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On the rebound: soil organic carbon stocks can bounce back to near forest levels when agroforests replace agriculture in southern India

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Abstract

Tropical agroforestry has an enormous potential to sequester carbon while simultaneously producing agricultural yields and tree products. The amount of soil organic carbon (SOC) sequestered is however influenced by the type of the agroforestry system established, the soil and climatic conditions and management. In this regional scale study, we utilized a chronosequence approach to investigate how SOC stocks changed when the original forests are converted to agriculture, and then subsequently to four different agroforestry systems (AFSs): homegarden, coffee, coconut and mango. In total we established 224 plots in 56 plot clusters across four climate zones in southern India. Each plot cluster consisted of four plots: a natural forest reference plot, an agriculture reference and two of the same AFS types of two ages (30–60 years and > 60 years). The conversion of forest to agriculture resulted in a large loss the original SOC stock (50–61 %) in the top meter of soil depending on the climate zone. The establishment of homegarden and coffee AFSs on agriculture land caused SOC stocks to rebound to near forest levels, while in mango and coconut AFSs the SOC stock increased only slightly above the agriculture stock. The most important variable regulating SOC stocks and its changes was tree basal area, possibly indicative of organic matter inputs. Furthermore, climatic variables such as temperature and precipitation, and soil variables such as clay fraction and soil pH were likewise all important regulators of SOC and SOC stock changes. Lastly, we found a strong correlation between tree species diversity in homegarden and coffee AFSs and SOC stocks, highlighting possibilities to increase carbon stocks by proper tree species assemblies.

1 Introduction

Land-use changes in the tropics are responsible for approximately 10 % of the human induced greenhouse gas emissions and are expected to remain the second largest source of carbon (C) emissions in the near future (Achard et al., 2014). Considering

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that tropical forest soils store a similar amount of organic carbon (692 Gt in the top 3 m; Jobbágy and Jackson, 2000) as the atmosphere (589 Gt C; Ciais et al., 2013), and that tropical climates foster rapid organic matter decomposition, land-use changes can result in strong carbon fluxes into or out of the soil. The conversion of tropical forests to agriculture causes both a release of stored soil organic carbon, often in the form of carbon dioxide, but it also results in a decline in soil productivity. To reduce carbon emissions from agriculture while simultaneously maintaining agricultural productivity it is necessary to identify and implement simple and cost effective measures to store and capture carbon. In this context agroforestry practices, which integrate trees into agricultural systems, offer a unique opportunity to sequester atmospheric carbon while also growing food, diversifying incomes (e.g. from sale of wood, fruit and staple foods), and simultaneously providing numerous environmental benefits. These include mitigating soil erosion (Montagnini and Nair, 2004), improving soil structure (Lal, 2007), pumping up nutrients from the subsoil (Das and Chaturvedi, 2008) and sequestering atmospheric carbon (Lal, 2007; Nair et al., 2009). Agroforestry systems (AFSs) have higher SOC sequestration rates than conventional agricultural systems (Nair et al., 2009) as the trees they have comparatively higher litter inputs and are capable of inserting carbon deep in the soil with their root systems (Montagnini and Nair, 2004).

Furthermore, tree species diversity in AFSs can have a large impact on organic matter turnover as diverse species mixtures can add different qualities of organic matter which correspondingly influence soil microbial communities and decomposition processes (Six et al., 2002; Acker et al., 2002). Niche differentiation and resource partitioning may lead to a better use of space and nutrient uptake and thus increase ecosystem carbon inputs (Thakur et al., 2015). Although it is recognized that AFSs have many benefits, their C sequestration potential, especially belowground, remains largely unexplored (Montagnini and Nair, 2004). Concentration and SOC turnover rates in AFSs vary significantly with biophysical site properties such as climate (Liu et al., 2011), vegetation, land-use types (Cadotte, 2013; Saha et al., 2010), soil type and texture (Six et al., 2002; Chaplot et al., 2010), land management (Hevia et al., 2003) and their interac-

tions (Powers and Schlesinger, 2002). It is generally recognized that temperature and precipitation are the most important variables regulating SOC (Chaplot et al., 2010; Liu et al., 2011). Since both affect the type of vegetation cover, the quantity of biomass production and the rate of SOM turnover (Hevia et al., 2003).

It is estimated that there are approximately 25.3 million hectares (Dhyani et al., 2013) of AFSs established across India, whereby the type of AFS established depends on the biophysical site conditions and the socioeconomic status of the owners. Despite this, regional-scale studies evaluating the impacts the establishment these land-use types have on SOC stocks remain relatively scarce (Albrecht and Kandji, 2003; Mutuo et al., 2005; Saha et al., 2010). Here in this study, we quantified SOC changes associated with the conversion of forest to agriculture and subsequently from agriculture to four different AFS types (homegarden, coffee, coconut and mango). Our plots were established across southern India in a broad range of biophysical conditions, ranging from semi-arid to humid climates and in soils with low and high activity clays. The objectives of this study were as follows:

1. to quantify SOC stocks and SOC stocks changes along a forest – agriculture – AFS trajectory, and
2. to determine the biophysical drivers regulating SOC stocks and its changes.

