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RESEARCH ARTICLE

Exploring tropical forest aboveground carbon dynamics via modelled landscapes of varied food production, past and present

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Societal Impact Statement

Contemporary land use studies often place food production in direct conflict with tropical forests, with forest land use for human needs exiting in conflict with carbon-related forest conservation and biodiversity protection efforts. We highlight the more nuanced, mixed activities possible in the space between primary forest and fixed, monocultures that were, and are, practiced by Indigenous communities from the deep past into the present. Given the increasingly clear importance of the tropics to human history and contemporary human sustainability, this work has key implications for understanding past human-environment processes, empowering Indigenous stewardship and informing forest conservation policy.

Summary

- Tropical forests are key components of the global carbon cycle given their considerable carbon stocks. Agriculture is often seen as in major conflict with tropical forests, with carbon budget models highlighting dramatic carbon stock losses with the conversion of land for food. However, these models often focus on monocultural cropping systems, while the archaeological and historical records highlight more varied forms of food production in tropical forests from at least 8,000 years ago.
- Here we develop a simple model to simulate relative aboveground carbon (AGC) values for a tropical forest anthrome with varied food production practices. We examine past examples of tropical land use activities including understory thinning, selective agroforestry and various swidden patterns. We compare these to old-growth forests, open cropping and plantation systems.
- Results highlight the importance of retaining large trees to AGC. Understory thinning practices have a limited effect on AGC by mainly impacting small trees. Regular, short fallow swidden drastically reduces AGC, while irregular, long fallow swidden can maintain AGC half that of old growth forest.
- A mosaic landscape of forest food production can maintain much higher long-term mean AGC values than is typically assumed for carbon budgets of past land use.

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KEYWORDS
aboveground carbon, large trees, past land use, swidden, tropical forests

1 | INTRODUCTION

Tropical forests play a key role in various parts of the Earth system (Lewis, 2006; Mitchard, 2018), being home to over half of the planet's biodiversity and modulating regional and global hydrological cycles (Lawrence & Vandecar, 2015; Malhi et al., 2014; Roberts et al., 2023). Tropical forests are also key components of the global carbon cycle, with their combined soil and biomass carbon stocks totalling upwards of 450 Pg and comprising ~25% of global terrestrial carbon (Baccini et al., 2012; Bonan, 2008; Pan et al., 2011). So significant are the contributions of tropical forests to planetary health that they, and particularly the Amazon rainforest, have been identified as a key 'tipping element' (Wang et al., 2023; Wunderling et al., 2024) and protecting these habitats is seen as a critical part of addressing global carbon emissions (Koh et al., 2021; Saatchi et al., 2011). Here, Earth system and climate scientists have recognised the importance of factoring the effects of different land use activities on tropical forests into models of carbon stocks and fluxes, as a means of predicting their future extent under different economic and political scenarios, as well as the associated climatic feedbacks (Li et al., 2022; Spera et al., 2016). Agricultural land use activities have been seen as particularly significant in this regard, with plantation and monoculture systems, as well as combined smallholder activities, being associated with wide-scale deforestation and terrestrial carbon loss into the atmosphere (Goh et al., 2016; Pendrill et al., 2022). However, these models generally simplify the wide variety of land use activities related to food production that have existed in the tropics from 8,000 years ago (Roberts et al., 2017), if not earlier (Ellis et al., 2021), and which are still practiced by many local communities today (Schmidt et al., 2021). Many of these land use behaviours involve different relationships to the carbon cycle, and archaeological, historical and palaeoecological data, as well as Indigenous consultation, can provide a wealth of insights into alternative tropical forest land use pathways that should be considered when comparing modelled scenarios that inform policy and conservation priorities.

The anthrome concept has become increasingly useful in understanding ecosystems with various human activities as a part of the landscape (Ellis, 2011), particularly for more nuanced human-influenced ecosystems in the past (Scerri et al., 2022). It has become increasingly clear that tropical forests have a long history of human occupation and management (Hunt et al., 2012; Roberts et al., 2017). Growing evidence ties this human history to significant thresholds in land use change including the emergence of major centres of domestication in the tropics (Clement et al., 2010; Denham et al., 2020), blooming urbanism across all of the tropical continents by the Late Holocene (Chase et al., 2011; Evans & Fletcher, 2015; Prümers et al., 2022) and new approaches to land use brought by European, and later US, colonialism, between the 15th and 19th centuries (Ellis, 2021; Findley et al., 2022). These changing socioeconomic contexts had the potential to have major impacts on tropical forests and the global carbon cycle. Modelling of these historical land use/carbon stock interactions has only recently been attempted as large-scale estimates. Koch et al. (2019), for example, recently presented a high-profile study exploring the impacts of European colonialism on land use in the Americas. European invasion of the Americas brought diseases estimated to have potentially resulted in up to 90% mortality in Indigenous populations within 2–3 generations (Lewis & Maslin, 2015; Nevle et al., 2011). Koch et al. (2019) and others argue that the resulting reduction in land use would have resulted in forest regrowth significant enough to induce a notable reduction of CO_2 in the atmosphere and help to catalyse the coldest period of the Little Ice Age. This hypothesis remains controversial (Bush et al., 2021; Hamilton et al., 2021). A key point is that large-scale estimates like Koch et al. (2019) generally estimate a land-use area under cultivation and then use typical carbon uptake rates for tropical afforestation to compute biomass carbon recovered after the large population loss. This assumption is problematic, however, given ample evidence that even large Indigenous urban populations in tropical forests regularly made use of mosaics of primary forest, arboriculture, mobile field systems, more open fields and use of aquatic resources (Roberts, 2019), each maintaining a range of carbon stocks. In addition to the rate of carbon uptake during succession, constraining the relative carbon stored on a landscape with mixed food production versus that of a mature recovered forest is therefore also critical for understanding potential changes in carbon stock.

The persistence of models that place food production in direct opposition to tropical forests is problematic as it positions land use possibilities in tropical forests needed to meet human needs in conflict with the recent focus on reforestation as a key form of carbon capture (Ameray et al., 2021; Chazdon et al., 2016). In the same way that the effectiveness of reforestation is closely linked to where and how it is done (Arroyo-Rodríguez et al., 2017), as well as the land use activities that preceded it, trajectories of food production in the tropics can have a variety of different forms (Chazdon et al., 2016) which may help to balance concerns with carbon stocks, economic benefits, food security and biodiversity (Feliciano et al., 2018; Padoch & Pinedo-Vasquez, 2010). Indeed, it has been clearly shown that Indigenous stewardship of tropical forests, where peoples have both the physical ability and legal autonomy to manage forests, has been key to the maintenance of these ecosystems as carbon sinks (Pratzer et al., 2023; Soto-Pinto et al., 2010; Walker et al., 2014). If we are to minimise the growing tension between an increasing proportion of the world's population living in the tropics (State of the Tropics, 2020) and the need to preserve carbon stocks in tropical forests, we need to broaden our understanding of the relationship between different forms of food production, land cover change (e.g. degrees of deforestation) and

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potential carbon dynamics. Although some models have been developed for contemporary arboriculture and smallholder systems (Blyth et al., 2021; Braakhekke et al., 2019) they tend not to include detailed insights from local communities, and neglect the wealth of insights into tropical food production, and its ecological consequences, available in the archaeological, historical and palaeoecological record.

