fig. 1; Fig. S4) herbaceousC played a role similar to litterC in the system, albeit it did not respond significantly to diversity (Table 2). None of the two MANOVAs performed on soil-related C compartments detected a significant effect of tree diversity (Table 1).

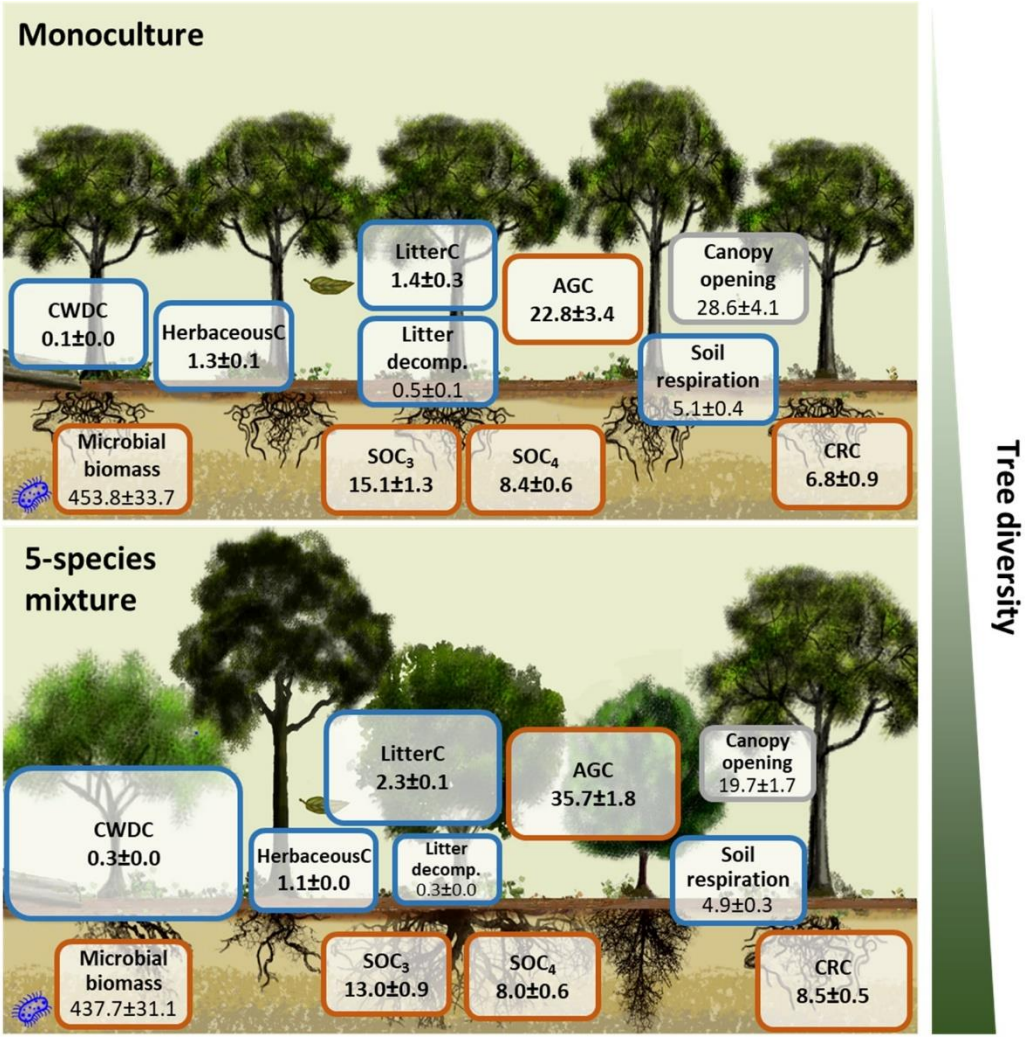

Fig. 1 C stocks and fluxes after 16 years of tree growth. Shown are means and standard errors of the C stocks in Mg C ha^{-1} (brown boxes) and fluxes in Mg C ha^{-1} $year^{-1}$ (blue boxes); numbers printed in bold. Variables in other units, including canopy opening and litter decomposition given in (%), soil respiration given in µmol m^{-2} s^{-1} and microbial biomass given in µg C_{mic} g soil dw^{-1} are not printed in bold to allow for separation. The size of the boxes in the 5-species mixture are scaled relative to the monoculture, with diversity-induced increases or decreases in C stocks and fluxes indicated by larger or smaller boxes, respectively. An overview of all analysed mixtures (2-, 3- and 5-species mixtures) is shown in Fig. S4. The sum of SOC_3 and SOC_4 gives SOC. AGC: aboveground tree C, CRC: coarse root C, CWDC: coarse woody debris C, SOC_4: C_4 derived soil organic C (SOC), SOC_3: C_3 derived SOC.

Table 1 MANOVAs for C stocks and fluxes after 16 years of growth. The main effect tested was tree diversity with 4 different levels (1, 2, 3 and 5 species per plot). Abbreviations are given in Fig. 1. Significant effects ($p < 0.05$) printed in bold.

Compartments	Roy's Greatest Root	$F_{3,18}$	p-value
AGC/CRC/CWDC	0.8975	5.39	**0.0080**
LitterC/Canopy opening	0.5974	3.58	**0.0343**

$SOC/SOC_4/SOC_3$	0.2059	1.24	0.3260
Microbial biomass/Soil respiration	0.1722	1.03	0.4015

Diversity effects on changes in C stocks and fluxes across time

With a least-squares mean of 0.140 kg C m^2 yr^{-1}, tree ΔAGC increment was significantly slower in monocultures than in most mixtures, which had increments of 0.140, 0.232, and 0.226 kg C m^2 yr^{-1} in 2-, 3-, and 5-species mixtures, respectively (Table 2, Fig. 2). The positive tree diversity effect on ΔAGC tended to strengthen over time in the 5-species mixtures (p = 0.16 for the time × diversity interaction). CWDC was significantly lower in monocultures (least-squares mean of 0.010 kg C m^2 yr^{-1}) than in all mixtures, with 0.012, 0.024, and 0.021 kg C m^2 yr^{-1}, for 2-, 3- and 5-species mixtures, respectively. In contrast, ΔCRC increment did not significantly differ between monocultures and mixtures (Table 2, Fig. 2).