2 Materials and methods

2.1 Study area

The study was conducted across three states in Southern India (Kerala, Karnataka and Andhra Pradesh; Fig. 1), in an area that has a long-standing history of diverse agroforestry-based land-use practices. The region has a tropical monsoon climate, with a rainy season from May to October and a distinct dry season from November to April. The mean annual precipitation (MAP) ranges from 627 to 3422 mm and mean annual

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temperature (MAT) ranges between 21.9°C in the highlands to 27.2°C at lower elevations (Hijmans et al., 2005). The soils were classified as Luvisols, Acrisols or Nitisols.

2.2 Sampling design and site selection

In this study we investigated how SOC stocks changed when forests are converted to agriculture and subsequently to agroforestry systems in four different climatic zones along a precipitation gradient (humid, moist sub-humid, dry sub-humid and semi-arid; based on classification by ICAR (1984). Each AFS type was sampled in two of four climatic zones based on its relative importance in terms of area, production and income in the region (Table 1). Using a chronosequence approach we established 56 plot clusters (Fig. 1). A plot cluster consisted of four land-use types: a natural forest reference and an agriculture reference and two AFS plots at different ages, medium (30–60 years) and old (> 60 years). Seven plot clusters were established for each AFS type in two climatic zones. In total 224 plots were set up (4 AFSs × 2 climate zones × 7 clusters × 4 land-use types).

The plot clusters were always centered around the natural forest reference plot. To reduce edge effects, the forest plots were selected at least 40 m from the forest edge. Clusters were chosen to only include plots with similar biophysical conditions (e.g. soil texture, landscape position, elevation, slope). Furthermore we chose sites which were well drained, had deeply weathered soils (no stones) and had not been limed.

2.3 Land-use systems and forest reference

Each AFS type consisted of a unique combination of trees and crops (Table 1) and originated from former agricultural land with the exception of 19 coffee plots and one homegarden plot which replaced forests directly. Pictures of the investigated land-use types in the different climate zones are found in Fig. A1 in Appendix A.

The homegarden AFS has a multilayered canopy, consisting of a diverse tree-admixture of different ages and sizes. The multipurpose trees grown here are found

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to calculate the soil carbon stock of the agroforestry and agriculture plots within each the cluster (Veldkamp et al., 1994). Additionally, we determined the pH of air-dried soil in a 1 : 2.5 soil-to-water solution for all sampling depths, and soil texture for two depths (0–10, 10–30 cm) using the pipette sedimentation method.

At each plot, we measured tree basal area for all trees with a diameter at breast height greater than 10 cm. These tree species were identified to the species level. Furthermore, we recorded information on slope, elevation and geographical coordinates of each plot. Through informal interviews with the land-owners we got information on current and past land-uses and their management practices. Meteorological data such as mean annual temperature and mean annual precipitation for the selected plots was retrieved from the WorldClim database (Hijmans et al., 2005).

2.5 Statistical analysis

To verify that plots were satisfactorily selected in the field and that the soils of the plot pairs were inherently similar we did an a posteriori comparison of soil clay percentages in the subsoil (10–30 cm) of the plot pairs using a paired *t* test analysis. To estimate the size of SOC stock changes following land-use change (either from forest to agriculture or from agriculture to AFS), we calculated the difference in SOC stocks between plot pairs. The percent-difference in SOC stocks was then expressed as the relative change to the respective reference SOC stock (forest reference for agriculture; agriculture reference for AFSs) ($\text{Relative change} = (\text{SOC}_{\text{converted}} - \text{SOC}_{\text{reference}}) / \text{SOC}_{\text{reference}} \times 100$). The influence of climate and site variables on SOC stocks and relative SOC stock changes was evaluated by linear and non-linear regression analyses across AFSs for single variables and with stepwise linear multivariate analyses for each system.

The residuals of all models were checked for normality with *Q-Q*-plots; models were considered significant at the $p \geq 0.05$ level. All statistical analyses were done using the software package R – version 2.15.0 (R Development Core Team, 2014).

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3 Results

3.1 Comparability of plot pairs

Based on the assumption that land-use changes do not directly affect soil texture, we found that the clay percent changes for the forest-to-agriculture conversion in agricultural plots were slightly lower than in the forest reference (difference of $-5.5 \pm 0.5\%$), while for the agriculture-to-AFSs conversion, clay percentages were slightly higher in the AFSs (difference of $2.3 \pm 0.4\%$). Considering how small these differences are, we feel confident to attribute any differences in SOC stocks to land-use changes.