In this study, we introduce a simple, generalised model to demonstrate the impacts on aboveground carbon (AGC) of various human practices related to food production. We seek to reproduce the mosaic nature of a tropical forest anthrome as a combination of human activities across a landscape. Though soil carbon plays a critical role in tropical forest dynamics and human activities influence these carbon reservoirs (Rahman et al., 2018), we limit our study to aboveground carbon, both because it comprises the majority of total carbon stocks in tropical forest systems (Pan et al., 2011) and to simplify the modelling approach given the differing processes and timescales involved with belowground carbon (Marín-Spiotta & Sharma, 2013). In this way, we focus on human activities that are interacting directly with the trees, as opposed to more indirectly with soil carbon. We explore land uses including traditional agroforestry, varied swidden/shifting patterns, and a more open cropland system, which we then compare to models of monoculture plantation as well as primary forest cover. We draw on ongoing research in Southeast Asia to inform the various modelled parameters for these land uses (Amano et al., 2020; Findley et al., 2022), however, these forms of land use are designed to be broadly applicable across the tropics. We argue that approaching past land use in and around forests as mosaics of varied food production activities might provide insights into contemporary carbon stock challenges in an Anthropocene context.

2 | DESCRIPTION

In the model introduced here, an idealised old-growth forest is established as an arbitrary grid of tree stands where each square plot in the grid corresponds to one hectare. Since our focus is on changes in total AGC, we prescribe AGC per hectare and then distribute this carbon into each tree stand following realistic tropical forest allometrics. Tree-stand structure in each plot is described by distributions of tree diameter at breast height (DBH), tree height and wood carbon density typical of old-growth tropical forests. We then emulate a range of human activities as two main processes: 1) selective tree removal or 'thinning' and 2) specified rotations of swidden clearing and fallow periods. A simple form of succession is implemented to allow regrowth in each plot. The impact of specific practices can then be evaluated as a time-independent change, such as the direct effect of a given tree thinning practice, or as a time-evolving change, such as for various swidden patterns. We define long-term mean AGC as being at least 50 years, at least twice the longest swidden rotation period, ensuring that landscape mean values stabilise for each simulation. We compute time-evolving cases in 1-year timesteps. By tracking the AGC of the trees through time, we demonstrate relative changes in the long-term mean AGC across the landscape.

2.1 | Modelled forest structure and composition

Distributions for stem density, DBH, maximum height and biomass carbon density vary widely across the tropics (Jucker et al., 2017). In this paper, tree DBH is the main stand structure metric and is described in each plot by a simple random gamma distribution $G(\alpha_{DBH},\beta_{DBH})$. Here, we set both α and β to a value of 0.3. The relationship of DBH to height is complex (Jucker et al., 2017). Here, we simply scale tree height to DBH as $\alpha_{DBH}\tan^{-1}(DBH * z(\mu,\sigma))$ where z is a random normal distribution and μ and σ here are set to 4 and 0.5, respectively. The maximum DBH and height are restricted to 1.5 m and 30 m, respectively, to avoid unrealistically large trees. Combined, these formulations and parameter values yield realistic DBH-Height distributions typical of the tropics (Corona-Núñez et al., 2018; Piponiot et al., 2022, see Figure 1). Using these size distributions, tree volumes are idealised as cones. A fixed wood density (600 kg m^{-3}) and a wood carbon fraction (0.5) typical of the tropics (Phillips et al., 2019; Yeboah et al., 2014) are used to compute AGC per tree. AGC is summed for all the trees in a plot giving MgC ha^{-1}, and averaging the AGC across the grid yields the mean for the forest landscape. To set a specific initial mean AGC for the modelled forest, an initial tree count is set for each plot and then iteratively scaled until the grid mean AGC matches the desired value. This allows natural variability in stem densities and stand structure between plots while constraining the modelled landscape to a realistic, prescribed AGC. The final stem densities are compared to typical tropical values and serve as a realism check for the forest AGC and stand structure values selected. Tropical forest aboveground carbon densities vary widely across the tropics, from 100 to more than 500 Mg ha^{-1} (Jucker et al., 2018; Piponiot et al., 2022). Here we constrain the modelled old-growth forest to a large, but typical, value of 200 Mg ha^{-1}.

To model land use behaviours that treat tree types differently, an initial old-growth forest is composed of three tree categories: "*promote*" trees as those that may be selectively kept for their food, medicinal or cultural value, "*harvest*" trees as those selectively removed for firewood or structural use and "*general*" trees which make up the remainder of the population. The *promote* category is useful in modelling agroforestry that has selective tree use but does not necessarily include domestication (Kennedy, 2012). In this study, trees in the three categories share the same coefficients for their DBH, height and carbon density distributions, and therefore are functionally the same. However, in future work, differing properties could be prescribed to each category to model the impacts of differing species groups. The forest composition of these categories is set by an initial proportion of trees from each category. In this study, we arbitrarily set these proportions as 0.3, 0.3 and 0.4, for the *promote*, *harvest* and *general* categories to simply demonstrate land use that is selective, but proportions emulating specific tropical forest sites could be used as well in future work. Table 1 summarises the model parameter values used in this study, and Figure 1 shows the corresponding modelled old growth DBH-Height distribution we examine.

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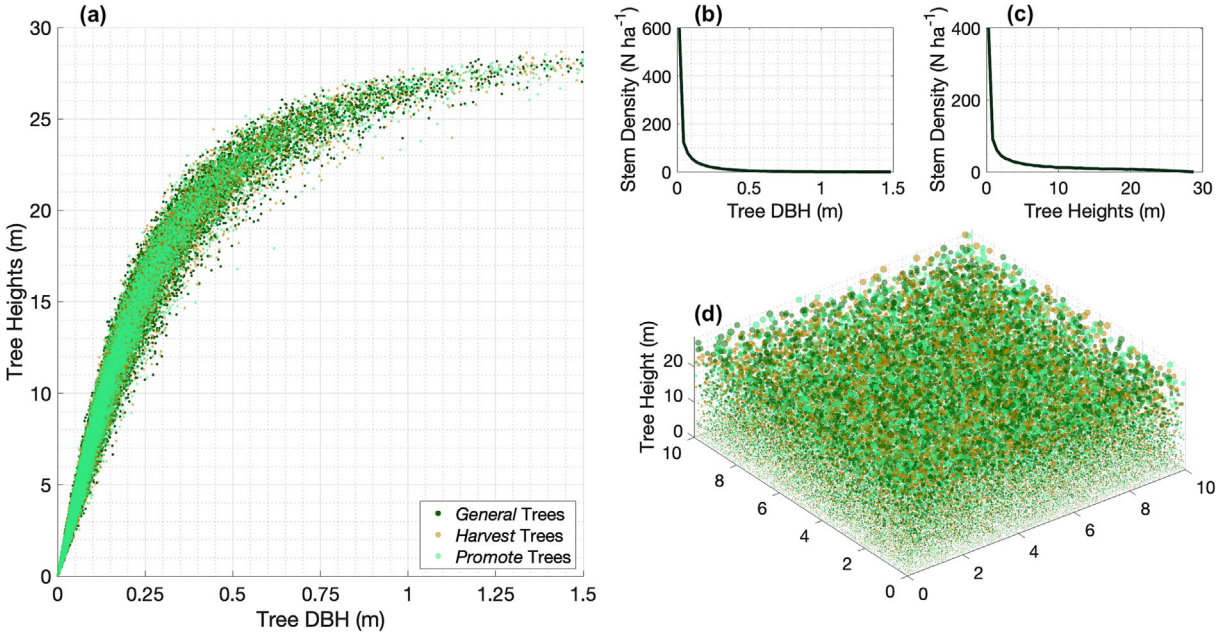

FIGURE 1 Example modelled old growth forest for a 100 ha grid (10 × 10). Modelled trees are described by (a) the distribution of tree height versus diameter at breast height (DBH) coloured by tree category, (b) a histogram of DBH by stem density (tree count), (c) a histogram of tree heights by stem density and (d) 3D depiction of the 100 ha domain, where tree heights are exaggerated. Trees in (d) are shown as circles sized by DBH but are represented in the model as cones for calculations.

