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RESEARCH



Modelling carbon stock and carbon sequestration ecosystem services for policy design: a comprehensive approach using a dynamic vegetation model

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ABSTRACT

Ecosystem service (ES) models can only inform policy design adequately if they incorporate ecological processes. We used the Lund-Potsdam-Jena managed Land (LPJmL) model, to address following questions for Mexico, Bolivia and Brazilian Amazon: (i) How different are C stocks and C sequestration quantifications under standard (when soil and litter C and heterotrophic respiration are not considered) and comprehensive (including all C stock and heterotrophic respiration) approach? and (ii) How does the valuation of C stock and C sequestration differ in national payments for ES and global C funds or markets when comparing both approach? We found that up to 65% of C stocks have not been taken into account by neglecting to include C stored in soil and litter, resulting in gross underpayments (up to 500 times lower). Since emissions from heterotrophic respiration of organic material offset a large proportion of C gained through growth of living matter, we found that markets and decision-makers are inadvertently overestimating up to 100 times C sequestered. New approaches for modelling C services relevant ecological process-based can help accounting for C in soil, litter and heterotrophic respiration and become important for the operationalization of agreements on climate change mitigation following the COP21 in 2015.

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Introduction

A plethora of methods and tools for quantifying, modelling and mapping ecosystem services (ESs) has been developed and evaluated for their utility in policy design (Bagstad et al. 2013; Grêt-Regamey et al. 2017; Harrison et al. 2018). However, the most of these methods and tools have ignored key ecological processes (i.e. the flows and fluxes of carbon, energy, water and nutrients between ecosystem components) which ultimately determine the supply and delivery of ES (Karp et al. 2015; Hallouin et al. 2018). Advances in ES modelling and mapping will depend on integrating relevant ecological processes (de Groot et al. 2010; Tallis et al. 2012) into the characterization of spatial and temporal variation in the provision of ES resulting from land-use change (Nelson and Daily 2010).

One approach for incorporating ecological processes into ES models is the use of dynamic global vegetation models (DGVMs). These models quantify essential

processes and ecosystem functions related to carbon and water under different land-use conditions from which the supply of ES can be calculated (Prentice et al. 2007; Quillet et al. 2010). The Lund-Potsdam-Jena managed Land (LPJmL) model is one such example (Sitch et al. 2003; Bondeau et al. 2007). LPJmL output variables associated with carbon (C) and water balances and other underpinning processes have been used as proxies for many ES (Haberl et al. 2007; Elkin et al. 2013; Krausmann et al. 2013), and are well suited for processes linked to the C cycle (Karp et al. 2015).

Comprehensive models, which explicitly incorporate the functional roles of vegetation dynamics and land-use change, are especially needed for quantifying C stocks and C sequestration for the design and implementation of regional and national public policies linked to climate change mitigation (Crossman et al. 2011). A number of standard methods and tools are available for modelling these ES (Egoh et al. 2012; Martínez-Harms and

Balvanera 2012; Grêt-Regamey et al. 2017), but most of them omit some key ecological components or processes underpinning C dynamics and its role in climate regulation (Lavorel et al. 2017), and many rely solely on look-up tables of C stocks, applied to different land cover classes. The explicit incorporation of these ecological processes has direct implications for social and economic valuation of ES, and thus for associated policies (Grêt-Regamey et al. 2017).

Standard C stocks assessments in the ES literature have largely focused on aboveground biomass (AGB) (450–650 PgC globally), ignoring the 70% of C global total that is stored in soils (1500–2400 PgC; Ciais et al. 2013). Similarly, standard estimates of C sequestration have focused only on the balance between net primary productivity (NPP, ~60 PgC/yr globally; Ciais et al. 2013) and C losses caused by fires and human removal of vegetation (~3.5 PgC/yr; Le Quéré et al. 2016). These standard approaches have not really addressed C sequestration balance at the ecosystem level, defined as the net balance between the uptake (removal) of C by terrestrial ecosystems and the emissions (release) of terrestrial C into the atmosphere (Chapin et al. 2006). Consequently, heterotrophic respiration (i.e. the decomposition or decay of dead organic material), which accounts for 20–40% of total C emissions or ~60–75 PgC/yr has been grossly under-represented (Schlesinger and Andrews 2000; Bond-Lamberty et al. 2004).

Various national policies and global instruments have been developed to foster maintenance of C stocks and to increase ecosystem C sequestration balance, i.e. to increase uptake relative to emissions. The United Nations policy on Reducing Emissions from Deforestation and Forest Degradation (REDD+) focuses on reducing C emissions from deforestation and degradation and increasing C uptake from reforestation and forest restoration (<http://redd.unfccc.int/>). Global funds compensate developing countries that are able to reduce their carbon emissions by abating tropical forest disturbance from land clearing and/or by increasing C uptake associated with vegetation regrowth (FCPF 2013; Peters-Stanley and Gonzalez 2014). Many countries in Latin America, Africa and Asia (Wunder et al. 2008; Ezzine-de-Blas et al. 2016) have developed national payment schemes for ES to foster the maintenance of biodiversity and that of vegetation cover, thus protecting C stocks from land-use change (Engel et al. 2008). Such global funds and national payments for ES, however, have not taken into account spatially explicit estimates of C stocks in soil and C releases from heterotrophic respiration.

Quantification of C stocks and C sequestration in response to large-scale and rapid land-use change is particularly relevant in Latin America for informing policy development of REDD+ initiatives and similar schemes. In the last 30 years, C has been lost as a result of deforestation in tropical Latin America (Aide et al. 2013; Hansen et al. 2013; Kim et al. 2015), but at the

same time many forested areas are gaining C because of regrowth of woody vegetation (Kim et al. 2015; Liu et al. 2015; Chazdon et al. 2016). Standard ES models, which are based mainly in allometric equations and the field data from permanent plots in the region are the response variables, suggest that Neotropical forests are important C sinks (Pan et al. 2011; Brienen et al. 2015; Poorter et al. 2015; Chazdon et al. 2016). Key uncertainties remain, however, as to how well these ES models represent actual C stocks and ecosystem-level balances because they fail to consider soil C stocks and heterotrophic respiration.