3.2 Land-use change impacts on SOC stocks

Among the land-use types investigated, SOC concentrations (data not shown) and SOC stocks were highest in natural forest, lowest in agriculture and intermediate for the different AFSs (Fig. 2). Deforestation for agriculture resulted in a strong decrease in SOC stocks across all climate zones, creating a loss of 50 to 61 % of the original SOC stock. The resulting SOC stocks of AFSs however were dependent on AFS type. While SOC stocks in homegarden and coffee AFSs rebounded to near forest levels, the SOC stocks in both coconut and mango AFSs increased only marginally compared to the agricultural reference (Figs. 2 and 3).

Of the AFSs studied, SOC stocks in the top meter of soil were highest in coffee ($156 \pm 10 \text{ Mg C ha}^{-1}$) followed by homegarden ($151 \pm 5 \text{ Mg C ha}^{-1}$), coconut ($98 \pm 7 \text{ Mg C ha}^{-1}$) and lowest in mango AFSs ($76 \pm 3 \text{ Mg C ha}^{-1}$). AFS establishment on agricultural land caused SOC stocks to increase significantly in all AFSs, with SOC gains ranging from $\sim 45\%$ in coconut in dry sub-humid zones to $\sim 103\%$ in homegarden in humid zones (Fig. 3). Furthermore, significant SOC stock gains were measured at all soil depths (with the exception of coffee in the subsoil (60–100 cm)). Homegardens exhibited the highest overall SOC stock gains, being relatively uniform throughout the soil profile. This was followed by coffee which, in contrast, had highest SOC stock

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gains at the soil surface and decreased with depth. Lastly, SOC stock gains in mango and coconut AFSs were comparatively low, but constant throughout the soil profile (Fig. 3).

The climate zone had a marginal influence on overall SOC stocks of a given AFS where only coconut and mango AFSs showed a tendency towards higher SOC stocks in the respective wetter climate zone (Fig. 2). Also the SOC stocks of the AFSs did not differ among the two age categories sampled (Fig. 2).

3.3 Predicting SOC stocks and relative changes in SOC stocks

In undisturbed forest ecosystems 82% of the variance in SOC stocks could be significantly explained by five variables (MAP, MAT, basal area, clay fraction and soil pH) using stepwise multivariate regression analyses (Table 2). While tree basal area and clay fraction exhibited positive linear correlations with SOC stock, both soil pH and MAP exhibited parabolic and inverse parabolic relationships respectively (Fig. 4a–d). For pH, SOC stocks were lowest at a near-neutral conditions while SOC stocks peaked between 2000 and 3000 mm yr⁻¹ MAP.

Basal area was the single best predictor of forest SOC stocks. This is evident in both, the scatterplot graphs in Fig. 4b and from its dominant position in the multivariate regressions for all land uses investigated (Table 2), except in agriculture which had no trees. Likewise, soil clay fraction was also an important predictor of soil SOC and was present in all AFSs regression equations except homegardens. Although MAT was an influential predictor of forest SOC stocks in the stepwise regression (found in 3 of the 6 prediction models; Table 2), yet taken as single predictor its influence on SOC stocks remains insignificant. SOC stocks in both homegarden and coffee AFSs are further positively correlated to the Shannon Wiener species diversity index of trees (Fig. 5). Coconut and mango AFSs however were not included as they are monocultures in terms of tree or palm species admixture.

The SOC stock losses attributed to the conversion of forests to agriculture could be predicted by two variables: clay fraction and MAT (Table 2). Thereafter, when agricul-

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positive correlation between SOC stocks and clay fraction (Table 2, Fig. 4c). Next, the parabolic relationship we observed between soil pH and forest SOC stocks (Fig. 4d) reflect how the soil biochemical environment is critically important for soil microbial communities that decompose organic matter (van Noordwijk et al., 1997). The high SOC stocks which we found under acidic conditions indicate that decomposition processes declined, perhaps due to the accumulation of toxic cations such as aluminum which hindered microbial populations (Pietri and Brookes, 2009). At a near-neutral soil pH, conditions were ideal for microbial communities and accordingly decomposition rates were high, resulting in little SOC accumulation. Finally, at a pH of above seven the SOC stocks were again slightly higher and such trends have previously been attributed to differences in soil mineralogy (van Noordwijk et al., 1997).