TABLE 1 An overview of model parameter values used in this study and references to typical values measured in the tropics.

Model parameter	Value	Units	Reference
Grid size	100 (10 × 10)	Ha	-
Succession time	100	Years	(Aryal et al., 2014; Velasco-Murguía et al., 2021)
Wood carbon density	300	Kg m^{-3}	(Pan et al., 2011; Yeboah et al., 2014)
Aboveground carbon density (AGC)	200	Mg ha^{-1}	(Jucker et al., 2018; Piponiot et al., 2022)
Model distributions	*Min-max*		
Diameter at breast height (DBH)	0.01–1.5	m	(Corona-Núñez et al., 2018; Ledo et al., 2016; Piponiot et al., 2022)
Height	0.5–30	m	(Jucker et al., 2017; Vaglio Laurin et al., 2019)

2.2 | Tree removal and regrowth

With a landscape of idealised trees established, we can then assess changes to forest structure, composition and AGC relative to this old-growth reference. The main mechanism for human activities to affect the forest is thinning processes which remove trees within a defined DBH range, specified for each tree category. Within a DBH range to be thinned, either all trees or a fraction of those trees can be removed which is handled as a random fractional probability of removal. For example, removal of 10% of understory trees is described by randomly removing 1 in 10 trees of 0–0.2 m DBH. Forest "clearing" of a grid plot, as in the case of swidden, is merely a special case of thinning where trees of all or most tree sizes are removed.

Succession is treated as a simple incremental forcing of the DBH and height distributions for each plot back to that of the initial old-growth forest. If at the start of a year, a plot has a lower tree count than that of the corresponding initial old growth plot, then the difference is added as new trees with the minimum set values for DBH and height, here 0.01 m and 0.5 m, respectively. Succession is defined by recovery time in years and a recovery coefficient that follows a logarithmic progression from 0 (first pioneer year) to 1 (fully recovered) across the recovery time. Using this approach for a 100 year succession yields growth curves comparable to various tropical sites (Aryal et al., 2014; Poorter et al., 2016; Rozendaal et al., 2019). The category composition of the new trees during succession can simply follow the initial old-growth category proportions or can be set as a composition reflecting human preferences, e.g. higher proportions of firewood, food or medicinal trees, i.e. *harvest* or *promote* category trees, at the expense of *general* category trees. In this way, future work could model compositional change from human selection.

Finally, swidden behaviour is described as a cycle of complete or partial clearing followed by successional regrowth. Swidden rotation is specified by the number of years spent cleared and the number of

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years spent fallow. Modern swidden systems often follow shorter and more regular rotations (Bruun et al., 2009; Dressler et al., 2017), however traditional systems under lower population pressure often have much longer fallow periods with more irregular return intervals (Bruun et al., 2018; Schmidt et al., 2021). Swidden rotations in a plot can simply repeat the pattern of years cleared and then years fallow, or the initiation of swidden clearing can follow a 0–1 normal probability of return after the given fallow period has elapsed. At the beginning of the fallow period, new sapling trees are added and trees follow succession each year until the return of clearing.

2.3 | Carbon scenarios in past Forest Anthromes

To explore the model behaviour and resulting AGC, we test a series of abstract human activities. Ethnohistorical and archaeological evidence points to forest management of small understory trees by hunter-gatherer groups to clear paths for access and open undergrowth for boosting prey numbers. This was done either by hand or particularly through the use of small-scale fire, from potentially 60,000 years ago or earlier through the late pre-colonial period on to modern Indigenous peoples (Coughlan et al., 2024; Hunt et al., 2012; Pivello, 2011; Roberts et al., 2021). Thinning was also often a result of wood harvesting for fuel or structural use (Roos et al., 2021). Given these practices, we first examine carbon outcomes for various thinning activities which include a limited path clearing for hunting, more widespread understory clearing by low-intensity fire, and the harvesting of wood represented by trees cleared from the *harvest* tree category alone. As shown below, large trees play an outsized role in AGC, and we therefore compute thinning with and without the largest 1% of trees. Thinning patterns are summarised in Table 2. Similarly to thinning activities, there is considerable evidence for a diverse range of swidden practices often with long fallow periods into the decadal scale and irregular patterns of return to a particular area, considerably different than regular, short fallow rotations common in modern contexts (Bredero et al., 2023; Downey et al., 2023; McNeil, 2012; Schmidt et al., 2021; Velasco-Murguía et al., 2021). Based on these more varied cycles of clearing and regrowth, a range of swidden patterns is also tested for short and long fallow periods with variable return intervals.

We present our model simulations in order of increasing complexity from the plot level up to a mixed, anthrome landscape. We begin by comparing individual, uniform thinning and swidden patterns separately to understand the relative influence of each on AGC. We then proceed to compare individual thinning and swidden patterns that vary spatially and temporally across a landscape to compare the integrated long-term AGC for each activity. Finally, we combine activities to simulate a landscape with a mosaic of multiple land uses to highlight the carbon dynamics for a realistic tropical forest where humans are carrying out a range of food-production practices. This combined landscape is similar to Indigenous land use systems around the world, such as the *muyong-uma-payo* complex of the Philippines (Findley et al., 2022), which have distinct fixed cropland among unmanaged, managed and swidden/fallow forests. For comparison, AGC values typical of modern oil palm, rubber and banana plantations are referenced. The results presented below highlight the behaviour of the model for a certain configuration of old-growth forest tree properties, succession and AGC. However, these values could be adjusted in future work to represent forest stand structure for specific regions of the tropics or other certain succession patterns.

3 | RESULTS

Figure 2 demonstrates the total carbon per tree and the cumulative AGC varies by tree size. Consistent with observational studies (Lutz et al., 2018; Martínez Cano et al., 2019), AGC increases exponentially with tree DBH and a small number of the largest trees makeup a substantial proportion of the total AGC. For the tree allometrics in this study, the largest 1% of individual trees hold approximately one-third of the total carbon, while including the largest 5% of trees accounts for two-thirds of the total carbon. Therefore, the fate of larger trees will dominate the carbon outcomes from various human modifications. The largest 1% of trees here have a lower DBH bound of ~0.76 m which will be used in further analysis to select out these trees.

With the significant role of large trees on carbon in mind, we focus on the impact of various thinning activities on tree size distribution and carbon for a 100 ha landscape (Figure 3). Agroforestry practices that only affect the smallest trees have a relatively small impact

TABLE 2 Idealised human activities simulated in this study and their corresponding model parameter values as trees removed, as all or per category, by each activity and the minimum and maximum limits of tree size removed in each case in terms of diameter at breast height (DBH).