The aim of our work is to show how the explicit integration of key ecosystem components and processes underpinning C dynamics in the assessment of ES has profound consequences for the assessment of the supply of ES and for the design and implementation of climate mitigation policies. In particular, we use LPJmL to model the supply of total C stock and C sequestration balance and thus, incorporate important ecosystem components and processes, namely soil C stocks and heterotrophic respiration. The study focuses on two countries and one region – Mexico, Bolivia and the Brazilian Amazon – because of: (1) their recognized potential for climate change mitigation (Asner et al. 2010; Brienen et al. 2015; Sakschewski et al. 2016), (2) high loss of forest cover in past (Aide et al. 2013; Hansen and Pauleit 2014; Kim et al. 2015) and (3) the availability of robust C dynamic assessments conducted with LPJmL for a similar time period (1981–2000). Two key questions guided the quantification and mapping of these ES (Figure 1):

- (i) when taking current land-use conditions into account, how different are C stock and C sequestration ecosystem service quantifications under the standard approach (when soil C stocks and heterotrophic respiration are not considered) and the comprehensive approach (including all C stocks and heterotrophic respiration)?
- (ii) How does the valuation of C stock and C sequestration differ in national payments for ES and global C funds or markets when comparing the standard and the comprehensive approach?

Material and methods

Study areas

Mexico, Bolivia and the Amazon region in Brazil are among the target areas of the project ‘the Role Of Biodiversity In climate change mitigation (ROBIN)’ which aims to evaluate the trade-offs between biodiversity, climate change mitigation, human well-being and the supply of ES, as well as to provide key information to decision-makers (ROBIN 2011). The study areas

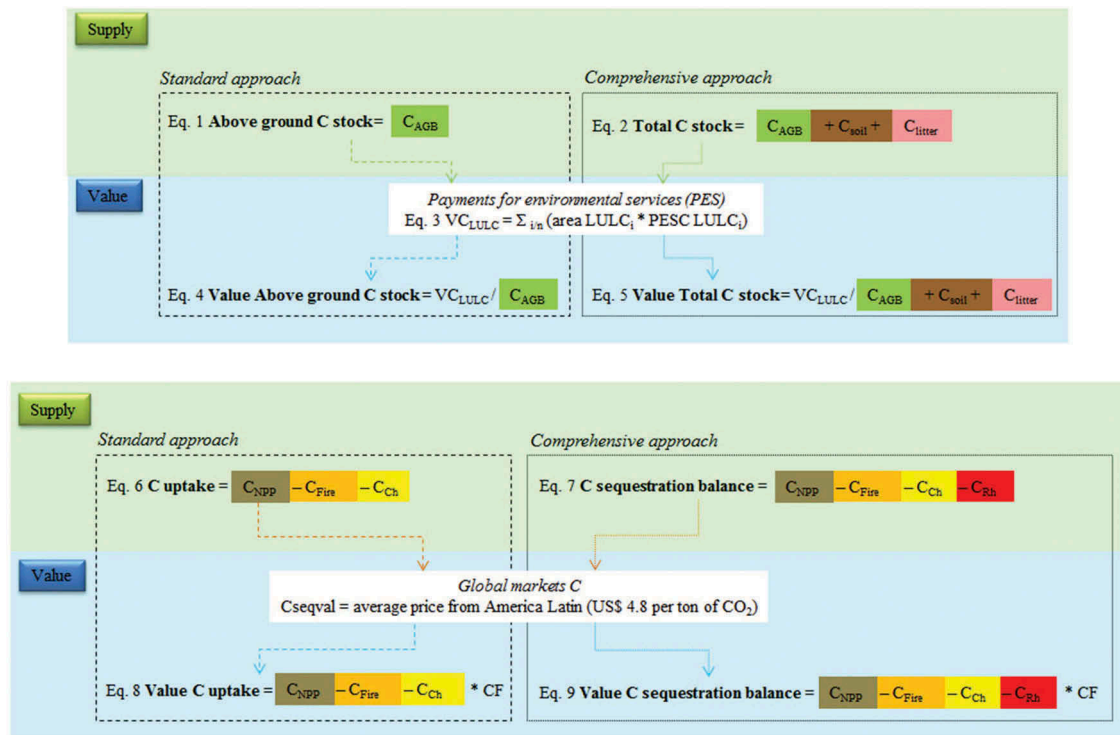


Figure 1. Schematic representation of standard and comprehensive approaches to modelling C stock and C sequestration.

Standard approach only includes aboveground carbon stock (Equation 1), and does not include heterotrophic respiration into carbon sequestration estimates (Equation 6). The comprehensive approach includes C stocks in soil and litter (Equation 2) and assesses ecosystem-level C sequestration including heterotrophic respiration (Equation 7). See details of each equation, pools and processes in Data S1. AGB = aboveground biomass; NPP = net primary productivity; Rh = heterotrophic respiration; Fire = C emissions by fire; Ch = C emissions from crop harvest; VCLULC = values of carbon stock considering the price (US\$) per kilogram C per hectare paid per land use and land cover (as equivalent of aboveground C stock) in payments for ESs (PES) conservation schemes; CF = conversion factor to consider average global price of C sequestration (Cseqval) and to transform C units into CO₂ equivalent units. See details in Tables 1 and 2 as well as Supplementary Materials 1 and 3.

cover nearly the full latitudinal range of Neotropical forest and different land use and land cover (LULC) categories. In Mexico (1,960,189 km² and 119,938,473 inhabitants in 2015; (INEGI 2015), 27% of its territory is covered by grazed shrubland, 26% by forests and 22% by cropland (van Eupen et al. 2014). For Bolivia (1,102,500 km² and 10,059,856 inhabitants in 2012; (INE 2013), LULC categories include forests (55%) and grazed shrubland (9%) (van Eupen et al. 2014). The Brazilian Amazon (5,013,186.89 km² and 26,190,759 inhabitants in 2010; (IBGE 2013) has 46% forest coverage and 19% covered by non-forest. In the deforested areas, large-scale mechanized agriculture occupies 1%, the pasture 10% and the secondary vegetation occupies 1%. These areas are located mainly in the Cerrado Biome (http://www.inpe.br/cra/projetos_pesquisas/arquivos/TerraClass_2014_v3).