As expected, regions of higher rainfall stored more SOC than drier zones (Fig. 2). This is likely because the natural forests in the humid zone have higher net primary production given the favorable year-round water availability compared to forests in the drier regions. Unexpectedly however, at very high levels of precipitation ($> 3000 \text{ mm yr}^{-1}$) SOC stocks declined again (Fig. 4a). We suspect that this decrease at high precipitation is related to the corresponding lower ecosystem biomass (using basal area as a proxy; Fig. A2, Appendix A). Both the decrease in SOC stocks and basal area at high precipitation could be explained by the torrential monsoon rains. Although the overall rainfall amount may be higher, its intensity and distribution over time causes much of it to runoff, which is then not available to plants when they need it. Meanwhile, it has been reported that the leachate from these soils may also contain high DOC concentrations (Lal, 2003).

Although MAT is a significant predictor of forest SOC stocks, its influence can only be evaluated in interaction with other variables (Fig. A3a, Appendix A). Although one would expect a strong correlation between MAT and MAP, it was not present here. While MAT is mainly driven by altitude, MAP depends on more complex weather phenomena that differ among climate zones. This might also explain why there is no clear

relationship between MAT and SOC when other variables are not included in the analysis.

4.2 Agriculture establishment causes up to 61 % SOC losses

In comparison to a large pool of studies on this land-use conversion conducted in the tropics, the SOC losses detected here for the different climate zones were at the higher end (50–61 %). Results from two meta-analyses report SOC stock decreases on average between 18 % (Powers et al., 2011) and 25 % (Don et al., 2011) for this land-use conversion in the tropics. Powers et al. (2011) however report that large SOC losses are possible (to a maximum of 76 %), but the losses depend on the clay mineralogy and precipitation regimes. Nevertheless, in our study we measured significant decreases in SOC stocks irrespective of soil type and precipitation regimes. We primarily attribute these large SOC losses to the frequent tilling and low organic matter inputs. Tillage exposes SOC to microbial activity through the destruction of aggregates which as a result makes SOC complexes vulnerable to decomposition (Six et al., 2002; Mangalassery et al., 2013). Furthermore, SOC stocks in agriculture systems can also be lost through erosion, runoff and leaching due to a lack of soil protection measures (Lal, 2003). However since all our plots were established on gentle slopes, erosion is of minor importance.

As previously reported by van Straaten et al. (2015), we also found that SOC stock losses were proportional to the initial forest SOC stock, whereby the higher the SOC stock was initially, the larger the corresponding SOC stock loss when converted to agriculture (Fig. A4, Appendix A).

4.3 SOC stocks rebound when agroforestry systems are established

Increases in SOC stocks resulting from agroforestry establishment are ultimately attributed to higher organic matter inputs from above- and belowground sources (leaves, wood, roots, fungi, animals, etc.; Montagnini and Nair, 2004) and a reduction of SOC

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losses from decomposition and leaching. Similar to the carbon stocks in forests, MAP, basal area, clay fraction and pH also control carbon stock changes when agricultural land is converted to agroforestry (Table 2, Fig. 4e–h). Furthermore, the accumulation of SOC depends highly on the quality of incoming litter (Lemma et al., 2006) and is reflected in the significantly higher soil C : N ratios in homegarden, coconut and mango AFSs (Fig. A5, Appendix A). In comparison to litter from agricultural crops, which generally have low C : N ratios and decompose rapidly, organic matter inputs from trees are generally of poorer quality (higher C : N ratios) because of the higher lignin and polyphenolic contents, which in turn results in slower decomposition rates and more SOC accumulation (Davidson and Janssens, 2006).

The relatively constant SOC stocks increases throughout the soil profile for each respective AFS (Fig. 3) indicate that belowground carbon inputs from roots and/or leaching of organic acids and soluble humus fractions to deeper layers are important processes for SOC accumulation. Considering the trees of the four AFSs have deeper rooting profiles than agricultural crops and that often more than half of the carbon assimilated by trees is transported belowground for root production (Montagnini and Nair, 2004), it is no surprise that SOC stocks also increased substantially at depth. Furthermore, tillage activities will have mixed soils in the top 30 cm and therein homogenized soil carbon concentrations to a certain extent (Yang and Kay, 2001).

However, the size of the SOC stock change hinges on the type of AFS established and its management practices. While all AFSs gained carbon compared to agriculture, the amounts gained varied strongly between the different types (Fig. 2). While coconut and mango SOC stocks increased just marginally above the agriculture reference, homegarden and coffee SOC stocks rebounded to forest levels. Clearly, the carbon cycling dynamics of both homegarden and coffee AFSs resemble that of natural forests since both AFSs support many different tree species of different ages, have varied stand structures and have high basal areas.

However, not only carbon input, but also losses are a function of AFS type, especially in terms of the plantation management schemes. In coconut and mango AFSs

(especially in the dry regions), the low SOC stock increases are linked to the removal of crop residues (including leaves) from the site which are used as fodder or fuel. In coconut, even the tree leaves are removed and utilized.