Human activity	Proportion of trees removed	Minimum DBH (m)	Maximum DBH (m)
Thinning - path clearing for hunting and gathering	0.1	0	0.25
Thinning - harvesting for firewood or building	0.5 (only *harvest* trees)	0	1.5
Thinning – Understory, small-scale fire	1	0	0.2
Thinning – Non-*promote* trees	1 (only *general* and *harvest* trees)	0	0.25
Swidden clearing	1	0	1.5
Swidden clearing – Leave largest 1% of trees	1	0	0.76
Clearing – Removing largest 1% of trees	1	0.76	1.5

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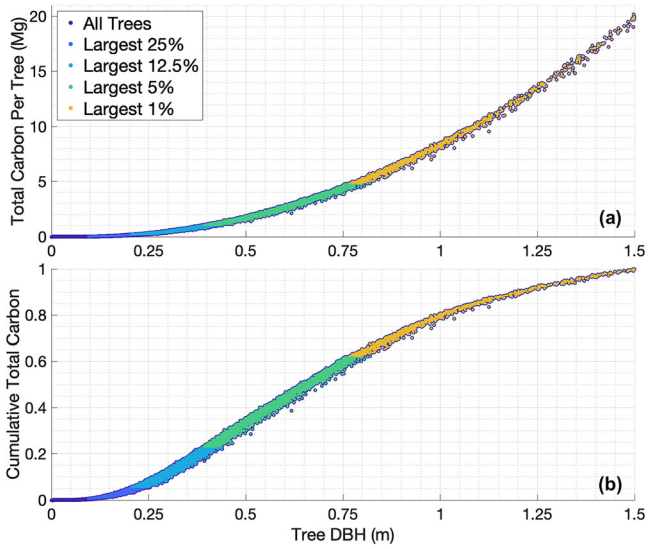

FIGURE 2 Distributions of total carbon per tree (a) and cumulative total aboveground carbon (b) in terms of diameter at breast height (DBH) across an initial old-growth forest.

on AGC. Thinning by forest path clearing, here set as 10% of trees smaller than 0.125 m DBH, lowers the stem density by ~1% with only a marginal effect on AGC. Small-scale fire, represented here by 50% clearing of trees smaller than 0.25 m DBH, has a large impact on the tree population and structure, yet only ~10% decrease in AGC. Carbon outcomes of human activities that impact tree-categories differently will depend on the proportion of each category on the overall tree population. For example, removing 50% of all trees in the *harvest* category, for moderate firewood and structure needs, for example, results here in a 10–15% reduction in AGC. We can also imagine agroforestry that keeps all *promote* trees but removes *general* and *harvest* category trees smaller than 0.25 m. This would lower AGC by ~10%, however long-term preferential selection and regrowth of *promote* trees could offset this 10% loss such as in the case of a managed food forest such as Philippine Muyong (Avtar et al., 2019; Camacho et al., 2016). Preferentially removing the largest 1% of trees or removing the smallest 99% of trees, as in Figure 2, corresponds to a loss of one-third and two-thirds of the old-growth AGC, respectively.

We next test the impact of various swidden rotational patterns, first for a single tree stand (Figure 4). Here we compare both the time

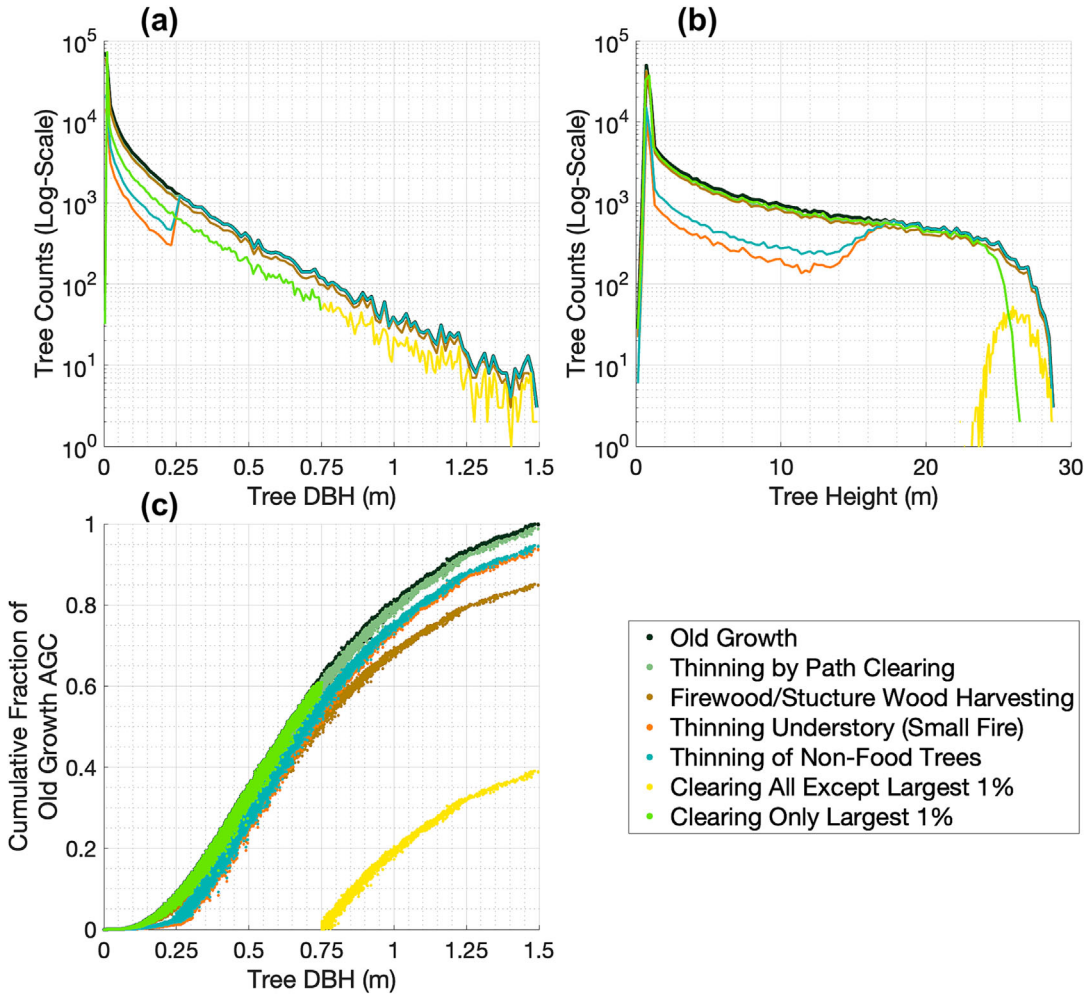

FIGURE 3 Distributions of tree counts for a simulated 100 ha forest landscape before and after various human "thinning" activities in terms of (a) diameter at breast height (DBH), (b) tree height and (c) cumulative aboveground carbon (AGC) as a fraction of the initial old growth forest.