ES components

C stock and ecosystem C sequestration balance were quantified and mapped for their *supply* and *value* components (Tallis et al. 2012; Villamagna et al. 2013). *Supply* is the capacity of an ecosystem to provide services (Burkhard et al. 2012). *Value*, in this study, refers to the price that society, including social actors

and decision-makers national, as well as corporations and markets global, set for the delivery of ES (Tallis et al. 2012), in this case, in US\$ per kilogram of carbon per hectare for C stocks and US\$ per kilogram of carbon per hectare per year for C sequestration. Our definition of value does not refer to economic value in the more general sense or to the social costs resulting from climate change (van Den Bergh and Botzen 2015) and is explicitly linked to existing policy instruments in the region associated with climate change mitigation.

Using the LPJmL model data

We applied the LPJmL model to map C stocks and ecosystem C sequestration balance in the study areas. LPJmL simulates global C dynamics and the interactions between the atmosphere, soil and vegetation (Sitch et al. 2003; Bondeau et al. 2007). It considers the growth, production and phenology of different plant functional types (PFTs) competing for light and water to represent the dynamics of plant communities at the biome level. The model was run at a grid resolution of 0.5° × 0.5° (approximately 50 × 50 km at the equator) using combinations of climate data, soil data and land-use change scenarios. Historical climate time-series data derived from the global circulation model HadGEM2-ES were

Table 1. Components of C stock and ecosystem C sequestration balance.

Definition	Components (code)	Description of the components (code)	Unit
C stock			
Amount of C stored in the landscape	Carbon in aboveground biomass (C_{AGB})	Carbon in the leaves, branches and aerial stems	kgC/m ²
	Soil carbon (C_{soil})	Carbon in the biomass of roots and the soil	kgC/m ²
	Litter carbon (C_{litter})	Carbon in the dead vegetation and soil organic matter. Turns into soil carbon in ~2–3 years.	kgC/m ²
Ecosystem C sequestration balance			
Amount of C sequestered through time (balance between uptake and release)	Uptake Release	Net primary productivity (C_{NPP})	kgC/m ² yr
		C emissions by fire (C_{fire})	kgC/m ² yr
		Heterotrophic respiration, including C emissions from deforestation (C_{Rh})	kgC/m ² yr
		C emissions through crop harvesting (C_{ch})	kgC/m ² yr

Table 2. Prices assigned in payment for ecosystem services for C stock. LULC = Land Use and Land Cover. See details about values for each LULC in the study areas in supplementary materials 3.

Definition	Components	Description of the components	Unit	Years	Source
Prices of C stock derived from national payments for ecosystem services	LULC for Mexico	16 LULC ranging from agriculture, shrubland to cloud forest	Polygon (ha)	2013	INEGI 2013
	Payment for ES in Mexico LULC in Bolivia	Prices between 0 and 85 US\$/ha	US\$/ha	2013	CONAFOR 2013
		9 LULC ranging from crops, managed grassland to cloud forest	Polygon (ha)	2007	Baldiviezo 2010
	Payment for ES in Bolivia LULC in the Brazilian Amazon	Prices between 0 and 2.25 US\$/ha	US\$/ha	2008	Asquith et al. 2008
		6 LULC ranging from annual agriculture, reforestation to forest	Polygon (ha)	2008	EMBRAPA 2014
Payment for ES in Brazil	Prices between 0 and 234 US\$/ha	US\$/ha	2011	Guedes and Seehusen 2011	

taken from the Inter-Sectoral Impact Model Intercomparison Project (Warszawski et al. 2014). Soil data were based on the Harmonized World Soil Database (Schaphoff et al. 2013). Land-use data were taken from the land-cover change model CLUE (Conservation of Land Use and its Effects), which was used in the ROBIN project (van Eupen et al. 2014; Boit et al. 2016). A spin-up period of 1000 years was used to bring the carbon pools and fluxes of the vegetation into equilibrium with historic climate and atmospheric CO₂ concentration while starting from bare ground.

We integrated LULC changes by simulating 100 years of historic trends (1901–2000), while the models used here rely on the period 1981–2000; the simulation data over the 20-year period were averaged across years to smooth out interannual climate variability. We used the so-called vegetation scenario to assess the reduction of a fraction of natural vegetation and the foliage projected cover of PFTs (Bondeau et al. 2007). The land-use change history was assessed (biomass removed by anthropic land-use change and by natural fire regimes) from the fraction of each grid cell that had been modified into one of each current land-use type; it also models the dynamics of 16 crop functional types including managed grass, in addition to the 9 PFTs, behaving as natural vegetation within the remaining fraction of natural vegetation (Bondeau et al. 2007).

C stock supply and ecosystem C sequestration balance

C stocks supply and ecosystem C sequestration balance were calculated for each grid cell and for the total area of

each study region; see Figure 1, Tables 1, 2 and text below for details.

Standard vs. comprehensive approach

C stock supply was defined as the average amount of carbon stored in the terrestrial ecosystem during the period studied (Table 1, Figure 1). C stock supply for 1981–2000 was calculated by using the current vegetation scenario (Figure 1; see details in Supplementary Materials 1). Three different C pools were assessed: vegetation (i.e. aboveground biomass, C_{AGB}), soil (i.e. roots and C within the soil at 100 mm depth, C_{soil}) and litter (i.e. above- and belowground litter pool and soil organic matter decomposition, C_{litter}). Since litter is very dynamic and cannot be considered *sensu stricto* as a long-term C stock, it was considered as a constant fraction of soil C (Bruun et al. 2009).

To assess how estimates of C stocks are biased by not explicitly including soil C, we contrasted two approaches. In the first approach, named here as ‘the standard approach’ (Equation 1 in Figure 1), we considered only aboveground biomass (C_{AGB}), which is the most common approach used for most C stock estimations (Gibbs et al. 2007; Pan et al. 2013). In the second approach, named here as ‘the comprehensive approach’ (Equation 2 in Figure 1), we considered all components, i.e. total C (C stock) was calculated as the sum of C in vegetation (C_{AGB}), in soil (C_{soil}) and in litter (C_{litter}).