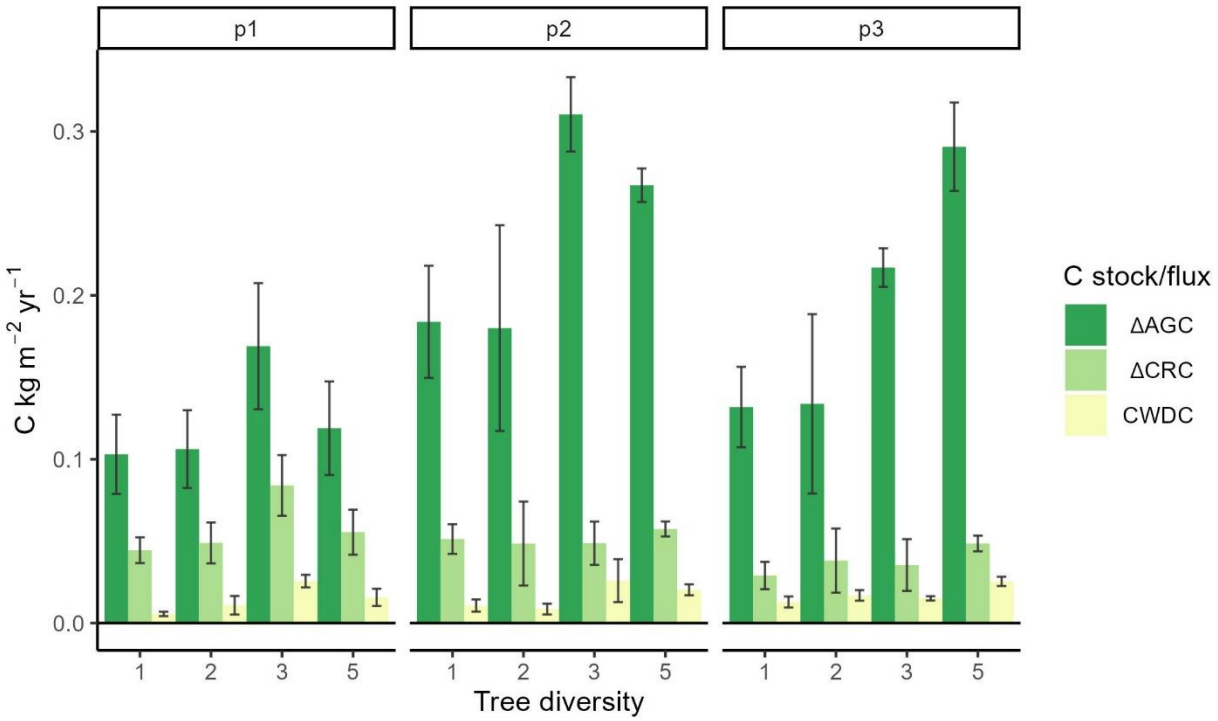

Fig. 2 Mean changes in aboveground tree C (ΔAGC), coarse root C (ΔCRC) and coarse woody debris C (CWDC) over time and with diversity. The analyses considered three time-intervals, early (p1), mid (p2), and late period (p3). Coloured bars show means and error bars standard errors of the mean for the examined C stocks and fluxes calculated as detailed in Eq. 1 and Fig. S1.

Table 2 Mixed-effects ANOVAs on changes in C stocks and fluxes over time. The analyses considered up to three time-intervals, early, mid, and late period across a total of 16 years, see the timeline in Supplementary Fig. S1 for details. Abbreviations are as in Figure 1. Entries in the table are F and p values, with p <0.05 *, p< 0.01 **, p<0.001 ***, and ns = not significant. Significant effects printed in bold. For root decomposition and soil respiration, ANOVA results are shown.

C stock/flux	Diversity	Time	Time × Diversity
ΔAGC	**5.07***	**11.25 *** **	1.67 ns
ΔCRC	1.11 ns	2.74 ns	0.72 ns
CWDC	**3.30 ***	0.23 ns	2.01 ns
HerbaceousC	0.98 ns	**47.10 *** **	0.37 ns
LitterC	0.81 ns	**100.74 *** **	**6.25 *** **
ΔSOC_3	0.92 ns	**29.10 *** **	1.61 ns
ΔSOC_4	0.67 ns	**44.57 *** **	**5.35 ** **
ΔSOC	0.62 ns	0.01 ns	2.55 ns
Litter decomposition	0.71 ns	**30.32 *** **	**5.15 ***
Root decomposition	0.69 ns	-	-
Microbial biomass	0.81 ns	**46.32 *** **	0.90 ns
Soil respiration	0.45 ns	-	-
Canopy opening	2.06 ns	**31.73 *** **	1.29 ns

We further compared the strongest aboveground C fluxes to the soil (herbaceousC and litterC, which were an order of magnitude higher than CWDC; Fig. 1) with observed changes in ΔSOC (Fig. 3). Across the plantation, herbaceousC did not vary with diversity but decreased significantly with time, with 0.201, 0.105, and 0.125 kg C m^2 yr^{-1} for the early, mid, and late period, respectively (Table 2, Fig. 3). Conversely, litterC increased significantly over time, with diversity effects depending on the period of plantation development (Table 2): In the early period, litterC was lowest and similar across diversity levels, while in the mid and late period litterC was lowest in monocultures with 0.149 and 0.141 kg C m^2 yr^{-1} and highest in 5-species mixtures, with 0.225 and 0.232 kg C m^2 yr^{-1} (Table 2, Fig. 3).

The predominately tree-derived ΔSOC_3 showed a significant change over time but not with diversity (Table 2): in the mid period all plots – irrespective of their diversity – showed a net increase in ΔSOC_3 while most plots did not show any SOC_3 loss or increment in the late period (Fig. 3). A notable exception are the 5-species mixtures, which tended to lose SOC_3 in the late period (Fig. 3). The indication of enhanced SOC_3 loss in 5-species mixtures in the late period coincided with the slowest leaf litter decomposition in this treatment (Fig. 4). Overall, leaf litter decomposition changed significantly over time and with diversity (Table 2; Fig. 4). Litter decomposition was slowest in the early and fastest in the mid period but did not respond to diversity in either period; in contrast, we observed a pronounced decline in leaf litter decomposition with diversity in the late period, particularly in 5-species mixtures (note that decomposition was only measured in 3- and 5-species mixtures in the mid and late period). A similar decrease in decomposition with diversity – but non-significant – was observed for root decomposition (Table 2, Fig. 4; note that root decomposition was only measured in the mid period).

ΔSOC_4, which is associated mainly with the C_4 grasses that existed before the plantation establishment, varied significantly in response to both time and the time by diversity interaction (Table 2). Between 2001 and 2011 the reduction in C_4 in the upper 0–10 cm of soil was around twice as fast as between 2011 and 2017 with least-square means of -0.13 kg C m^2 yr^{-1} and -0.055 kg C m^2 yr^{-1}, respectively (Fig. 3). The significant time by diversity interaction was driven by the three-species mixtures where the decrease in ΔSOC_4 was strongest in the mid period and disappeared in the late period while the other treatments experienced continued loss in ΔSOC_4 in the late period (Fig. 3). Overall, reductions in predominately pasture-derived SOC_4 were larger than any observed gains in tree-derived SOC_3 resulting in a net negative SOC-balance of reforestation (Fig. 3).

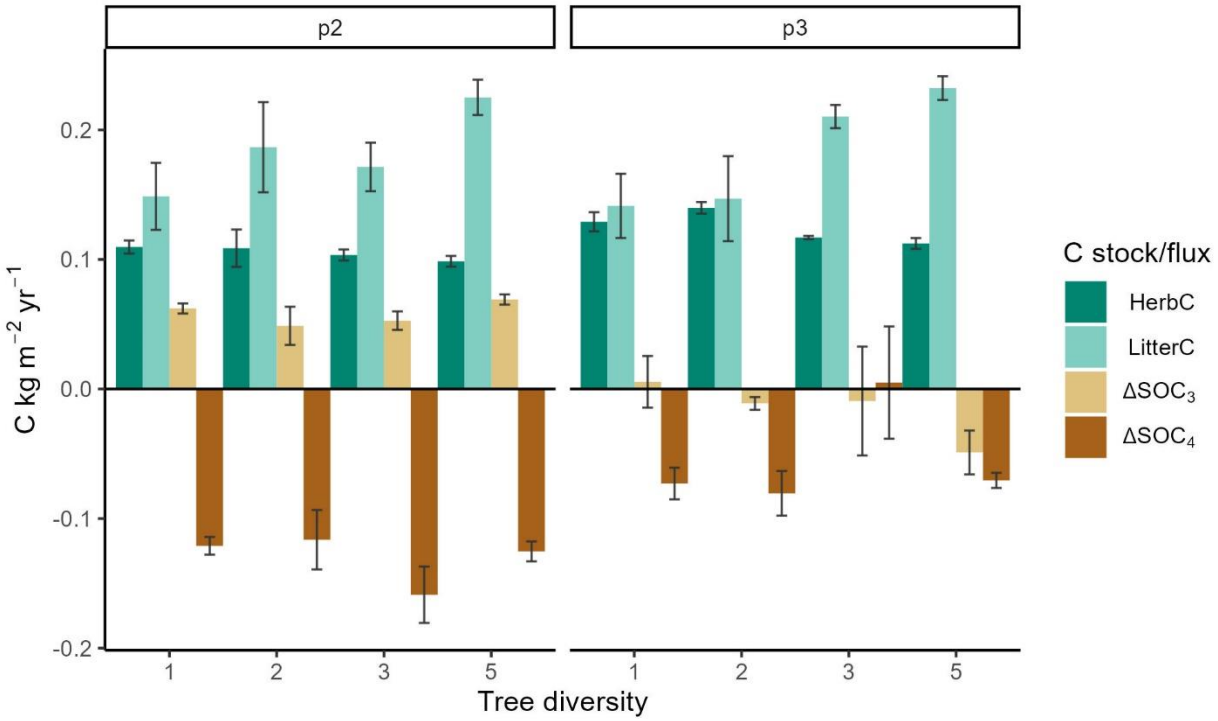

Fig. 3 Mean changes of dominant aboveground C fluxes to the soil with time and diversity and corresponding observed changes in soil organic carbon (ΔSOC). Coloured bars show means and error bars standard errors of the mean of herbaceous C and leaf litter C and changes in C_3 and C_4-derived SOC (SOC_3 and SOC_4). The analyses considered two time-intervals, mid (p2), and late period (p3), as SOC data was only measured in these two periods (Supplementary Fig. S1). The examined SOC changes were calculated as detailed in Eq. 1 and Fig. S1.