The effect of climate zone on SOC stock changes can only be quantified within each AFS type. While the climate zone did not affect SOC stock changes in either coffee or homegarden AFSs, only a slight difference were found for coconut and mango (Fig. 2). This is however more likely attributed to the implementation of different management practices and cannot be disentangled from climate itself. For instance, in humid climates coconut farmers utilize a “planted fallow system” which includes a fallow period in the cropping cycle where organic matter is reintegrated into the soil. Such systems have been shown to improve soil fertility and maintain SOC stocks (Salako et al., 1999). In contrast, in the dry sub-humid climate farmers use a continuous cropping system which inevitably results in lower organic matter inputs and therein lower SOC stocks. The age of each respective AFS also had no significant effect on SOC stocks (Fig. 2), indicating that soil carbon had already reached a new equilibrium within the first 30–60 years. This is consistent with literature which report that a new SOC equilibrium can be attained in 20 to 40 years following land-use conversion (Detwiler, 1986; de Blécourt et al., 2013; Chiti et al., 2014).

Lastly, tree species diversity (Shannon Wiener index) correlated strongly positively with SOC stocks in homegarden and coffee AFSs (Fig. 5), highlighting the role that species and resource complementarity have in maximizing biomass production (Cadotte, 2013). Interestingly, both homegarden and coffee AFSs investigated in this study had similar tree diversities as natural forests. Since plant diversity was also positively correlated with basal area (data not shown) it is possible that the favorable climatic conditions where these AFSs exist can allow both high species diversity and high ecosystem productivity. Literature has shown that plant diversity is integrally linked to ecosystem productivity (Cadotte, 2013) and ecosystem resource utilization (Tilman et al., 2012), which both affect SOC storage potential (Thakur et al., 2015). In contrast,

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Table 1. Environmental variables and structural characteristics of agroforestry systems in the study area (mean \pm SE).

AFS	Climatic zone*	Tree/palm species	Soil classification ¹	Elevation (m a.s.l.)	MAP ² (mm)	MAT ² (°C)	Clay content ³ (%)	Tree density ³ (tree ha ⁻¹)
Homegarden	Humid	<i>Artocarpus</i> spp., <i>Mangifera indica</i> ,	Nitisols (<i>n</i> = 4) Acrisols (<i>n</i> = 3)	90 \pm 17	3422 \pm 277	27.2 \pm 0.15	20.8 \pm 1.4	362 \pm 21
	Moist sub-humid	<i>Myristica</i> spp. and mixed species	Nitisols (<i>n</i> = 6) Luvisols (<i>n</i> = 1)	940 \pm 17	1744 \pm 52	22.1 \pm 0.15	22.6 \pm 1.2	328 \pm 17
Coffee	Humid	<i>Artocarpus</i> spp. <i>Terminalia</i> spp. and mixed forest species	Nitisols (<i>n</i> = 4) Acrisols (<i>n</i> = 2), Luvisols (<i>n</i> = 1)	956 \pm 42	2718 \pm 90	21.9 \pm 0.15	23.1 \pm 1.2	291 \pm 14
	Moist sub-humid		Nitisols (<i>n</i> = 6) Luvisols (<i>n</i> = 1)	981 \pm 36	1666 \pm 61	22.0 \pm 0.19	22.1 \pm 1.0	285 \pm 14
Coconut	Humid	<i>Cocos nucifera</i>	Nitisols (<i>n</i> = 4) Acrisols (<i>n</i> = 3)	90 \pm 17	3422 \pm 277	27.2 \pm 0.15	21.4 \pm 1.3	166 \pm 6
	Dry sub-humid		Luvisols (<i>n</i> = 4) Nitisols (<i>n</i> = 3)	860 \pm 20	688 \pm 49	23.5 \pm 0.15	19.4 \pm 1.4	177 \pm 6
Mango	Dry sub-humid	<i>Mangifera indica</i>	Luvisols (<i>n</i> = 6) Nitisols (<i>n</i> = 1)	875 \pm 29	703 \pm 29	23.3 \pm 0.19	17.9 \pm 1.3	104 \pm 6
	Semi-arid		Luvisols (<i>n</i> = 5) Nitisols (<i>n</i> = 2)	844 \pm 34	627 \pm 28	24.6 \pm 0.26	16.9 \pm 1.3	116 \pm 6

* ICAR (1984)

¹ FAO world reference base soil classification derived from Harmonized World Soil Database (FAO, 2009)² Derived from WorldClim dataset (Hijmans et al., 2005) (*n* = 7)³ Mean \pm standard error; data derived from respective agroforestry plots (*n* = 14).

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Table 2. Multivariate regression models predicting SOC stocks in different land-use systems and the relative changes in SOC stock (%) from either forest or agriculture references in the 100 cm soil profile. MAP is mean annual precipitation (mm), MAT is mean annual temperature (°C), Clay fraction (%) and basal area ($\text{m}^2 \text{ha}^{-1}$).