Ecosystem C sequestration supply was defined as the ecosystem-level balance between the amount of carbon that was taken up by vegetation and the amount of carbon that was released into the atmosphere (Table 1; Figure 1), both per unit

area per year, as well as a total across the whole study area (Chapin et al. 2006). CO₂ is absorbed by the vegetation from the atmosphere through photosynthesis, so that net primary productivity (C_{NPP}) is equal to the gross primary productivity (GPP) minus the respiration of primary producers (i.e. autotrophic respiration). NPP in LPJmL includes both the growth of natural vegetation and the annual regrowth of crops. C released is liberated into the atmosphere as a result of: (a) heterotrophic respiration (C_{Rh}), defined as the amount of C released by the decomposition of dead organic material, (b) deforestation (clearing forest completely and permanently), (c) fires (C_{Fire}) and (d) crop harvesting (C_{Ch}) (see details of pools and fluxes in Bondeau et al. 2007; Thonicke et al. 2008). C_{Rh} subsumes simulated microbial decomposition processes within the litter layer in LPJmL, which result in time-delayed CO₂ emissions over several years, although a fraction of this input is mineralized into the soil into slow decomposing pools. Simulated decomposition processes include dead biomass produced by the natural mortality of plants as well as deforestation and other land-use activities, which result in short-term or long-term CO₂ release through forest loss. The amount of C lost from the ecosystem by timber harvesting was not differentiated further into different components (e.g. a separation between losses from deforestation and selective logging) because this information is not available from the land-use scenario at country scale. C_{Ch} accounts for the amount of C temporarily stored in (non-woody) crop biomass and lost from the ecosystem by harvesting.

To assess how estimates of ecosystem C sequestration are biased by not explicitly incorporating heterotrophic respiration, we contrast standard approach (Equation 6 in Figure 1) that only includes net primary productivity (C_{NPP}), emissions from fire (C_{Fire}) and from crop harvesting (C_{Ch}), with the comprehensive approach (Equation 7 in Figure 1) that also includes emissions from heterotrophic respiration (C_{Rh}).

Model validation and comparison

The validity of the models is important if they are to be used for policy design and implementation (Peng et al. 2009). Only for aboveground C stocks, we used formal validation of our spatial models (see details in Supplementary Materials 2) as well as simple comparisons of total national estimates. Our results of total C stock were compared with currently available national-level estimates of total aboveground C from modelled estimations (IPCC in Gibbs et al. 2007), biomass harvest compilations and forest inventories (Gibbs et al. 2007), as well as remotely sensed data

(Liu et al. 2015). No analogous data were available to calibrate our ecosystem C sequestration balance models.

Implications for the valuation of C stock and ecosystem C sequestration

Effects of the inclusion of soil and litter carbon on price paid for carbon stock

Based on the most widely used approaches for calculating the price of C stock, we assessed them from the flat rate payments per hectare currently issued by existing PES (or Payment for ESs) conservation schemes in each country (Table 2, Supplementary Materials 3) and then divided by typical C stocking rates of different forest types. A specific price per unit area (VCLULC; Equation 3 in Figure 1) was associated with each category of LULC. For Mexico, public and government sectors distinguish nine types of LULC for payments for ESs (CONAFOR 2013), where LULC data are derived from remote sensing (INEGI 2013). Since Bolivia does not have payments for ESs programmes, the price per area for each LULC type was derived from one-time payments that had been made for bird habitat and watershed protection in the Los Negros valley, Santa Cruz Department in three types of LULC (Asquith et al. 2008). These were extrapolated to the same LULC elsewhere, based on LULC data from remote sensing (Baldiviezo 2010). For Brazil, an analogous procedure was used based on payments for ESs for five types of LULC in the Mata Atlantica (Guedes and Seehusen 2011), for which data were also obtained from remote sensing (EMBRAPA 2014).

To assess how the inclusion of soil carbon affects the way in which C stocks are valued, we compared the standard with the comprehensive approaches. Although in PES schemes and payments are not usually made in terms of C, the resulting value or 'price' of the C is invariably calculated on the basis of AGB, and does not include the soil carbon stocks that are also present in these ecosystems. If all the C stocks were to be included, the estimated price per ton C would be much lower.

We thus compared current estimated values per ton C using the standard approach, based solely on the AGB (Value aboveground C stock; Equation 4 in Figure 1), with those based on the total C stocks, using the comprehensive approach, including AGB, soil and litter stocks (Value total C stock; Equation 5 in Figure 1).

To obtain the difference of the C stock value if soil and litter C are included in the calculation, we followed the next steps. First, we converted kgC/m² to

kgC/ha for aboveground C stock and total C stock. For example, to Mexico, we have the following data:

Equation 1: Aboveground C stock = $C_{AGB} = 5.71 \text{ kgC/m}^2$.

Equation 2: Total C stock = 14.31 kgC/m^2 .

$$\begin{aligned} \text{Above ground C stock} &= C_{AGB} \\ &= 5.71 \frac{\text{kgC}}{\text{m}^2} \\ &\quad * \frac{10,000 \text{ m}^2}{1 \text{ ha}} \\ &= \frac{5.71 * 10,000}{1} \\ &= 57,100 \frac{\text{kgC}}{\text{ha}} \end{aligned} \quad (1)$$

$$\text{Total C stock} = 14.31 \frac{\text{kgC}}{\text{m}^2} = 143,100 \frac{\text{kgC}}{\text{ha}} \quad (2)$$

Second, we obtained the value of aboveground C stock and the value of total C stock considering the specific price per unit area (VCLULC; Equation 3 in Figure 1):

$$VC \text{ LULC} = 29.38 \text{ US\$ ha} \quad (3)$$

(grid with tropical rain forest and tropical dry forests for Mexico, see value for each LULC in Table 2, Supplementary Materials 3).

$$\begin{aligned} \text{Value Above ground C stock} &= \frac{VC_{LULC}}{C_{AGB}} \\ &= \frac{29.38 \text{ US\$/ha}}{57,100 \text{ kgC/ha}} = 0.0005 \text{ US\$/kgC ha} \end{aligned} \quad (4)$$

$$\begin{aligned} \text{Value Total C stock} &= \frac{29.38 \text{ US\$/ha}}{143,100 \text{ kgC/ha}} \\ &= 0.0002 \text{ US\$/kgC ha} \end{aligned} \quad (5)$$

Finally, we calculated the difference (as ratio) between aboveground C stock (Equation 4) and the total C stock values (Equation 5).