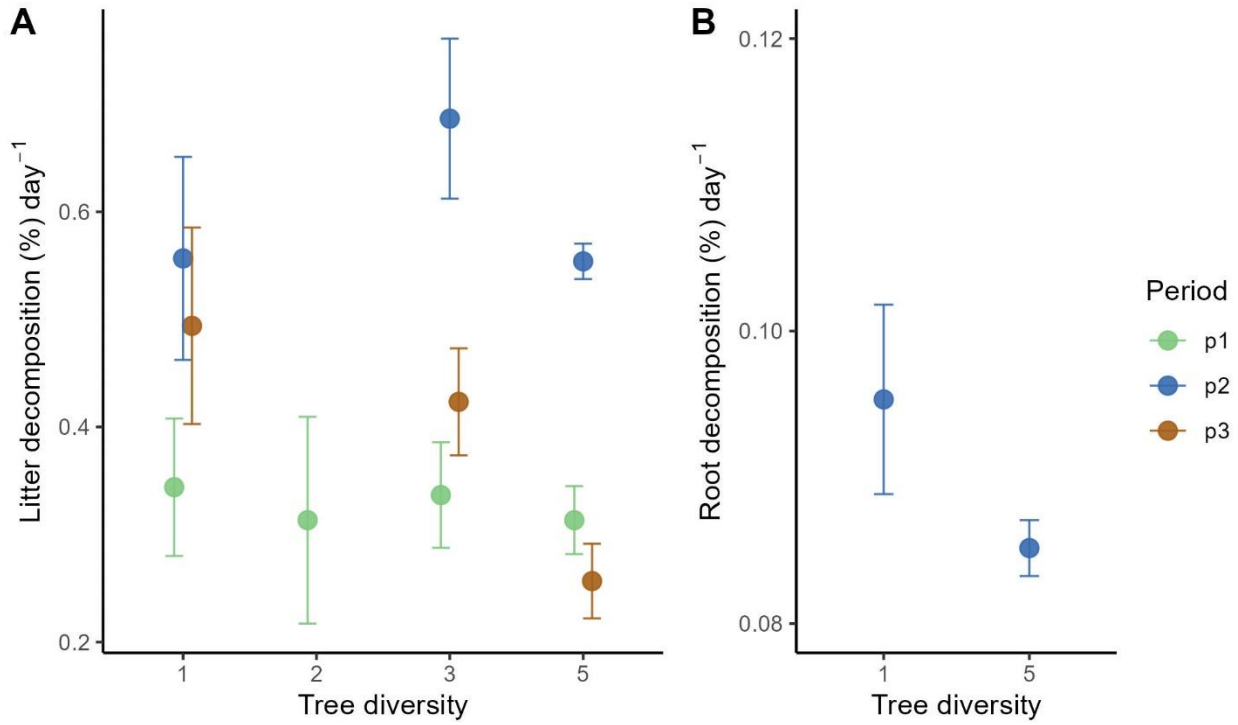

Fig. 4 Mean changes in leaf litter and root decomposition with time and diversity. Coloured points show means and error bars standard errors of the mean. The analyses considered three time-intervals, early (p1), mid (p2), and late period (p3). Leaf litter decomposition but not root decomposition responded significantly to tree diversity (Table 2).

Finally, none of the remaining variables, including microbial biomass, soil respiration and canopy opening responded significantly to diversity (Table 2), even though canopy opening tended to be lower in 5-species mixtures compared to monocultures ($F = 2.06$, $p = 0.14$), particularly in the mid- and late period. However, for soil microbial biomass and canopy opening, for which we had repeated measurements, we observed pronounced temporal changes (Table 2). Soil microbial biomass increased significantly from 315 to 453 µg C_{mic} g soil dw^{-1} from the mid to the late period. Not surprisingly, canopy opening, and thus light transmission, declined strongly with progressing stand development from a least-squares mean of 47.8% in the early to 21.1% in the mid period to than increase slightly again to 27.2% in the late period.

Effects of diversity on C stock-flux relationships

Using structural equation models, we explored the effect of tree diversity on linkages amongst C stocks and fluxes above- and belowground (Fig. 5). In both periods of plantation development (mid and late period), tree diversity significantly decreased canopy opening and increased ΔAGC with standardized path coefficients of -0.41 and 0.42 in the mid period and -0.4 and 0.71 in the late period (Fig. 5). Tree diversity effects on ΔAGC thus increased by ~70% from the mid to the late period. Canopy opening exerted a significant positive effect on herbaceousC but decreased litterC with standardized path coefficient of 0.57 and -0.40 in the mid period and 0.52 and -0.43 in the late period. ΔAGC significantly increased both litterC and CWDC with standardized path coefficients of 0.51 and 0.68 in the mid period and 0.53 and 0.62 in the late period. Hence, we observed a consistent control of diversity on aboveground C stocks and fluxes and their linkages across time. Aboveground, tree diversity led to a net increase of C fluxes to the soil through its indirect effects on herbaceousC, litterC and CWDC of -0.23, 0.38, 0.29 and -0.21, 0.55, 0.44 respectively for the mid- and late period (see Lefcheck, 2016 for calculation of indirect effects).

In contrast, we observed few significant linkages between aboveground and belowground C stocks and fluxes and only one indirect effect of diversity on belowground changes in C stocks (Fig. 5). In the mid and late period, the significant effect of litterC on belowground ΔC stock (expressed as sum of ΔCRC and predominately tree-derived SOC fraction, ΔSOC_3) had a standardized path coefficient of 0.91 and 0.71, respectively. The indirect effect of tree diversity on belowground ΔC stock via litterC was 0.36 and 0.39 for the mid and late period, respectively. SEMs expressing belowground ΔC stock using SOC instead of SOC_3 yielded similar results, except for a disappearance of the significant effect of litterC in the late period and overall lower explained variation (R^2) in ΔC stock (Fig. S5). Overall, belowground changes in C stocks were largely disconnected from the diversity-controlled C stock and flux network observed aboveground.