Land-use	Statistical model	R^2	n
SOC stock (Mg C ha^{-1})			
Forest	SOC stock = $71.7 + 4.9$ (Basal area) $- 4.3$ (MAT) $+ 1.6$ (Clay) $+ 9.0$ (pH) $+ 0.006$ (MAP)	0.82**	56
Homegarden	SOC stock = $95.1 + 3.5$ (Basal area)	0.29**	28
Coffee	SOC stock = $680.5 + 4.5$ (Basal area) $+ 4.2$ (Clay) $- 34.7$ (MAT) $+ 0.03$ (MAP)	0.64**	28
Coconut	SOC stock = $-186.7 + 11.5$ (MAT) $- 1.1$ (pH)	0.40**	28
Mango	SOC stock = $42.3 + 4.3$ (Basal area)	0.34**	28
Agriculture	SOC stock = $-25.1 + 4.4$ (Clay) $+ 0.006$ (MAP)	0.47**	56
Relative change in SOC stock (%) from forest to agriculture			
Agriculture	$\Delta\text{SOC} = -144.8 + 2.1(\text{Clay}) + 2.1(\text{MAT})$	0.34**	56
Relative change in SOC stock (%) from agriculture to AFS			
All AFSs	$\Delta\text{SOC stock} = 228.8 + 2.7$ (Basal area) $- 8.9$ (MAT) $+ 0.01$ (MAP)	0.15**	92
Homegarden	$\Delta\text{SOC stock} = 228.3 + 7.1$ (Clay) $- 4.8$ (Basal area) $- 37.1$ (pH)	0.29**	27
Coffee	$\Delta\text{SOC stock} = -8.7 - 7.1$ (Basal Area) $+ 7.7$ (Clay)	0.44	9
Coconut	$\Delta\text{SOC stock} = -223.5 + 6.3$ (Basal area) $+ 0.002$ (MAP) $+ 24.7$ (pH)	0.24 ^a	28
Mango	$\Delta\text{SOC stock} = -66.7 + 13.9$ (Basal area) $- 0.2$ (MAP) $+ 30.6$ (pH) $- 3.0$ (Clay)	0.58**	28

^a marginally significant at $p \leq 0.1$,

* significant at $p \leq 0.05$ and

** highly significant at $p \leq 0.01$

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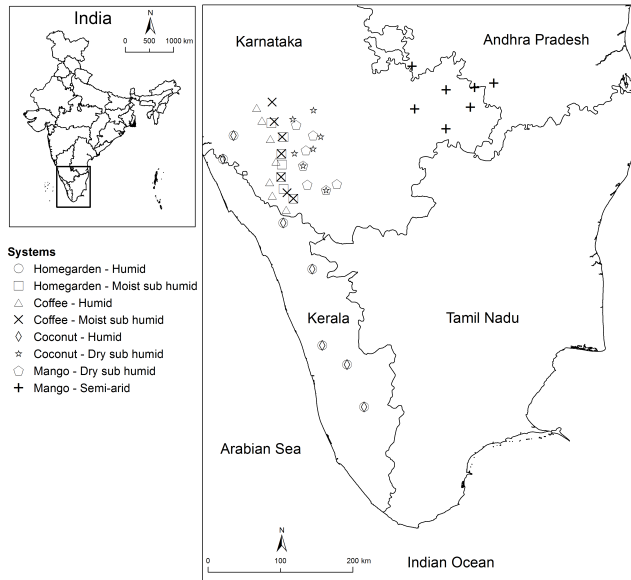


Figure 1. Geographical location of the plot clusters in southern India. Each point represents a cluster of four plots: natural forest, agriculture and the AFSs at two ages (medium and old).

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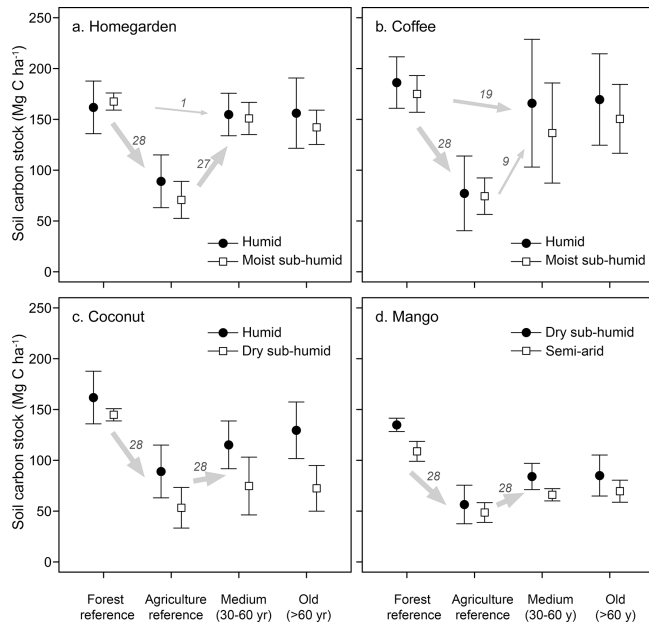