Prices of C sequestration from global markets

Standard C sequestration projects in the voluntary and other carbon markets (Value C uptake; Equation 8 in Figure 1) calculate the price of C on the basis of increases in AGB. We used the global average price of C of different types of projects including projects that pay for the following: (i) C sequestration, i.e. increasing C stock over time as a result of forest regrowth (AR = afforestation/ reforestation) and improved forest management (FM = improved forest management) and (ii) reductions in CO₂ emissions, i.e. reducing activities that cause C releases to the atmosphere as a result of land-use change and forest combustion through improved forest management, without necessarily increasing C stock. The average global price of C (shown as C_{sequal} in Figure 1) from all market projects in Latin America for 2015 was US\$ 4.8

per ton of CO₂e per hectare (Hamrick and Allie 2015). To apply this price, we used a conversion factor (CF) that in the first step transforms CO₂ units (in price of C market) into equivalent C units, considering that 3.67 tons of CO₂ is equivalent to 1 ton of C (Ciais et al. 2013). In a second step, it converts 1 ton of C per hectare into kgC per m² (unit used for ecosystem C sequestration balance maps). The resulting CF was US\$ 0.131 per 1.0 kg C/m² yr.

To assess how the inclusion of heterotrophic respiration affects the way in which ecosystem C sequestration is valued, we compared the resulting price of C sequestration using the standard approach, taking into account only carbon uptake by vegetation (Value C uptake; Equation 8 in Figure 1), with our comprehensive approach in which the C flux would also take into account heterotrophic respiration (Value C sequestration balance; Equation 9 in Figure 1). We did not include soil carbon in this analysis since increases in soil carbon are slow and would not be measureable over the time interval of most projects.

To show if overall sequestration has been overestimated, and that payments could have been realized in areas that are net emitters, we followed the next steps. First, we considered the data for C uptake and C sequestration balance for Mexico, for example:

$$C \text{ uptake} = 0.912 \text{ kg C/m}^2 \text{ yr} \quad (6)$$

$$C \text{ sequestration balance} = 0.058 \text{ kg C/m}^2 \text{ yr} \quad (7)$$

Second, we obtained the value of C uptake and the value C sequestration balance considering the average global price of C (shown as C_{sequal} in Figure 1) from all market projects in Latin America, but as CF, before described:

C_{sequal} = US\$ 4.8 per ton of CO₂e per hectare = US\$ 0.131 per 1.0 kg C/m² yr

$$\begin{aligned} \text{Value C uptake} &= 0.912 \text{ kg C/m}^2 \text{ yr} \\ &\quad * 0.131 \text{ US\$ kgC/m}^2 \text{ yr} \\ &= 0.119 \text{ US\$/kgC/m}^2 \text{ yr} \end{aligned} \quad (8)$$

$$\begin{aligned} \text{Value C sequestration balance} \\ &= 0.008 \text{ US\$/kgC/m}^2 \text{ yr} \end{aligned} \quad (9)$$

Finally, we calculated the difference (as ratio) of value between C uptake (Equation 8) and the C balance sequestration value (Equation 9).

Results

How are estimates of C stocks biased by not including soil C?

We found that standard approach of C stocks have been neglecting between 49.5% and 65% of the total C stocks, relative to the comprehensive approach, by

failing to incorporate the amount of C stored in soil and litter. The relative contributions of the different pools (AGB, soil and litter) were similar between countries, according to the comprehensive approach. The largest total C stock was found in the Brazilian Amazon (total of 348.2 PgC), followed by Bolivia (51.3 PgC) and Mexico (37.8 PgC) when averaged for 1981–2000 (Figure 2, Table S1 and Table S2 in Supplementary Materials 1). The largest soil C stocks were found in the Brazilian Amazon (144 PgC), followed by Bolivia (23.5 PgC) and Mexico (21.6 PgC), but the relative contribution of soil C to the total in each country is in the reverse order: 41% in the Brazilian Amazon, 46% in Bolivia and 57% in Mexico. Litter C contributed 8% to total C stocks in the region (59.6 tonC/ha, 8.2% for Brazilian Amazon, 38.1 tonC/ha, 8.1% for Bolivia, and 14.6 tonC/ha, 8.3% for Mexico; Table S2 in S1 Appendix). Underestimations of total C stock due to non-inclusion of soil and litter C were highest for Mexico (65.4%), following of Bolivia (53.9%) and Brazilian Amazon (49.6%) (Figure 2, Table S1 and Table S2 in Supplementary Materials 1).

Aboveground carbon stocks modelled by LPJmL, and obtained for standard approach, are higher than those reported by previous studies, and show a partial match with the corresponding spatial patterns (Figure 3, S3 Appendix). Spatial correlations between our model (axis 'Calculated aboveground C stock') and remote-sensed data (axis 'Stimated aboveground C stock') were highest for Bolivia ($R^2 = 0.57$), followed by Mexico ($R^2 = 0.52$), then by the Brazilian Amazon ($R^2 = 0.35$). The discrepancies are largely due to the fact that satellite images become saturated at relatively low aboveground C stock levels (~ 13.5 – 15 kgC/m²) while our model predicted higher values (e.g. 29.6 kgC/m²) (Steininger 2000). As a result, fewer discrepancies were found for Mexico, more for Bolivia, while they were highest in the Brazilian Amazon. LPJmL values for aboveground C stocks were consistently higher than other sources (Figure 2), on average 59% higher than IPCC estimates, 72–88% larger than forest inventories (12% for the Brazilian Amazon). As a result, country-level estimates of aboveground C stocks from LPJmL models were higher than other estimates (shown in Figure 2) for Mexico (1–3 times), Bolivia (1–10) and the Brazilian Amazon (1–3 times) (Table S6 in S3 Appendix).

How are C sequestration estimates biased by not explicitly including heterotrophic respiration?