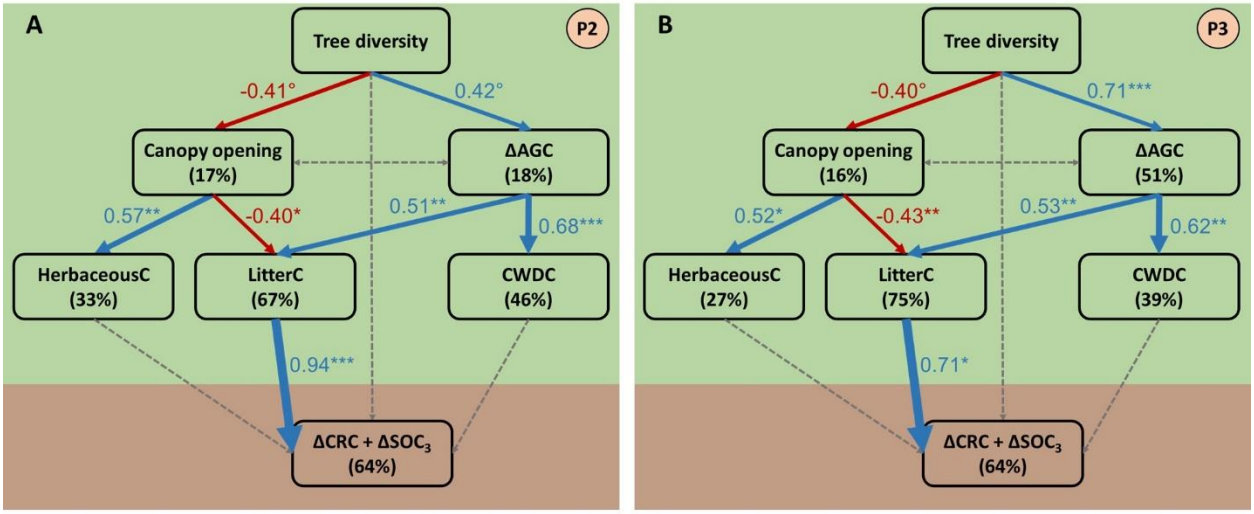

Fig. 5 Direct and indirect effects of tree diversity on C stocks and fluxes. The SEMs partition potential tree diversity effects on C stocks and fluxes into effects mediated via canopy space filling (expressed as canopy opening) and via aboveground tree C changes (expressed as ΔAGC), which are expected to influence herbaceous C, leaf litter C and coarse woody debris C (CWDC). These latter C fluxes are, in turn, hypothesized to influence changes in belowground C, expressed as the summed change in coarse root C (ΔCRC) and predominately tree-derived soil organic C (ΔSOC_3). SEMs were fit for the mid period (panel A, P2) and the late period (panel B, P3) with all variables being calculated as detailed in Eq. 1 and Fig. S1. The SEMs fit the data well (Fisher's C = 20.17, df = 20, P = 0.45, n = 22 plots for (A); Fisher's C = 21.17, df = 18, P = 0.27, n = 22 plots for (B)). Examined variables are shown as boxes and relationships as directional arrows with significant positive effects in blue, significant negative effects in red, and nonsignificant effects in dashed gray. The hypothesis-driven conceptual model is shown in Fig. S3. For each significant relationship, standardized path coefficients are shown next to each path with path-width scaled according to coefficient size and asterisks indicating the significance level (*P < 0.05, **P < 0.01, and ***P < 0.001). Bidirectional grey arrows show significant partial correlations. The variation explained in each variable (R^2) is shown below the variable name. The green and brown font indicates above- and belowground variables.

Discussion

As the first tropical site of TreeDivNet, the Sardinilla experiment provides a unique opportunity to evaluate temporal changes in C stocks and fluxes in the neotropics. Consistent with our hypothesis (H1), we observed that tree diversity can increase C stocks and fluxes. Specifically, we noted a remarkable increase in AGC stocks driven by tree diversity, with an average 57% increase in AGC in five-species mixtures compared to monocultures after 16 years (35.7±1.8 *vs* 22.8±3.4 Mg C ha^{-1}; Fig. 1). This observed effect aligns with a recent meta-analysis demonstrating that mixture plots sequestered up to 70% more carbon in aboveground biomass than monoculture ones (Warner et al., 2023). Comparing our results with chronosequences of secondary forests in Panama and the wider neotropics, we found that our C stock

estimates after 16 years (35.8 and 22.6 Mg C ha^{-1} stored respectively in trees and SOC (0–10 cm)) are comparable. For instance, Neumann-Cosel et al. (2011), working like us in the Panama Canal watershed, reported aboveground ranges of 20.55 Mg C ha^{-1} to 56.45 Mg C ha^{-1} with SOC in the first 0-10 cm adding 27.5±3.1 Mg C ha^{-1}. Similarly, Gardon et al. (2020) estimated that actively restored secondary forests in Brazil accumulated approximately 100 Mg biomass yr^{-1} after 16 years, roughly equivalent to 50 Mg C ha^{-1}, and akin to the AGC of our most productive mixture plot. Overall, these findings contribute to our understanding of the build-up of C stocks in tropical forest restoration and emphasize the importance of considering tree diversity in such initiatives.

The long-term C balance of reforestation in the face of progressing climate change may depend more on forest stability and thus C residence time within the forest than on average C accumulation rates. Here, we understand stability as a forest's ability to maintain functioning over time despite repeated perturbations, such as climate extremes (Schnabel et al., 2021), which is broadly consistent with the insurance hypothesis (Yachi and Loreau, 1999). In the Sardinilla experiment, observed climate extremes left the ecosystem little time to recover between perturbations. The extreme wet spell of 2010 was followed in 2015 by a severe drought (Fig. S2; see also Browne et al., 2021; Detto et al., 2018), and a hurricane in 2016. As Bhaskar et al. (2018) pointed out, it is important to understand forest resilience in the context of constant climatic disturbances. While our study design does not allow us to disentangle the effects of climate extremes from those of stand development on tree diversity effects, it does allow us to test whether positive tree diversity effects persist or even strengthen over time despite repeated climate extremes, which triggered growth reductions and elevated tree mortality (Hutchison et al., 2018; Schnabel et al., 2019). Consistent with our hypothesis (H2), and despite these repeated extremes, we uncovered significant positive effects of tree diversity on all the aboveground C stocks and fluxes (Fig. 5). Remarkably, the positive tree diversity effect not only persisted but tended to strengthen over time, at least for ΔAGC. Our previous findings (Hutchison et al., 2018; Schnabel et al., 2019) indicated that tree diversity increased the stability of tree productivity by enhancing growth, buffering temporal variations in growth, and reducing mortality vis-à-vis

monocultures. Although two- and three-species mixtures were the most productive in the early period of the Sardinilla experiment (e.g. Healy et al., 2008; Scherer-Lorenzen et al., 2007), our results demonstrate that five-species mixtures outperformed the less diverse mixtures in later years, as already observed in previous reports (Guillemot et al., 2020; Schnabel et al., 2019). Here, we moved beyond these earlier studies and similar findings in other ecosystems (e.g. Jucker et al., 2014; Schnabel et al., 2021), which focussed on single ecosystem functions, and leveraged a unique dataset on multiple C stocks and fluxes and their interrelationships. This approach allowed us to adopt an integrated ecosystem perspective on C stability in mixed compared to monospecific planted forests. C stability is particularly important considering that tree diversity increased C stocks and fluxes only aboveground, where C is particularly susceptible to climate-driven forest disturbances.

Using structural equation modelling we showed that the tree diversity directly or indirectly effected all the aboveground C stocks and fluxes that we measured (Fig. 5), suggesting that the aboveground components of the C cycle are linked. Canopy opening, a proxy for canopy space filling, played a central role in our SEMs with denser foliage at high diversity enhancing litterC but reducing herbaceousC. Tree architecture apparently plays a crucial role in explaining these effects of tree diversity on the aboveground system. After 16 years of growth, trees growing in mixture allocated a higher proportion of their biomass to branches (Guillemot et al., 2020), which is consistent with higher canopy space filling reported in other tree diversity experiments (Kunz et al., 2019; Williams et al., 2017). Similarly, tree productivity (captured here as ΔAGC) increased with tree diversity, as has been previously reported from our (Guillemot et al., 2020; Schnabel et al., 2019) and other tree diversity experiments (Guerrero-Ramírez et al., 2017). Enhanced tree productivity at high diversity, in turn, enhanced both litterC and CWDC and thus C fluxes to the soil. Likely drivers of these observed positive diversity effects aboveground are complementary species interactions in mixtures, such as higher community-level light capture or complementary water and nutrient uptake from different soil layers reported in Sardinilla (Oelmann et al., 2010; Sapijanskas et al., 2014; Schwendenmann et al., 2015; Zeugin et al., 2010). Litter manipulation experiments support the idea of significant leaf litter-driven

carbon and nutrient fluxes to the soil. Long-term experiments in Barro Colorado Islands Nature Monument in Panama removed litter from forest plots to add it to other identical plots, allowing to compare plots with litter removal and litter addition (Cusack et al., 2018; Sayer et al., 2024). After ten and 17 years of manipulation, soil C was significantly higher in the 0–5 cm layer in the litter addition plots (Cusack et al., 2018), while tree growth significantly declined in litter removal plots (Sayer et al., 2024). The authors explained their results by the fast carbon cycling and high C input into the soil in tropical forests. Our SEMs confirmed the positive link between litterC and the predominately tree-derived fraction of SOC (SOC_3) but no further linkages of SOC_3 with tree diversity nor herbaceousC or CWDC (Fig. 5). This means that the surplus of C fluxes to the soil in the high-diversity mixtures was largely not incorporated into the mineral soil phase, and thus, the multiple direct and indirect relationships of aboveground C stocks and fluxes largely did not extend belowground.