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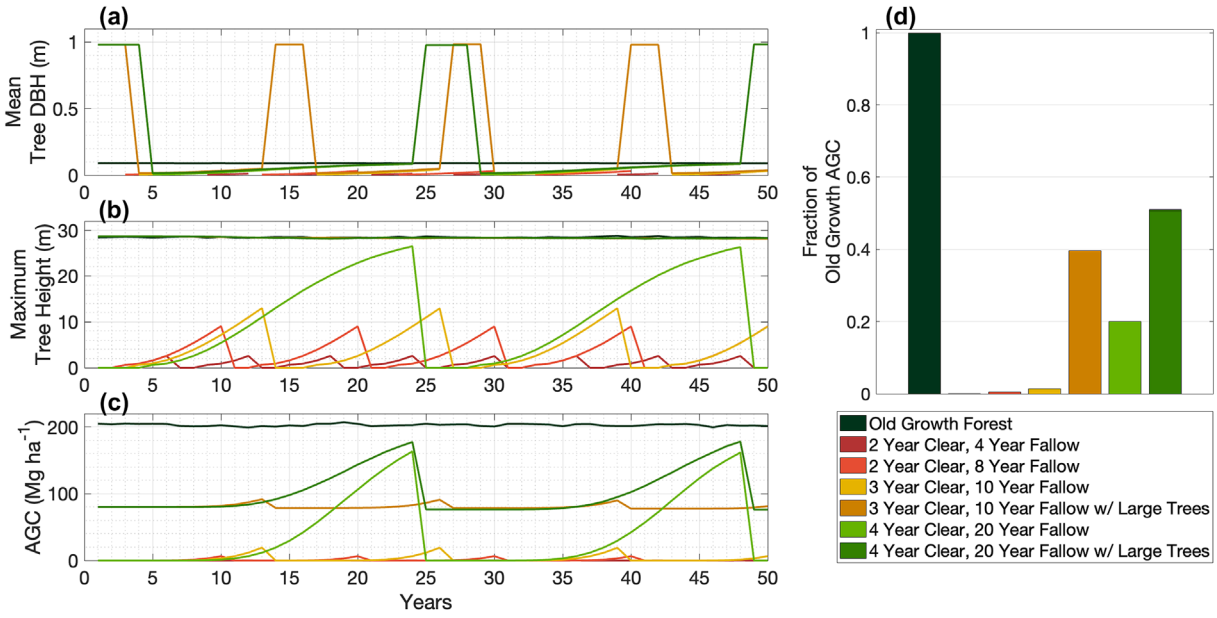

FIGURE 4 Time evolution for a forest plot (1 ha) undergoing various swidden clearing-fallow rotational patterns of (a) mean tree diameter at breast height (DBH), (b) maximum tree height and (c) aboveground carbon (AGC). Panel (d) shows the long-term (simulation length) mean aboveground carbon (AGC) for each swidden pattern as a fraction of the initial old-growth forest AGC.

evolution of annual AGC as well as the resulting long-term AGC means to a reference old growth stand. Regular short-swidden rotations with full clearing and fallow periods of 8 years or less result in drastic reductions in AGC greater than 95%. Even 10-year fallow periods with full clearing, though attaining around a third of the old growth height, only recover a maximum of ~10% of the old-growth AGC at peak succession and a mean of ~3% of old-growth AGC across the swidden cycle. Cleared cultivation period-length, being generally shorter than fallow, has a relatively small influence on recovered AGC. Extending the fallow period to 20 years in fully cleared stands allows enough successional carbon uptake to store upward of ~20% of the old growth stand.

Also shown are cases with and without the largest 1% of trees retained for medium (10-year) and long (20-year) fallow periods. Leaving large trees results in a consistent and markedly higher mean DBH and drives the maximum height to near that of the old growth value. Large trees also markedly raise the minimum and in turn also the long-term mean AGC values. Short to medium fallow rotations see the greatest increase, where the 10-year fallow case with large trees surpasses the AGC of the 20-year fallow without. For a given swidden pattern, the AGC trajectory during recovery and the peak AGC attained are highly dependent on how succession is treated, i.e., AGC is sensitive to the standard recovery time and the shape of the recovery curve. Interestingly for the longer 20-year fallow case, large tree retention only slightly increases the peak AGC compared to the case without those trees, indicating a tipping point where the importance of stand recovery approaches that of the largest trees.

Next, we examine how AGC varies across a grid of tree plots with a single land use. Here 100 years is simulated over a 100 ha grid for a reference old-growth forest (Figure 5a), a thinning treatment (Figure 5d) and four swidden patterns (Figure 5b,c,e,f). Panels in Figure 5 show the AGC at the last time step to demonstrate the typical spatial pattern. The start times of swidden rotations in each plot are randomised. Corresponding time series for individual plots in each panel are shown in Figure 6. The background variability of the reference old-growth forest is evident resulting from the randomness introduced in the DBH and height distributions each year. This variability is mainly a result of the presence or lack of large trees from the upper extreme of the DBH-Height distribution. The uniform thinning treatment in Figure 5d removes all trees <0.25 m DBH each year and results in ~20% drop in long-term AGC (Figure 6d). The landscape with regular 3 years cleared, 10 years fallow swidden rotation results in a drastic AGC reduction of ~1% that of the old-growth forest, with some slight variability depending on the stage of the rotation of each plot. The same swidden rotation, but with an irregular return interval, 10% probability each year after 10 years or longer, has a large range of fallow times (Figure 6c). This large range yields varied stand ages across the landscape and significantly raises the long-term mean AGC to ~25% that of the old-growth landscape (Figure 6c). In Figure 5e and 5f, the largest 1% of trees are retained preserving significant AGC on the landscape, here again around one-third of the old growth reference (Figure 6e and 6f), regardless of if using a short 4-year or medium 10-year fallow length.

Finally, we examine the AGC dynamics for a landscape of concurrent old-growth forests, a forest with thinning, irregular swidden and permanent cropland with large *promote/harvest* trees. Figure 7a shows the time series of all tree plots in the grid coloured by the land cover as well as the landscape mean in black for the entire grid. Figure 7b shows the spatial pattern of AGC for the last time step representing typical variability. As in Figures 5 and 6, the old-growth forest shows