Standard approach of C sequestration only takes into account C uptake from NPP (i.e. photosynthesis minus autotrophic respiration of primary producers; 1.92 PgC/yr for Mexico, 1.93 PgC/yr for Bolivia and

11.89 PgC/yr for the Brazilian Amazon) and emissions from fire (-0.10 PgC/yr for Mexico and Bolivia and -0.70 PgC/yr for the Brazilian Amazon), and crop harvest (-0.32 PgC/yr for Mexico, -0.08 PgC/yr for Bolivia and -0.39 PgC/yr for the Brazilian Amazon, all values in Table S1 in Supplementary Materials 1).

By explicitly including heterotrophic respiration a positive, yet at least 10 times smaller ecosystem C sequestration balance was found for all countries (when the comprehensive approach compared with the standard approach for the period 1981–2000), because heterotrophic respiration offsets the vast majority of the CO₂ uptake by vegetation growth given by NPP (Figure 4, Table S1 in Supplementary Materials 1). Ecosystem C sequestration balance was highest for the Brazilian Amazon (0.48 PgC/yr, equal to 1 tonC/ha yr), followed by Bolivia (0.14 PgC/year, equal to 1.3 tonC/ha yr) and finally by Mexico (0.03 PgC/yr, equal to 0.1 tonC/ha yr). Heterotrophic respiration (-1.48 PgC/yr for Mexico, -1.61 PgC/yr for Bolivia and -10.32 PgC/yr for the Brazilian Amazon), including decomposition of dead organic material (as well as the modelled deforestation prescribed by the land-use scenario which serves as an input to LPJmL), was in fact the major contributor to C emissions. Overestimation of the ecosystem C sequestration values was highest for Mexico (53-fold; Fig. S6 in Supplementary Materials 5 and Table S1 in Supplementary Materials 1), followed by Brazilian Amazon (22-fold; Fig. S14 in Supplementary Materials 7 and Table S1 in Supplementary Materials 1) and Bolivia (12-fold; Fig. S10 in Supplementary Materials 6 and Table S1 in Supplementary Materials 1).

How does the inclusion of soil C affect the way in which C stocks are valued in national payments for ES?

The effective price per ton of C that financial supporters of PES conservation schemes are paying today using standard approaches, which focus only on aboveground C stocks based on a flat rate per hectare, are up to 500 times lower if soil and litter C are included in the calculation. The other side of this coin is that they are in fact conserving far more carbon than they have calculated, since when the carbon in the soil and litter layers are included, this increases the total C stock considerably. As a result, in most PES, areas in Mexico C are being conserved at an equivalent price of only US\$0.1 per kg C per ha based on current PES per hectare payment levels (South-eastern part of the country Figure 5(e)), while in large fractions of the Brazilian Amazon (Central and western part of the Amazon Figure 7(e)), this is US\$ 0.01 per kg C per ha, and most areas in Bolivia (Central and Northern parts of the Country, Figure 6(e)), only US \$0.001 per kg C per ha because of the great, and up to now

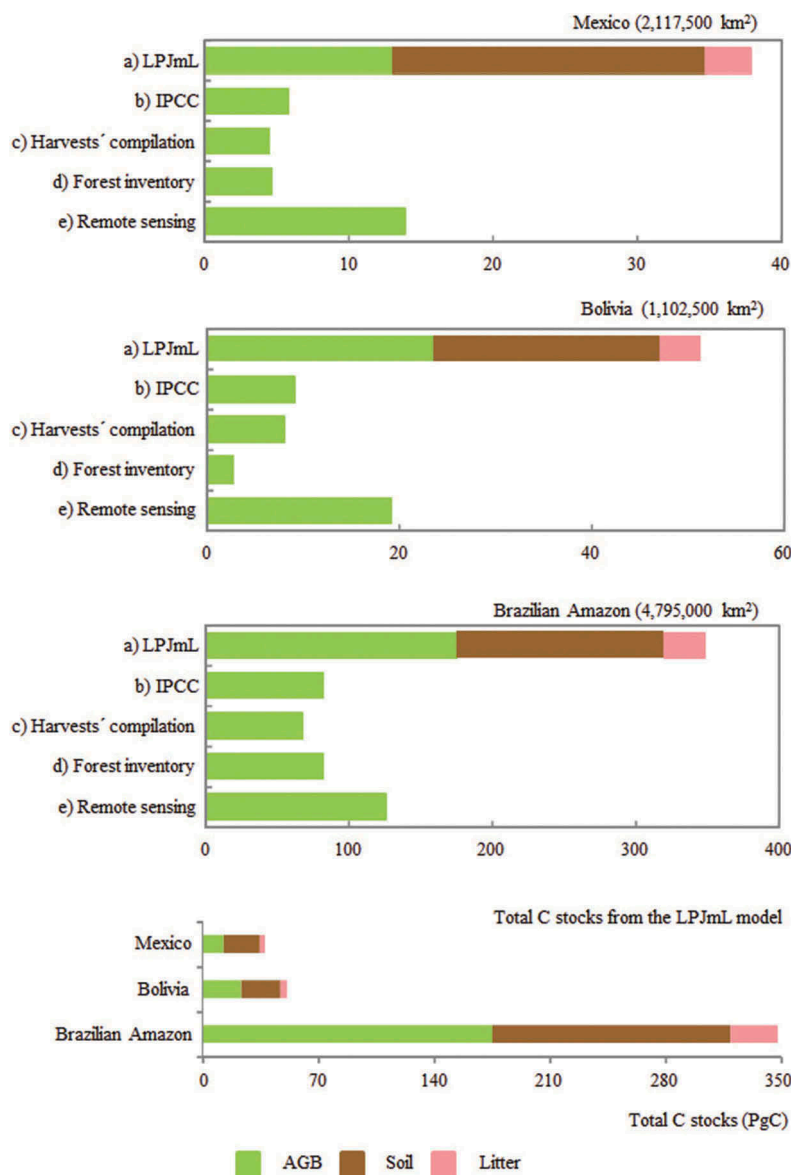


Figure 2. Magnitude of C stocks for Mexico, Bolivia and the Brazilian Amazon using dynamic vegetation model data (LPJmL) and range of other data sources.