Overall, the Sardinilla planted forest gained significant C aboveground, but we observed a loss of SOC in the 0–10 cm layer associated with a reduction in both bulk density and SOC concentration (Table S2). This loss occurred regardless of tree species richness levels, indicating that tree diversity may only sometimes exert a significant effect on SOC, as noted also in another temperate tree diversity experiment (Martin-Guay et al., 2022). Because the planted forest was established on an active pasture (Scherer-Lorenzen et al., 2005), we suggest that the removal of cows likely minimized compaction which resulted in decreased bulk density (Blanco Sepúlveda and Nieuwenhuyse, 2011). Several studies have identified the misrepresentation of changes in SOC mass associated with sampling to a fixed depth where there have been significant changes in bulk density to that depth (e.g. von Haden et al., 2020). Although variable among the treatments and the two sampling periods, comparison of relative changes in SOC concentration and bulk density suggest that about half of the apparent loss in SOC mass is associated with a loss of SOC concentration and the other half with a decrease in bulk density (Table S2) and thus the loss of SOC mass in the plantation may be an overestimate (Fig. 3). However, SOC concentrations in the 10 – 50 cm depth in the pasture prior to the establishment of the Sardinilla experiment ranged from 1 to 2% and a $\delta^{13}C$ value

between -17 and -21‰, suggesting a strong proportion of SOC_4, and thus there may be further losses in SOC from the subsoil (Moore et al., 2018), as also suggested by (Quartucci et al., 2023). The literature fails to reach a consensus about how reforestation affects SOC (Laganière et al., 2010), with climatic zone, species planted, clay content, past land use, and soil parent material all affecting the SOC balance of forest regrowth (Araujo et al., 2017; Wallwork et al., 2022). For example, in Brazil's Atlantic forest, SOC stock (0–10 cm) of 5-year old re-growing forests was half that of the remnant forest and similar to that of pastures (Zanini et al., 2021) while another Brazilian study (Camargo et al., 1999) reported similar SOC stocks at 0–10 cm for forest, secondary forest fallows, and pasture even though AGC varied 44-fold. Marín-Spiotta et al. (2009), who reported no changes in SOC during secondary forest establishment in Puerto Rico, explained this by a loss of pasture-derived SOC_4 which counterbalanced tree-derived gains in SOC_3. Finally, in a nearby Panamanian site, SOC stocks did not vary along a chronosequence of secondary forests (Neumann-Cosel et al., 2011). We propose that Sardinilla's clay-rich Cambisols, Tropudalfs and Vertisols (average clay content reaches 65% (Moore et al., 2018)) might have amplified compaction related to grazing while the establishment of trees likely loosened up the soil (Table S2) with follow-up effects like an increase in mineralization and thus, increased C loss. Important gaps in the understanding of SOC cycling and storage have restricted the ability to manage ecosystems to enhance soil C stocks (Wallwork et al., 2022). In the case of Sardinilla, we suggest that the land-use change effect (partly) overruled the effects of tree diversity and its C_3-derived C inputs to SOC stock. Given that high soil clay content is common in the tropics (http://hydro.iis.u-tokyo.ac.jp/~sujan/research/gswp3/soil-texture-map.html; Rasmussen et al., 2018) including soil C pool in the C assessments of forest restoration is likely to improve overall C storage estimates (Quartucci et al., 2023).

The importance of forest restoration for ecosystem C storage, a key ecosystem service for climate regulation, has not only been discussed in the scientific literature but has also triggered international commitment to reforestation. As we work on understanding how forest C stocks are being rebuilt through time at the ecosystem level, it is important to remain realistic about the potential of forest restoration to

contribute towards mitigating climate change. Sequestering C is a slow process (Baldocchi and Penuelas, 2019): the average yearly net CO_2 uptake in Sardinilla was 5.67 Mg CO_{2eq} ha^{-1} yr^{-1} or 1.54 Mg C ha^{-1} yr^{-1}. To illustrate, we estimated the emissions from a single one-way flight between Frankfurt and Panama City to 62.7 Mg CO_{2eq} using the ICAO carbon calculator. Hence, this flight demands a flux equivalent to that sequestered by ~11 ha in the Sardinilla planted forest in one year. Some have suggested that the enthusiasm for nature-based solutions risks putting excessive pressure on land use. For example, Dooley et al. (2022) estimated that countries' climate pledges for land-based carbon dioxide removal would demand 1.2 billion ha of land, an area globally equal to that used to grow food. Our thorough ecosystem-level analysis of C stocks and fluxes sheds some light on the challenges of using active reforestation projects to compensate for emissions. We note that Griscom et al. (2017) used higher sequestration potentials of 2.8 to 4.7 Mg C ha^{-1} yr^{-1} to estimate the potential of reforestation to act as a nature-based solution for climate mitigation. Therefore, while nature-based solutions are undeniably important for C sequestration and other ecosystem benefits, such as biodiversity and water regulation (Griscom et al., 2017; Seddon, 2022), co-benefits and potential trade-offs should be carefully assessed (Schuldt et al., 2023). Mixed planted forests as a nature-based solution may not only enhance carbon stocks and fluxes vis-à-vis monocultures, as we show here, but also decrease the restored forests susceptibility to stress and disturbances and, thereby, increase C permanence (Anderegg et al., 2020) while also providing higher levels of biodiversity and a broader range of ecosystem services (Messier et al., 2021).

Acknowledgements

We acknowledge the dedication of all fieldworkers who worked in the Sardinilla experiment over the last 16 years and contributions by Daniel Lesieur as data manager. For soil analyses, field and laboratory support was provided by Muriel Abraham and Meaghan Murphy. FS acknowledges support by the International Research Training Group TreeDì funded by the Deutsche Forschungsgemeinschaft (DFG, grant 319936945/GRK2324). JG acknowledges support by the French Agricultural Research Centre for

International Development (Cirad, CRESI program). NE acknowledges funding by the DFG (German Centre for Integrative Biodiversity Research, FZT118; and Gottfried Wilhelm Leibniz Prize, Ei 862/29-1). TM was supported by the Natural Sciences and Engineering Research Council of Canada (NSERC) and the FQRNT-supported Centre for Climate and Global Change Research at McGill University. NRGR and ITH acknowledge support from Fonds de recherche du Québec nature et technologies, NSERC, Quebec Centre for Biodiversity Science and the DFG (grant 316045089/GRK 2300). CP acknowledges support from NSERC, the Canada Research Chair Program and the Smithsonian Tropical Research Institute.

Author contributions

CP and FS conceived the goals and aims of the study and coordinate the Sardinilla experiment. FS, CP, JG, KEB, SC, NE, and CW developed the methodology. CP, FS, JG, MB, SC, NE, TG, NRGR, ITH, CM, LM, JM, TM, YO, MSL, LS, and AW collected and curated the data. FS and CP analysed the data. FS created the figures. FS and CP wrote the original manuscript draft and all authors contributed to reviewing and editing the manuscript.

Conflict of interest statement

The authors declare no conflict of interest.

Data availability

The data that support the findings of this study are openly available in Dryad at http://doi.org/tbd. Data will be made openly available upon acceptance.

References

Anderegg, W.R.L., Trugman, A.T., Badgley, G., Anderson, C.M., Bartuska, A., Ciais, P. et al, 2020. Climate-driven risks to the climate mitigation potential of forests. Science 368. https://doi.org/10.1126/science.aaz7005.