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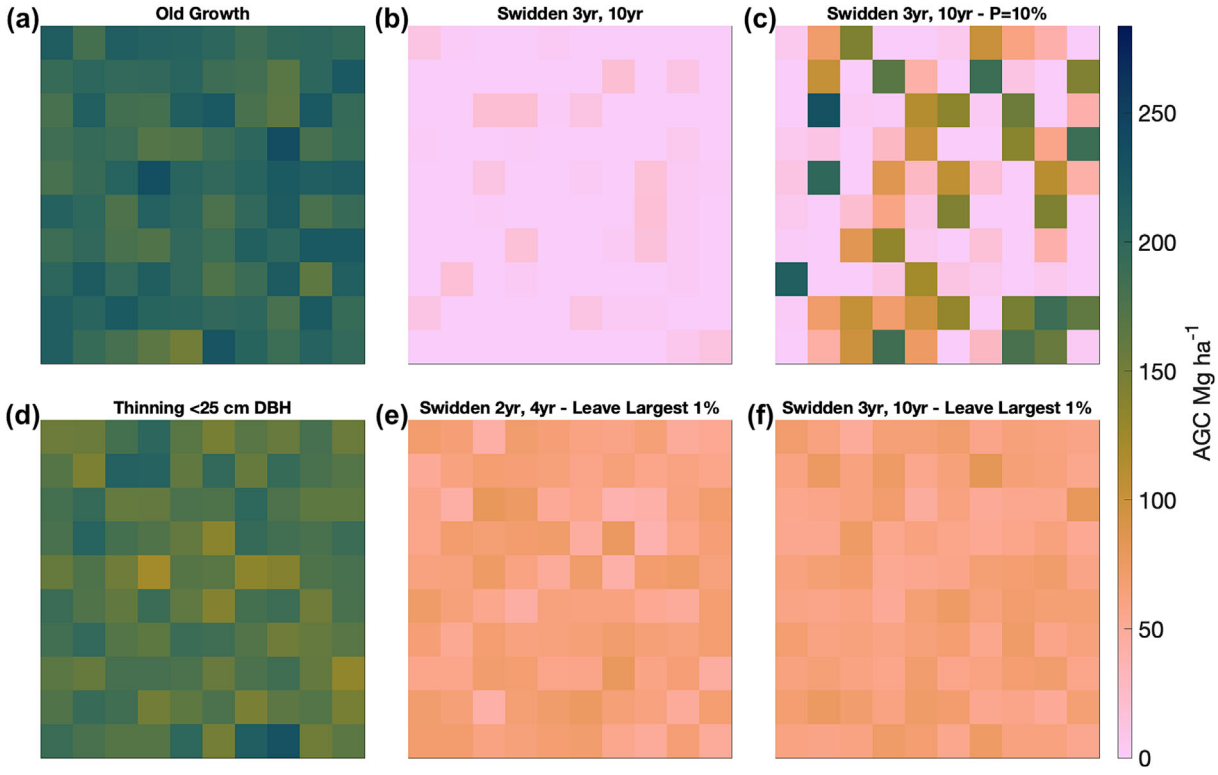

FIGURE 5 Aboveground carbon (AGC) across 100 ha forested landscapes, shown at the final time step of a simulation, for (a) an old growth reference, (b) a 3-year cultivated/10-year fallow swidden pattern, (c) a 3-year cultivated/10-year fallow swidden pattern with a 10% probability of return, (d) a consistent thinning of trees smaller than 0.25 m diameter at breast height (DBH), (e) a 2-year cultivated/4-year fallow swidden pattern that retains the largest 1% of trees, (f) a 3-year cultivated/10-year fallow swidden pattern that retains the largest 1% of trees.

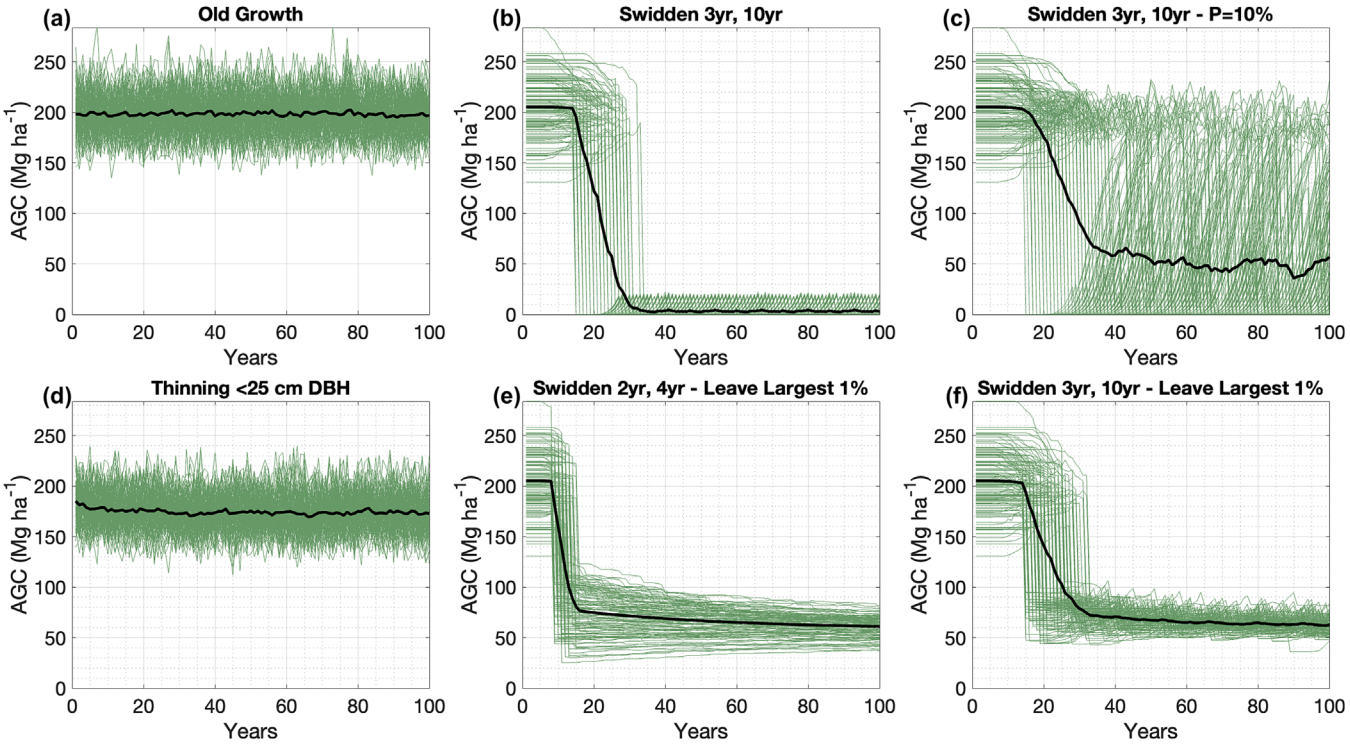

FIGURE 6 Simulated time series, corresponding to panels in Figure 5, of individual 1 ha tree plots (green) and the grid mean (black) for (a) an old growth reference, (b) a 3-year cultivated/10-year fallow swidden pattern, (c) a 3-year cultivated/10-year fallow swidden pattern with a 10% probability of return, (d) a consistent thinning of trees smaller than 0.25 m diameter at breast height (DBH), (e) a 2-year cultivated/4-year fallow swidden pattern that retains the largest 1% of trees, (f) a 3-year cultivated/10-year fallow swidden pattern that retains the largest 1% of trees.

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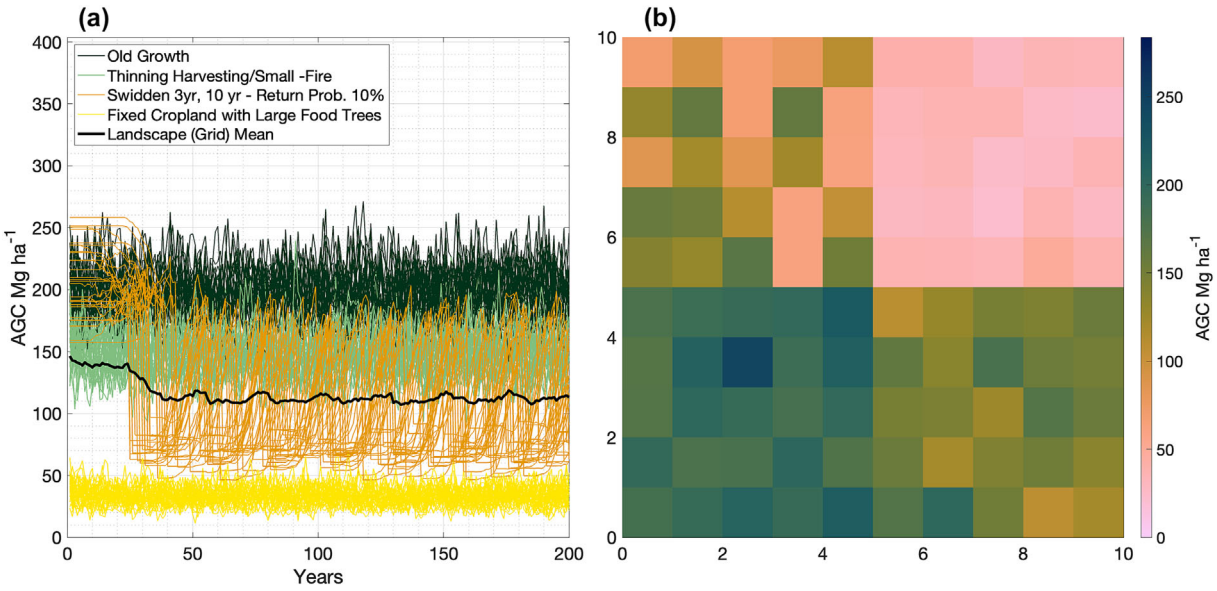