Total C stocks from (a) LPJmL model using compressive approach and average from 1981 to 2000; (b) IPCC (IPCC 2006); (c) compilations of point-based biomass harvest measurement data (Gibbs et al. 2007), (d) national forest inventory data (Gibbs et al. 2007) and (e) spatially explicit data derived from remote sensing (Liu et al. 2015).

unrecognized, contribution of C soil and C litter in these areas (Fig. S11 in Supplementary Materials 7).

How does the inclusion of heterotrophic respiration affect the way in which C sequestration is valued in global C funds or markets?

The inclusion of heterotrophic respiration, which is the amount of C released because of the decay of organic matter, dramatically changed the spatial distribution of areas that can be considered as actively sequestering C (Figure 8). In the case of Mexico, for example, the positive gains in C associated with the more humid parts of the country (e.g. within the states of Chiapas and Veracruz in the southeast of Mexico) are greatly modified by the effects of heterotrophic respiration, such that they are seen to be net emitters (0.01–

0.1 kgC/ha⁻¹ yr⁻¹) rather than net absorbers on the order of 0.25–0.96 kgC/ha⁻¹ yr⁻¹ (Figure 8 and Fig. S6 in Supplementary Materials 5). As a consequence, large parts of the study areas, 33% for Mexico (Figure 8(b)), 30% for the Brazilian Amazon (Figure 8(f)) and 6% for Bolivia (Figure 8(d)), are shown to be contributors to C emissions rather than sinks.

When heterotrophic respiration (C_{RH}), an ecosystem process routinely omitted by global markets, is included in the ecosystem carbon balance, the country-level balance remains positive (i.e. the countries remain sinks overall), but the sink effect is much smaller than that derived from standard calculations, which are based solely on living biomass. Figure 8 demonstrates the very large differences between the equivalent prices per ton of C sequestered in carbon projects based on estimates that do not include ecological decay processes (standard

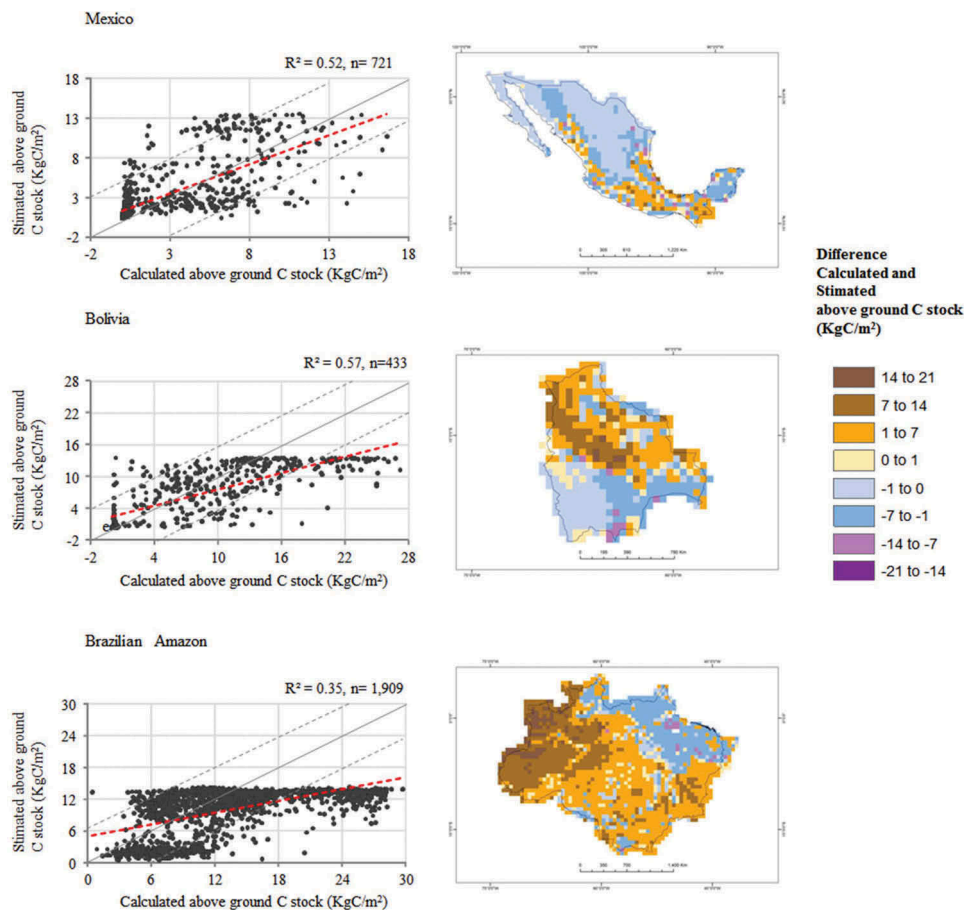


Figure 3. Validation of aboveground C stock for Mexico, Bolivia and the Brazilian Amazon.

We compared our values of aboveground C stock modelled here with LPJmL (axis 'Calculated aboveground C stock'), considering standard approach, with aboveground C stock from remote-sensed data (axis 'Stimated aboveground C stock'), by comparing: (a) the relationship between the data sets which fit a linear regression (red dashed line) and root-mean-square errors (grey dashed line) for each pixel (50 × 50 Km) and (b) the corresponding spatial patterns of each data set.

approaches) and comparing these with those that do include such processes (comprehensive approaches). The figures presented below illustrate this point, since in our analysis carbon emissions from deforestation are included in the C_{Rh} calculation (Figure 8(b,d,f)), while global market in carbon projects usually do not give accounting for decaying material or timber products, these are assumed from the overall calculation of C gained or lost.

However, since emissions from heterotrophic respiration of organic material offset a large proportion of the carbon gained through growth of living matter, in reality funds, markets and decision-makers are inadvertently overestimating the carbon that they think they are saving (Equation 9 in Figure 1), and are therefore, in effect, paying much higher prices for each ton of carbon that is in reality being saved.