Anderson, J., Domsch, K.H., 1978. A physiological method for the quantitative measurement of microbial biomass in soils. Soil Biol. Biochem. 10, 215–221. https://doi.org/10.1016/0038-0717(78)90099-8.

Araujo, M.A., Zinn, Y.L., Lal, R., 2017. Soil parent material, texture and oxide contents have little effect on soil organic carbon retention in tropical highlands. Geoderma 300, 1–10. https://doi.org/10.1016/j.geoderma.2017.04.006.

Baldocchi, D., Penuelas, J., 2019. The physics and ecology of mining carbon dioxide from the atmosphere by ecosystems. Glob. Chang. Biol. 25, 1191–1197. https://doi.org/10.1111/gcb.14559.

Barry, K.E., Mommer, L., van Ruijven, J., Wirth, C., Wright, A.J., Bai, Y. et al, 2019. The Future of Complementarity: Disentangling Causes from Consequences. Trends Ecol. Evol. 34, 167–180. https://doi.org/10.1016/j.tree.2018.10.013.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4. J. Stat. Softw. 67, 1–48. https://doi.org/10.18637/jss.v067.i01.

Bauhus, J., van der Meer, P., Kanninen, M. (Eds.), 2010. Ecosystem goods and services from plantation forests. Earthscan, London, UK.

Beck, T., Joergensen, R.G., Kandeler, E., Makeschin, F., Nuss, E., Oberholzer, H.R. et al, 1997. An inter-laboratory comparison of ten different ways of measuring soil microbial biomass C. Soil Biol. Biochem. 29, 1023–1032. https://doi.org/10.1016/S0038-0717(97)00030-8.

Bhaskar, R., Arreola, F., Mora, F., Martinez-Yrizar, A., Martinez-Ramos, M., Balvanera, P., 2018. Response diversity and resilience to extreme events in tropical dry secondary forests. For. Ecol. Manage. 426, 61–71. https://doi.org/10.1016/j.foreco.2017.09.028.

Blanco Sepúlveda, R., Nieuwenhuyse, A., 2011. Influence of topographic and edaphic factors on vulnerability to soil degradation due to cattle grazing in humid tropical mountains in northern Honduras. Catena 86, 130–137. https://doi.org/10.1016/j.catena.2011.03.007.

Browne, L., Markesteijn, L., Engelbrecht, B.M.J., Jones, F.A., Lewis, O.T., Manzané-Pinzón, E. et al, 2021. Increased mortality of tropical tree seedlings during the extreme 2015-16 El Niño. Glob. Chang. Biol. 27, 5043–5053. https://doi.org/10.1111/gcb.15809.

Camargo, P.B. de, Trumbore, S.E., Martinelli, L.A., Davidson, E.A., Nepstad, D.C., Victoria, R.L., 1999. Soil carbon dynamics in regrowing forest of eastern Amazonia. Glob. Chang. Biol. 5, 693–702. https://doi.org/10.1046/j.1365-2486.1999.00259.x.

CBD, 2022. COP15: Final text of Kunming-Montreal Global Biodiversity Framework. https://www.cbd.int/article/cop15-final-text-kunming-montreal-gbf-221222.

Cesarz, S., Craven, D., Auge, H., Bruelheide, H., Castagneyrol, B., Gutknecht, J. et al, 2022. Tree diversity effects on soil microbial biomass and respiration are context dependent across forest diversity experiments. Global Ecol. Biogeogr. 31, 872–885. https://doi.org/10.1111/geb.13461.

Chen, S., Wang, W., Xu, W., Wang, Y., Wan, H., Chen, D. et al, 2018. Plant diversity enhances productivity and soil carbon storage. PNAS 115, 4027–4032. https://doi.org/10.1073/pnas.1700298114.

Chen, X., Chen, H.Y.H., Chen, C., Ma, Z., Searle, E.B., Yu, Z. et al, 2020. Effects of plant diversity on soil carbon in diverse ecosystems: a global meta-analysis. Biol. Rev. 95, 167–183. https://doi.org/10.1111/brv.12554.

Chen, X., Taylor, A.R., Reich, P.B., Hisano, M., Chen, H.Y.H., Chang, S.X., 2023. Tree diversity increases decadal forest soil carbon and nitrogen accrual. Nature 618, 94–101. https://doi.org/10.1038/s41586-023-05941-9.

Coll, L., Potvin, C., Messier, C., Delagrange, S., 2008. Root architecture and allocation patterns of eight native tropical species with different successional status used in open-grown mixed plantations in Panama. Trees 22, 585–596. https://doi.org/10.1007/s00468-008-0219-6.

Cusack, D.F., Halterman, S.M., Tanner, E.V., Wright, S.J., Hockaday, W., Dietterich, L.H. et al, 2018. Decadal-scale litter manipulation alters the biochemical and physical character of tropical forest soil carbon. Soil Biol. Biochem. 124, 199–209. https://doi.org/10.1016/j.soilbio.2018.06.005.

Depauw, L., Lombaerde, E. de, Dhiedt, E., Blondeel, H., Abdala-Roberts, L., Auge, H. et al, 2024. Enhancing Tree Performance Through Species Mixing: Review of a Quarter-Century of TreeDivNet Experiments Reveals Research Gaps and Practical Insights. Curr. For. Rep., 1–20. https://doi.org/10.1007/s40725-023-00208-y.

Detto, M., Wright, S.J., Calderón, O., Muller-Landau, H.C., 2018. Resource acquisition and reproductive strategies of tropical forest in response to the El Niño–Southern Oscillation. Nat. Commun. 9, 913. https://doi.org/10.1038/s41467-018-03306-9.

Dooley, K., Keith, H., Larson, A., Catacora-Vargas, G., Carton, W., Christiansen, K.L. et al, 2022. The Land Gap Report 2022.

Elias, M., Potvin, C., 2003. Assessing inter- and intra-specific variation in trunk carbon concentration for 32 neotropical tree species. Can. J. For. Res. 33, 1039–1045. https://doi.org/10.1139/x03-018.

Frazer, G.W., Canham, C.D., Lertzman, K.P., 1999. Gap Light Analyzer (GLA), Version 2.0: Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation. Simon Fraser University, Burnaby, British Columbia, and the Institute of Ecosystem Studies, Millbrook, New York.

Gardon, F.R., Santos, R.F.d., Rodrigues, R.R., 2020. Brazil's forest restoration, biomass and carbon stocks: A critical review of the knowledge gaps. For. Ecol. Manage. 462, 117972. https://doi.org/10.1016/j.foreco.2020.117972.

Griscom, B.W., Adams, J., Ellis, P.W., Houghton, R.A., Lomax, G., Miteva, D.A. et al, 2017. Natural climate solutions. PNAS 114, 11645–11650. https://doi.org/10.1073/pnas.1710465114.

Guerrero-Ramírez, N.R., Craven, D., Messier, C., Potvin, C., Turner, B.L., Handa, I.T., 2016. Root quality and decomposition environment, but not tree species richness, drive root decomposition in tropical forests. Plant Soil 404, 125–139. https://doi.org/10.1007/s11104-016-2828-y.

Guerrero-Ramírez, N.R., Craven, D., Reich, P.B., Ewel, J.J., Isbell, F., Koricheva, J. et al, 2017. Diversity-dependent temporal divergence of ecosystem functioning in experimental ecosystems. Nat. Ecol. Evol. 1, 1639–1642. https://doi.org/10.1038/s41559-017-0325-1.

Guillemot, J., Kunz, M., Schnabel, F., Fichtner, A., Madsen, C.P., Gebauer, T. et al, 2020. Neighbourhood-mediated shifts in tree biomass allocation drive overyielding in tropical species mixtures. New Phytol. 228, 1256–1268. https://doi.org/10.1111/nph.16722.

Handa, I.T., Aerts, R., Berendse, F., Berg, M.P., Bruder, A., Butenschoen, O. et al, 2014. Consequences of biodiversity loss for litter decomposition across biomes. Nature 509, 218–221. https://doi.org/10.1038/nature13247.