FIGURE 7 Simulated aboveground carbon density (AGC) for a forest landscape undergoing a combination of activities. Panel (a) shows individual times series of four land uses: plots with old growth (dark green), plots with 100% thinning of trees <0.2 m diameter at breast height (DBH) and 50% *harvest* category trees <1 m DBH (light green), plots with a 3-year cultivated/10-year fallow swidden pattern with a 10% probability of return (orange) and plots with a fixed cropping system and the retention of *promote* category trees >0.5 DBH representing large fruit trees. Panel (a) also shows the landscape mean AGC (black). Panel (b) shows the landscape at the last time step of the simulation with the four partitioned land uses.

TABLE 3 Aboveground carbon density for various systems.

		Aboveground carbon density (mg ha^{-1})	References
Primary	Old growth forest	100–500+	
Secondary	Thinned forest	50–500	
	Agroforestry	100–500+	
	Swidden with full clearing	2–80	
	Swidden with large trees	20–150	
Monoculture/ Mixed plantation	Oil palm	20–100	(Goh et al., 2016; Kho & Jepsen, 2015; Málaga et al., 2021)
	Rubber	20–100	(Blagodatsky et al., 2016; Bruun et al., 2018; Wauters et al., 2008)
	Banana	2–40	(Ganeshamurthy, 2023; Ortiz-Ulloa et al., 2021)

realistic AGC variations both in space and time. This is paralleled by the thinned forest which maintains ~70–80% that of old growth. The open cropland plots have the lowest AGC values through time, though consistently around 20% of old growth values due to the retention of large *promote* trees. Table 3 summarises various modelled land uses compared to modern cropping systems.

4 | DISCUSSION

In this study, we developed a simple model of aboveground carbon (AGC) for a tropical forest anthrome and examined the impact of various conceptual food production activities on landscape-scale AGC. Our two key results are that 1) a mixed landscape of forest thinning and swidden activities can yield a wide range of long-term AGC outcomes, including preserving a large fraction of old-growth AGC for scenarios with long fallow time, irregular return interval and preferential small tree thinning, and 2) the retention of a small number of large trees has an outsized impact on how land use affects landscape AGC.

Existing models of human land use tend to place agriculture in direct opposition to tropical forests, suggesting that the introduction of food production into these environments results in significant carbon stock losses. However, these models are usually based on agricultural or plantation models of monoculture field systems. An important

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distinction our results highlight is the difference between the time-evolving AGC at the plot level and the long-term AGC integrated across a landscape. For example, many land use discussions still focus on AGC at certain stages of swidden rotation, often the low AGC during the cultivation period. However, the peak fallow recovery AGC can vary widely depending on fallow/succession length and the regularity of return in the swidden cycle. For a short, regular swidden rotation these factors do indeed yield very low AGC analogous to complete clearance, while the long-term mean AGC across several swidden cycles increases rapidly as fallow length increases. An irregular return interval further lengthens the effective fallow period and, in turn, AGC. This becomes especially true across a landscape where individual plots are at various stages of recovery. It is important to note the lack of a specified hydroclimate or species composition in the model, which will greatly vary the AGC and successional aspects of a given forest. However, since the AGC is based on the idealised trees present or not present, the key theme is not the absolute AGC values or changes, but instead how the AGC varies relative to old-growth reference, allowing these results to be generalised for food production across the tropics.

Our results support existing research that has demonstrated the importance of large trees within a tropical forest in terms of carbon dynamics (Burt et al., 2021; Lutz et al., 2018). We show that the top 1% of the trees in a realistic model tropical forest hold a third or more of the aboveground carbon (Figure 2). In a real forest, these large trees tend to also be the oldest, highlighting the importance of long timescales when thinking about carbon storage and dynamics in tropical forests (Flores & Staal, 2022). Large trees tend also to play an outsized role in nutrient cycling, soil anchoring and within the water cycle (Meakem et al., 2018). Furthermore, we show that a swidden system which includes maintenance of the top 1% of trees can maintain a third or more of the aboveground carbon stocks of an old-growth forest, regardless of short or long fallow times. Indeed many Indigenous/traditional swidden practices take exception to clearing the largest trees either for reasons of cultural/religious importance or for practical work required to remove the largest trunks (Camacho et al., 2016; Carrière et al., 2002; Lindenmayer, 2017).

In the interest of constraining model behaviour and making the results more general, the model in this study lacks several important forest dynamics such as a baseline tree mortality or interactive tree growth. The use of fixed stem densities greatly simplifies successional dynamics, but this could also cause underestimation of AGC early in succession when stem densities are typically higher. However, given the small contribution of the smallest trees to total volume, even introducing 10 times as many saplings at the beginning of succession would only yield total AGC values less than 1% of the mature old growth reference. Growth dynamics not present in the model could also be important for large trees, which often thrive in successional tree stands and their presence can also accelerate secondary recovery (Rivas-Alonso et al., 2021). Likewise, growth dynamics would play a role in traditional stand management practices, such as in a Philippine *Muyong* woodlot (Avtar et al., 2019; Findley et al., 2022; Rabena et al., 2015), which includes diligent managing of undergrowth and the planting of tree saplings to promote stand succession and health. These feedback would work to further increase the long-term mean AGC by enhancing fallow uptake and long-term storage.

Our approach highlights how more subtle and diverse models of forest management, agroforestry and swidden complexify traditional human-versus-forest land use models, emphasising the large space in between primary forest and cleared cropland or monoculture systems, such as in Table 3. These results have important implications for modelling both directions of deforestation and afforestation (Pavlick et al., 2013; Schaphoff et al., 2018). The relatively high long-term AGC possible for a mosaic of food production activities, typical of many past and present local communities, does not necessarily imply large AGC loss when old growth forest is modified by food production. Large, dense populations with limited regulation may certainly result in short fallow swidden scenarios, with rapid loss of forest cover and AGC on a regional scale (Figures 4, 5 and 6). By contrast, if cultural and social constraints are placed on the types of trees felled and duration of land use, as commonly exist among Indigenous societies, the impacts on regional AGC will be far lower (Avtar et al., 2019; Schmidt et al., 2021). Future research here could, for example, explore the ways in which Amazonian Garden City food production practices may have interacted with the carbon cycle based on palaeoecological insights into disturbance (Maezumi et al., 2018). This lends context to the modelling of major tropical transitions such as afforestation scenarios after European colonial arrival and the hypothesised forest regrowth resulting from documented mass Indigenous mortality in the Americas due to disease and European policy. For analyses of resulting carbon uptake (Koch et al., 2019), the potential carbon stock change could be significantly lower depending on the starting AGC maintained on the landscape by Indigenous practices, perhaps requiring other terrestrial sinks or human actions during this period to explain global changes in atmospheric carbon (Bush et al., 2021; Nevle et al., 2011).