Figure 2. Mean SOC stocks (0–100 cm) in the four different land-use systems, with each graph showing the respective forest and agriculture references and the two AFSs ages categories (medium and old) in the two different climatic zones. Each point represents the mean of seven plots, while error bars indicate the 95 % confidence intervals based on the Student's *T* distribution. The arrows with corresponding numbers indicate the trajectory of the land-use change and the number of plots originating from the respective references.

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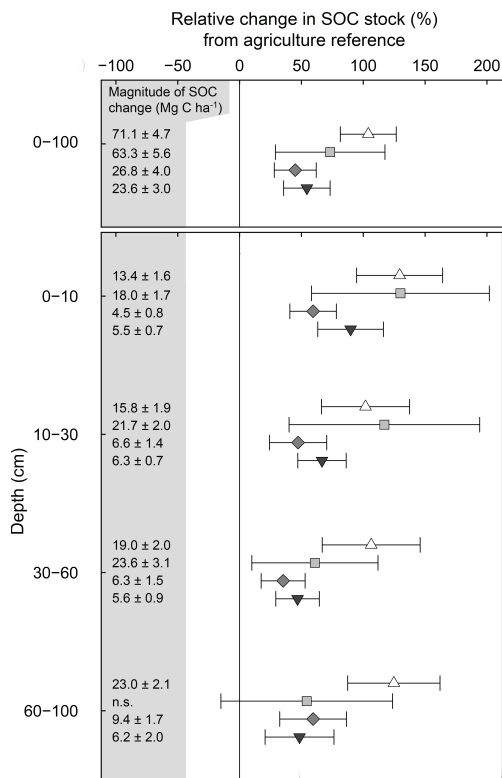


Figure 3. Relative change in SOC stock in the 1 m soil profile from agriculture to agroforestry systems (homegarden (Δ; $n = 27$), coffee (■; $n = 9$), coconut (◆; $n = 28$) and mango (▼; $n = 28$). Error bars indicate the 95% confidence intervals based on the Student's T distribution. Cumulative increase in SOC stocks (considering only the depths with significant changes). The magnitude of SOC stock increases for depths where significant changes are presented are presented in the gray-shaded area. (n.s. = not significant).

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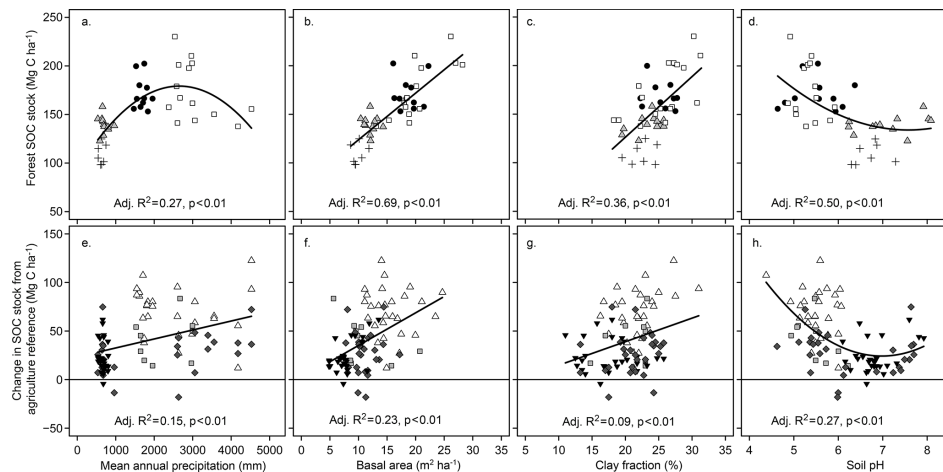


Figure 4. Scatterplots (a–d) showing the relationship forest SOC stock (top 1 m) exhibits with MAP (mm), basal area (m² ha⁻¹), soil texture (clay percent), and soil pH across humid (□), moist-sub-humid (●), dry sub-humid (▲) and semi-arid (+) climate zones. Scatterplots (e–h) show the relationship SOC stock changes (from agriculture reference) have with the same soil and biophysical variables in homegarden (Δ), coffee (■), coconut (◆) and mango (▼) AFSs.



Figure A1. Photos of the six land use types investigated in two climatic zones.