Healy, C., Gotelli, N.J., Potvin, C., 2008. Partitioning the effects of biodiversity and environmental heterogeneity for productivity and mortality in a tropical tree plantation. J. Ecol. 96, 903–913. https://doi.org/10.1111/j.1365-2745.2008.01419.x.

Huang, Y., Ma, Y., Zhao, K., Niklaus, P.A., Schmid, B., He, J.-S., 2017. Positive effects of tree species diversity on litterfall quantity and quality along a secondary successional chronosequence in a subtropical forest. J. Plant Ecol. 10, 28–35. https://doi.org/10.1093/jpe/rtw115.

Hutchison, C., Gravel, D., Guichard, F., Potvin, C., 2018. Effect of diversity on growth, mortality, and loss of resilience to extreme climate events in a tropical planted forest experiment. Sci. Rep. 8, 15443. https://doi.org/10.1038/s41598-018-33670-x.

Isbell, F., Cowles, J., Dee, L.E., Loreau, M., Reich, P.B., Gonzalez, A. et al, 2018. Quantifying effects of biodiversity on ecosystem functioning across times and places. Ecol. Lett. 21, 763–778. https://doi.org/10.1111/ele.12928.

Jucker, T., Bouriaud, O., Avacaritei, D., Coomes, D.A., 2014. Stabilizing effects of diversity on aboveground wood production in forest ecosystems: linking patterns and processes. Ecol. Lett. 17, 1560–1569. https://doi.org/10.1111/ele.12382.

Jucker, T., Koricheva, J., Finér, L., Bouriaud, O., Iacopetti, G., Coomes, D.A., 2020. Good things take time – diversity effects on tree growth shift from negative to positive during stand development in boreal forests. J. Ecol. 108. https://doi.org/10.1111/1365-2745.13464.

Kunert, N., Brändle, J., El-Madany, T.S., 2022. Carbon allocation and tree diversity: shifts in autotrophic respiration in tree mixtures compared to monocultures. Biologia 77, 3385–3396. https://doi.org/10.1007/s11756-022-01141-4.

Kunert, N., El-Madany, T.S., Aparecido, L.M.T., Wolf, S., Potvin, C., 2019. Understanding the controls over forest carbon use efficiency on small spatial scales: Effects of forest disturbance and tree diversity. Agric. For. Meteorol. 269-270, 136–144.

Kunz, M., Fichtner, A., Härdtle, W., Raumonen, P., Bruelheide, H., Oheimb, G. von, 2019. Neighbour species richness and local structural variability modulate aboveground allocation patterns and crown morphology of individual trees. Ecol. Lett. 22, 2130–2140. https://doi.org/10.1111/ele.13400.

Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2017. lmerTest Package: Tests in Linear Mixed Effects Models. J. Stat. Softw. 82, 1–26. https://doi.org/10.18637/jss.v082.i13.

Laganière, J., Angers, D.A., Paré, D., 2010. Carbon accumulation in agricultural soils after afforestation: a meta-analysis. Glob. Chang. Biol. 16, 439–453. https://doi.org/10.1111/j.1365-2486.2009.01930.x.

Lange, M., Eisenhauer, N., Sierra, C.A., Bessler, H., Engels, C., Griffiths, R.I. et al, 2015. Plant diversity increases soil microbial activity and soil carbon storage. Nat. Commun. 6, 6707. https://doi.org/10.1038/ncomms7707.

Lecina-Diaz, J., Alvarez, A., Regos, A., Drapeau, P., Paquette, A., Messier, C. et al, 2018. The positive carbon stocks-biodiversity relationship in forests: co-occurrence and drivers across five subclimates. Ecol. Appl. 28, 1481–1493. https://doi.org/10.1002/eap.1749.

Lefcheck, J.S., 2016. piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. Methods Ecol. Evol. 7, 573–579. https://doi.org/10.1111/2041-210X.12512.

Lefcheck, J.S., Orth, R.J., Dennison, W.C., Wilcox, D.J., Murphy, R.R., Keisman, J. et al, 2018. Long-term nutrient reductions lead to the unprecedented recovery of a temperate coastal region. PNAS 115, 3658–3662. https://doi.org/10.1073/pnas.1715798115.

Lenth, R., 2020. emmeans: Estimated Marginal Means, aka Least-Squares Means.

Lewis, S.L., Wheeler, C.E., Mitchard, E.T.A., Koch, A., 2019. Restoring natural forests is the best way to remove atmospheric carbon. Nature 568, 25–28. https://doi.org/10.1038/d41586-019-01026-8.

Li, Y., Liu, X., Xu, W., Bongers, F.J., Bao, W., Chen, B. et al, 2020. Effects of diversity, climate and litter on soil organic carbon storage in subtropical forests. For. Ecol. Manage. 476, 118479. https://doi.org/10.1016/j.foreco.2020.118479.

Liu, X., Trogisch, S., He, J.-S., Niklaus, P.A., Bruelheide, H., Tang, Z. et al, 2018. Tree species richness increases ecosystem carbon storage in subtropical forests. Proc. Biol. Sci. 285.

Madsen, C., Potvin, C., Hall, J., Sinacore, K., Turner, B.L., Schnabel, F., 2020. Coarse root architecture: Neighbourhood and abiotic environmental effects on five tropical tree species growing in mixtures and monocultures. For. Ecol. Manage. 460, 117851. https://doi.org/10.1016/j.foreco.2019.117851.

Marín-Spiotta, E., Silver, W.L., Swanston, C.W., Ostertag, R., 2009. Soil organic matter dynamics during 80 years of reforestation of tropical pastures. Glob. Chang. Biol. 15, 1584–1597. https://doi.org/10.1111/j.1365-2486.2008.01805.x.

Martin-Guay, M.-O., Belluau, M., Côté, B., Handa, I.T., Jewell, M.D., Khlifa, R. et al, 2022. Tree identity and diversity directly affect soil moisture and temperature but not soil carbon ten years after planting. Ecol Evol 12, e8509. https://doi.org/10.1002/ece3.8509.

Messier, C., Bauhus, J., Sousa-Silva, R., Auge, H., Baeten, L., Barsoum, N. et al, 2021. For the sake of resilience and multifunctionality, let's diversify planted forests! Conserv. Lett. 15, e12829. https://doi.org/10.1111/conl.12829.

Moore, T.R., Abraham, M., Kalácska, M., Murphy, M.T., Potvin, C., 2018. Changes from pasture to a native tree plantation affect soil organic matter in a tropical soil, Panamá. Plant Soil 425, 133–143. https://doi.org/10.1007/s11104-018-3574-0.

Murphy, M., Balser, T., Buchmann, N., Hahn, V., Potvin, C., 2008. Linking tree biodiversity to belowground process in a young tropical plantation: Impacts on soil CO2 flux. For. Ecol. Manage. 255, 2577–2588. https://doi.org/10.1016/j.foreco.2008.01.034.

Neumann-Cosel, L., Zimmermann, B., Hall, J.S., van Breugel, M., Elsenbeer, H., 2011. Soil carbon dynamics under young tropical secondary forests on former pastures—A case study from Panama. For. Ecol. Manage. 261, 1625–1633. https://doi.org/10.1016/j.foreco.2010.07.023.

Oelmann, Y., Potvin, C., Mark, T., Werther, L., Tapernon, S., Wilcke, W., 2010. Tree mixture effects on aboveground nutrient pools of trees in an experimental plantation in Panama. Plant Soil 326, 199–212. https://doi.org/10.1007/s11104-009-9997-x.

Parr, C.L., Te Beest, M., Stevens, N., 2024. Conflation of reforestation with restoration is widespread. Science 383, 698–701. https://doi.org/10.1126/science.adj0899.

Potvin, C., Dutilleul, P., 2009. Neighborhood effects and size-asymmetric competition in a tree plantation varying in diversity. Ecology 90, 321–327. https://doi.org/10.1890/08-0353.1.

Potvin, C., Mancilla, L., Buchmann, N., Monteza, J., Moore, T., Murphy, M. et al, 2011. An ecosystem approach to biodiversity effects: Carbon pools in a tropical tree plantation. For. Ecol. Manage. 261, 1614–1624. https://doi.org/10.1016/j.foreco.2010.11.015.