Closely linked to interactions between forest carbon and food production are how human activities impact forest composition and biodiversity. While we have focused here on carbon dynamics, the idealised tree categories in our model approach are useful to glean conceptual insights into how past land uses could have changed and maintained the makeup of a forest. Traditional agroforestry practices across the tropics have strong social, economic and cultural components, and data on Indigenous practices suggest that strategies will often minimise the loss of carbon while simultaneously maintaining biodiversity and managing domesticated plants (Camacho et al., 2016; Scerri et al., 2022; M. K. Sullivan et al., 2024). Conceptually in our model, selective pressure from humans takes the form of tree 'replacement', where activities remove trees and desired trees are left to grow. This replacement can be passive/subtractive, as in the case of understory thinning of specific tree types to promote other preferred species, or additive whereby desired trees are actively planted in agroforest wood lots or recovering fallows. Even mild selective pressure over great lengths of time, particularly by long-fallow swidden where plots see all or partial clearing and regrowth, could significantly alter the forest composition. This combined with any large-tree

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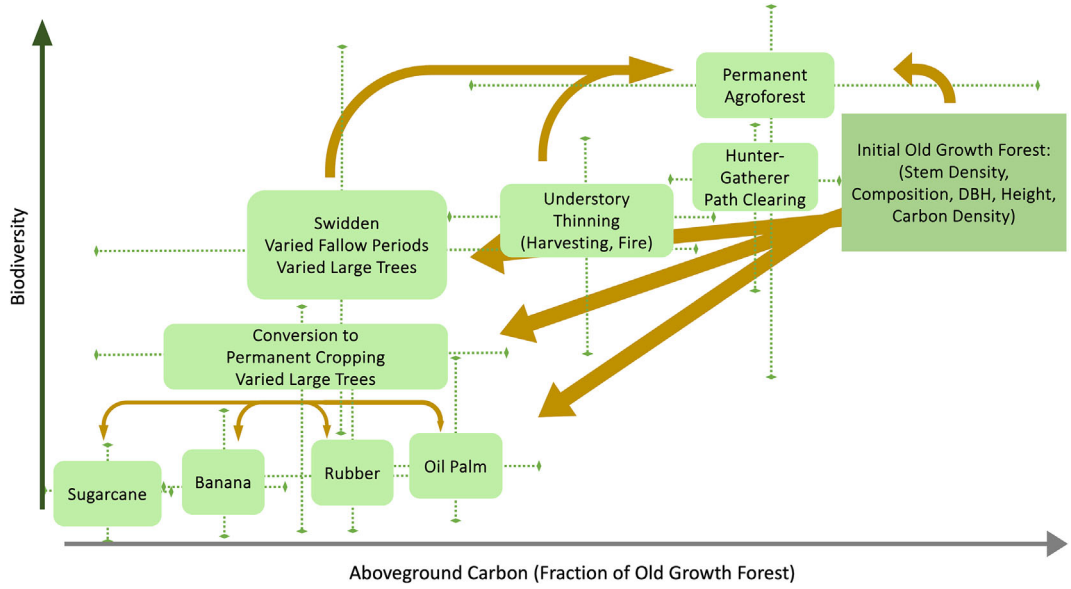

FIGURE 8 Conceptual diagram relating aboveground carbon (AGC) and biodiversity for a tropical old-growth forest and various activities related to food-production. An initial old-growth forest described by stem density, tree size distribution, AGC and tree species composition progresses along various conceptual pathways (orange) depending on human impacts on forest structure and specific tree types. This yields a spectrum of possible outcomes between old growth and common modern monocultures, depicted here as green uncertainty bars.

retention provides mechanisms connecting human activity with hyperdominant tree species, known to have been selected for in the Amazon rainforest (ter Steege et al., 2013; Unruh, 1990) and thereby the carbon makeup of the landscape (Fauset et al., 2015).

We summarise our results in the conceptual diagram in Figure 8. Across the tropics, the relationship between biomass carbon and biodiversity varies considerably by environment (Ferreira et al., 2018; Sullivan et al., 2017) but generally is positively correlated (L. Poorter et al., 2015; Lourens Poorter et al., 2017; Van Der Sande et al., 2017). Many human disturbances do indeed negatively impact forest biomass carbon, biodiversity or both. Path clearing and understory thinning have small effects while cultivation practices from various swidden patterns increasing to fixed cropping systems have stronger impacts. Some modern plantation systems such as oil palm systems can have comparable carbon stocks, but generally have significantly less biodiversity leading to different challenges (Zemp et al., 2023). However, swidden landscapes, especially irregular long-fallow swidden with large tree retention, occupy a large range of AGC relative to an old-growth forest and can support moderate to large biodiversity due to the varied successional landscapes they create as noted elsewhere (Deere et al., 2018; Padoch & Pinedo-Vasquez, 2010). Of note are traditional managed wood lot and forest garden systems of Southeast Asia or the Amazon (Camacho et al., 2016; Maezumi et al., 2018; Schmidt et al., 2021; Unruh, 1990; Walker et al., 2014) where mild thinning and selective pressure may induce a composition change but cause only small carbon or biodiversity changes if not increases compared to their primary forest counterpart.

Future use of this model may be able to apply more complex scenarios and incorporate additional features and datasets to simulate carbon pathways with land use change. Adding dynamic agent-based components which show how human practices from different agroforestry practices to different swidden fallow lengths, to different forms of plantation or even grazing of domesticated animals, can lead to certain path dependencies or new ecological dynamics that, in turn, constrain future human actions. Such an approach can also link tropical land use to hydrological dynamics (e.g. regional rainfall – see (Cook et al., 2012), soil erosion or biodiversity to determine how past human activities may have shaped other parts of the Earth system. Further study of this nuanced space between primary forest cover and varied land use anthromes can help to consider how food production might be productively incorporated within tropical environments today, balancing critical biodiversity and Earth system functions of forests (e.g. as carbon sinks) with potential for food security and the need to maintain a livelihood.

AUTHOR CONTRIBUTIONS

Sebastian A. Los, Ricarda Winkelmann and Patrick Roberts designed the research; Sebastian A. Los carried out model development, analysis and interpretation with assistance from Patrick Roberts and Ricarda Winkelmann; Sebastian A. Los and Patrick Roberts wrote the manuscript, which was reviewed by all co-authors.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Model code used in this study is available as MATLAB code via GitHub (https://github.com/SebastianALos/ForestAnthromeModel/ last access 8 November 2024) and Zenodo: (Los, S. A., Winkelmann, R., Roberts, P.; 2024; Forest Anthrome Model; SebastianALos/ForestAnthromeModel: Forest Anthrome Model; DOI 10.5281/zenodo.14094970).

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