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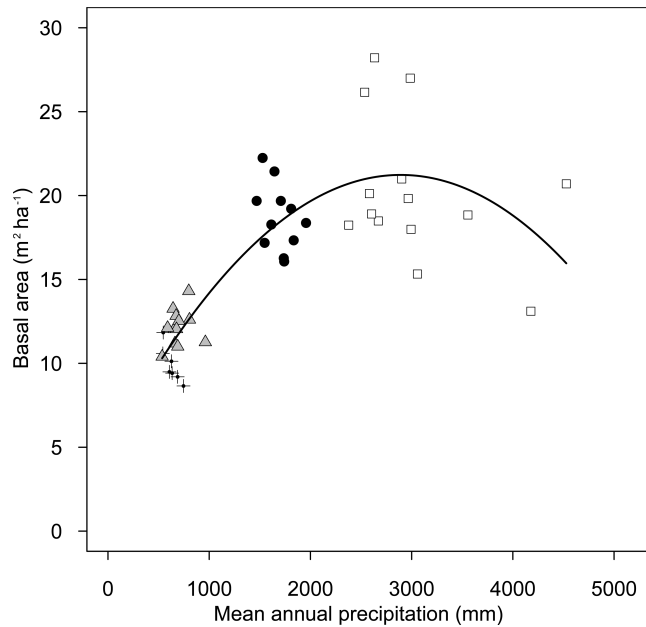
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Figure A2. Scatterplot showing the relationship between basal area ($\text{m}^2 \text{ha}^{-1}$) and MAP (mm) across humid (\square), moist-sub-humid (\bullet), dry sub-humid (Δ) and semi-arid ($+$) climate zones.

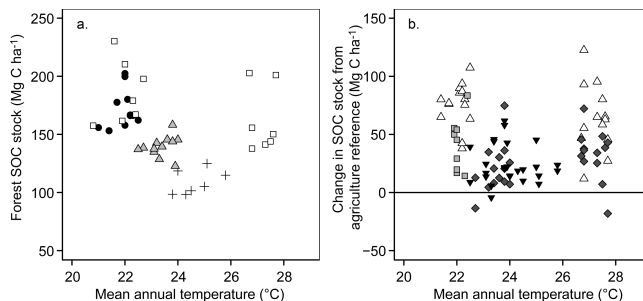


Figure A3. Scatterplots showing the relationship (or lack thereof) between MAT (°C) and **(a)** forest SOC stocks across humid (□), moist-sub-humid (●), dry sub-humid (▲) and semi-arid (+) climate zones and **(b)** changes in SOC stocks in in homegardens (Δ), coffee (■), coconut (◆) and mango (▼) AFS.

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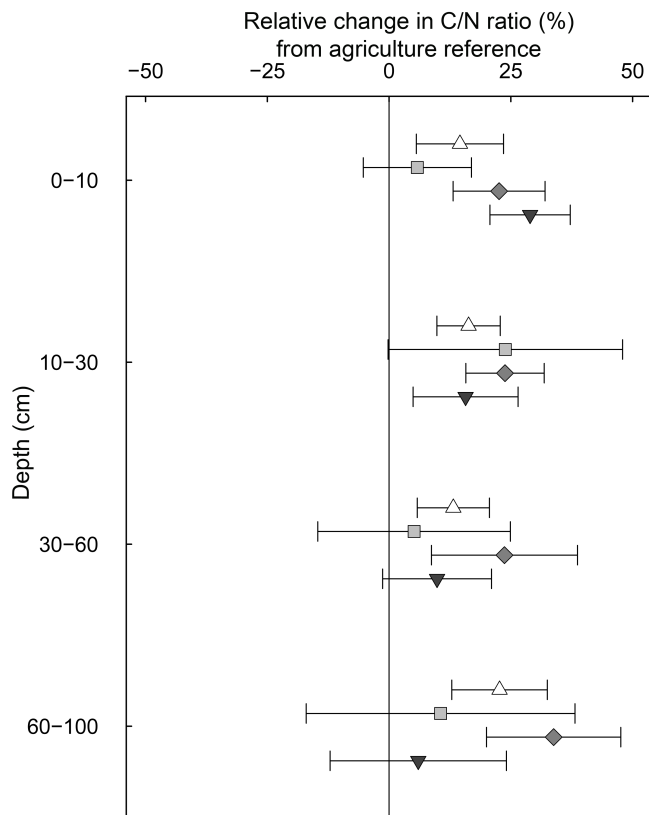


Figure A5. Relative change in C / N ratio in the 1 m soil profile from agriculture to agroforestry systems (homegarden (Δ ; $n = 27$), coffee (\blacksquare ; $n = 9$) coconut (\blacklozenge ; $n = 28$) and mango (\blacktriangledown ; $n = 28$). Error bars indicate the 95 % confidence intervals based on the Student's T distribution.

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