Quartucci, F., Gocke, M., Denich, M., Moraes Gonçalves, J.L. de, Amelung, W., 2023. Deep soil carbon loss offsets rapid aboveground carbon accumulation after reforestation. For. Ecol. Manage. 548, 121403. https://doi.org/10.1016/j.foreco.2023.121403.

Rasmussen, C., Heckman, K., Wieder, W.R., Keiluweit, M., Lawrence, C.R., Berhe, A.A. et al, 2018. Beyond clay: towards an improved set of variables for predicting soil organic matter content. Biogeochemistry 137, 297–306. https://doi.org/10.1007/s10533-018-0424-3.

Ravenek, J.M., Bessler, H., Engels, C., Scherer-Lorenzen, M., Gessler, A., Gockele, A. et al, 2014. Long-term study of root biomass in a biodiversity experiment reveals shifts in diversity effects over time. Oikos 123, 1528–1536. https://doi.org/10.1111/oik.01502.

Ruiz-Jaen, M.C., Potvin, C., 2011. Can we predict carbon stocks in tropical ecosystems from tree diversity? Comparing species and functional diversity in a plantation and a natural forest. New Phytol. 189, 978–987. https://doi.org/10.1111/j.1469-8137.2010.03501.x.

Sapijanskas, J., Paquette, A., Potvin, C., Kunert, N., Loreau, M., 2014. Tropical tree diversity enhances light capture through crown plasticity and spatial and temporal niche differences. Ecology 95, 2479–2492. https://doi.org/10.1890/13-1366.1.

Sapijanskas, J., Potvin, C., Loreau, M., 2013. Beyond shading: Litter production by neighbors contributes to overyielding in tropical trees. Ecology 94, 941–952. https://doi.org/10.1890/12-0337.1.

Sayer, E.J., Leitman, S.F., Wright, S.J., Rodtassana, C., Vincent, A.G., Bréchet, L.M. et al, 2024. Tropical forest above-ground productivity is maintained by nutrients cycled in litter. J. Ecol. 112, 690–700. https://doi.org/10.1111/1365-2745.14251.

Scherer-Lorenzen, M., Luis Bonilla, J., Potvin, C., 2007. Tree species richness affects litter production and decomposition rates in a tropical biodiversity experiment. Oikos 116, 2108–2124. https://doi.org/10.1111/j.2007.0030-1299.16065.x.

Scherer-Lorenzen, M., Potvin, C., Koricheva, J., Schmid, B., Hector, A., Bornik, Z. et al, 2005. The Design of Experimental Tree Plantations for Functional Biodiversity Research, in: Scherer-Lorenzen, M., Körner, C., Schulze, E.D. (Eds.), Forest Diversity and Function. Temperate and Boreal Systems. Springer, Berlin, Heidelberg. Ecological Studies, Analysis and Synthesis 176, pp. 347–376.

Schnabel, F., Liu, X., Kunz, M., Barry, K.E., Bongers, F.J., Bruelheide, H. et al, 2021. Species richness stabilizes productivity via asynchrony and drought-tolerance diversity in a large-scale tree biodiversity experiment. Sci. Adv. 7. https://doi.org/10.1126/sciadv.abk1643.

Schnabel, F., Schwarz, J.A., Dănescu, A., Fichtner, A., Nock, C.A., Bauhus, J. et al, 2019. Drivers of productivity and its temporal stability in a tropical tree diversity experiment. Glob. Chang. Biol. 25, 4257-4272. https://doi.org/10.1111/gcb.14792.

Schuldt, A., Liu, X., Buscot, F., Bruelheide, H., Erfmeier, A., He, J.-S. et al, 2023. Carbon-biodiversity relationships in a highly diverse subtropical forest. Glob. Chang. Biol. 29, 5321–5333. https://doi.org/10.1111/gcb.16697.

Schwendenmann, L., Pendall, E., Sanchez-Bragado, R., Kunert, N., Hölscher, D., 2015. Tree water uptake in a tropical plantation varying in tree diversity: Interspecific differences, seasonal shifts and complementarity. Ecohydrology 8, 1–12. https://doi.org/10.1002/eco.1479.

Searle, E.B., Chen, H.Y.H., Paquette, A., 2022. Higher tree diversity is linked to higher tree mortality. PNAS 119, e2013171119. https://doi.org/10.1073/pnas.2013171119.

Seddon, N., 2022. Harnessing the potential of nature-based solutions for mitigating and adapting to climate change. Science 376, 1410–1416. https://doi.org/10.1126/science.abn9668.

van der Sande, M.T., Poorter, L., Kooistra, L., Balvanera, P., Thonicke, K., Thompson, J. et al, 2017. Biodiversity in species, traits, and structure determines carbon stocks and uptake in tropical forests. Biotropica 49, 593–603. https://doi.org/10.1111/btp.12453.

Vicente-Serrano, S.M., Beguería, S., López-Moreno, J.I., 2010. A Multiscalar Drought Index Sensitive to Global Warming: The Standardized Precipitation Evapotranspiration Index. J. Clim. 23, 1696–1718. https://doi.org/10.1175/2009JCLI2909.1.

von Haden, A.C., Yang, W.H., DeLucia, E.H., 2020. Soils' dirty little secret: Depth-based comparisons can be inadequate for quantifying changes in soil organic carbon and other mineral soil properties. Glob. Chang. Biol. 26, 3759–3770. https://doi.org/10.1111/gcb.15124.

Wallwork, A., Banin, L.F., Dent, D.H., Skiba, U., Sayer, E., 2022. Soil carbon storage is related to tree functional composition in naturally regenerating tropical forests. Funct. Ecol. 36, 3175–3187. https://doi.org/10.1111/1365-2435.14221.

Warner, E., Cook-Patton, S.C., Lewis, O.T., Brown, N., Koricheva, J., Eisenhauer, N. et al, 2023. Young mixed planted forests store more carbon than monocultures—a meta-analysis. Front. For. Glob. Change 6. https://doi.org/10.3389/ffgc.2023.1226514.

Weisser, W.W., Roscher, C., Meyer, S.T., Ebeling, A., Luo, G., Allan, E. et al, 2017. Biodiversity effects on ecosystem functioning in a 15-year grassland experiment: Patterns, mechanisms, and open questions. Basic Appl. Ecol. 23, 1–73.

Williams, L.J., Paquette, A., Cavender-Bares, J., Messier, C., Reich, P.B., 2017. Spatial complementarity in tree crowns explains overyielding in species mixtures. Nat. Ecol. Evol. 1, 63. https://doi.org/10.1038/s41559-016-0063.

Wolf, S., Eugster, W., Potvin, C., Turner, B.L., Buchmann, N., 2011. Carbon sequestration potential of tropical pasture compared with afforestation in Panama. Glob. Chang. Biol. 17, 2763–2780. https://doi.org/10.1111/j.1365-2486.2011.02460.x.

Xu, S., Eisenhauer, N., Ferlian, O., Zhang, J., Zhou, G., Lu, X. et al, 2020. Species richness promotes ecosystem carbon storage: evidence from biodiversity-ecosystem functioning experiments. Proceedings. Biological sciences 287, 20202063. https://doi.org/10.1098/rspb.2020.2063.

Yachi, S., Loreau, M., 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. PNAS 96, 1463–1468. https://doi.org/10.1073/pnas.96.4.1463.

Zanini, A.M., Mayrinck, R.C., Vieira, S.A., Camargo, P.B. de, Rodrigues, R.R., 2021. The effect of ecological restoration methods on carbon stocks in the Brazilian Atlantic Forest. For. Ecol. Manage. 481, 118734. https://doi.org/10.1016/j.foreco.2020.118734.

Zeugin, F., Potvin, C., Jansa, J., Scherer-Lorenzen, M., 2010. Is tree diversity an important driver for phosphorus and nitrogen acquisition of a young tropical plantation? For. Ecol. Manage. 260, 1424–1433. https://doi.org/10.1016/j.foreco.2010.07.020.