Discussion

Importance of using dynamic vegetation models for ES

The use of DGVMs allowed us to explicitly incorporate soil C into estimates of total C stocks and heterotrophic

respiration into ecosystem C sequestration balance, which together allowed us to deliver what we feel is a more realistic representation of C dynamics than is currently available using standard tools. The LPJmL model delivered values for aboveground C stock that were comparable in area and resolution with the most reliable and recent data sources available (Liu et al. 2015), and reported on areas with particularly high aboveground C stock (as in the case of the forest in Bolivia).

It is important to note that there is still considerable uncertainty in estimating total biomass carbon based on remote sensing of up to 45% (Saatchi et al. 2011) which calls for comparing simulation results against several available observation products. The total C stock for each of the countries and the pixel-by-pixel aboveground C obtained with LPJmL were highly correlated (R^2 between 0.35 and 0.57) with values obtained from remote sensing data (Liu et al. 2015) for low aboveground C values. Areas with very high aboveground C content (>14.2 kgC/m²) could be detected with LPJmL, but not with remote sensing because of saturation over highly dense areas; the saturation values reported here (15 kgC/m²) match those reported by a study for Brazil and Bolivia

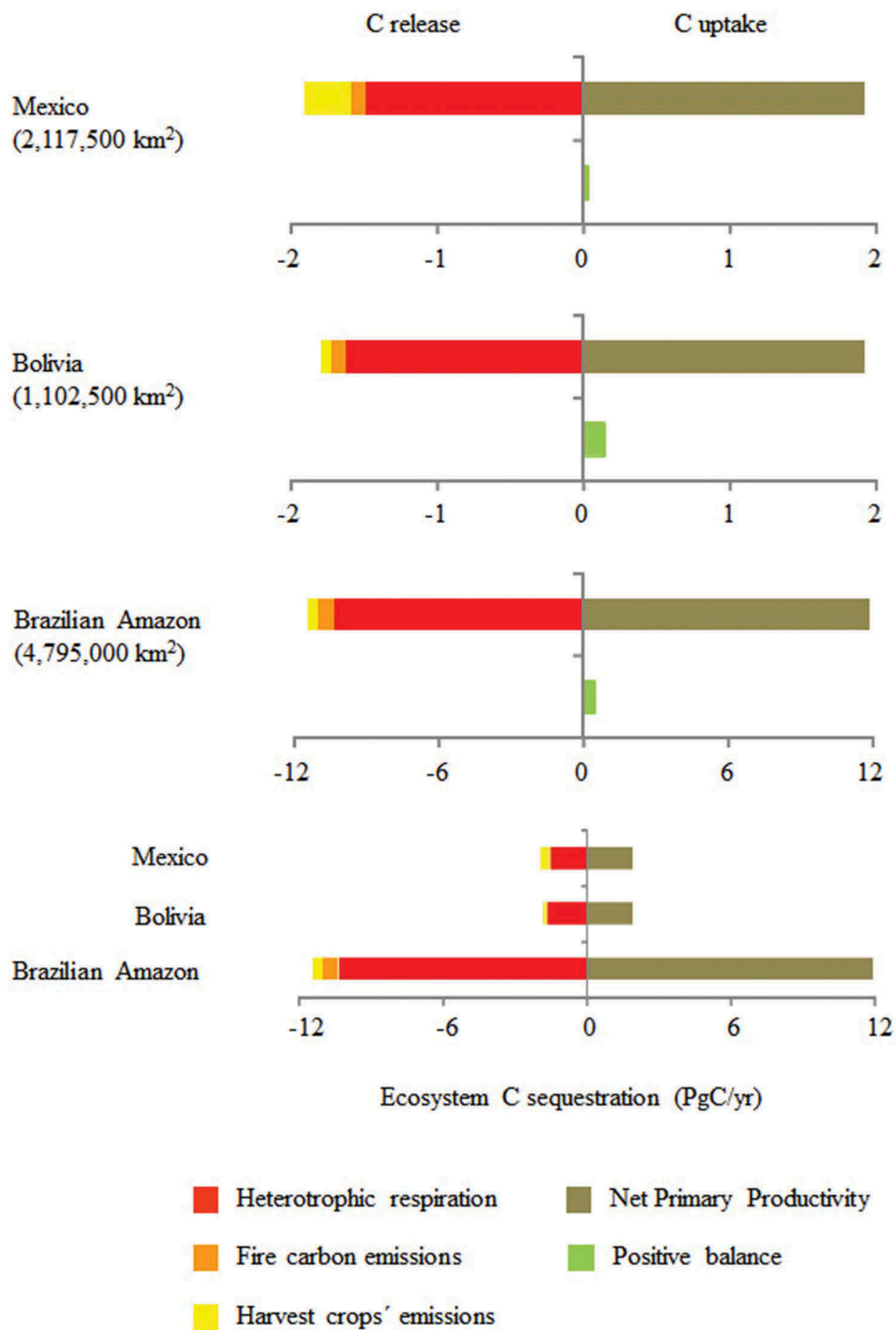


Figure 4. Magnitude of ecosystem C sequestration balance for Mexico, Bolivia and the Brazilian Amazon based on the comprehensive approach and using dynamic vegetation model data (LPJmL).

Ecosystem C balance (green bars) calculated as the difference between C uptake from NPP (brown bars) and release from heterotrophic respiration (decomposition of organic material including deforestation by the land-use scenario – red bars), fire (orange) and crop harvest (yellow) for Mexico, Bolivia and the Brazilian Amazon.

(Steininger 2000). In turn, highest LPJmL predicted C stock values (144 PgC) are smaller than the highest total aboveground C biomass values reported from field in sites such as Maraca' forests (Amazonian forest) to be about 350 PgC (Nascimento et al. 2007). In fact, extrapolations of plot-level data over large areas (Poorter et al. 2015) confirmed that the aboveground C stocks per unit area as estimated by LPJmL were slightly higher than those from forest plots and

site data for Bolivia (differences of 4%), and the Brazilian Amazon (7%), and only lower for Mexico (81%) for being data derived mainly from tropical dry forest.

LPJmL also contributed to an assessment of C in litter. The importance of C in litter in vegetation and soil dynamics is well known in the carbon dynamics literature (Ciais et al. 2013), but its contribution to ES associated with climate change mitigation needs to be reassessed.

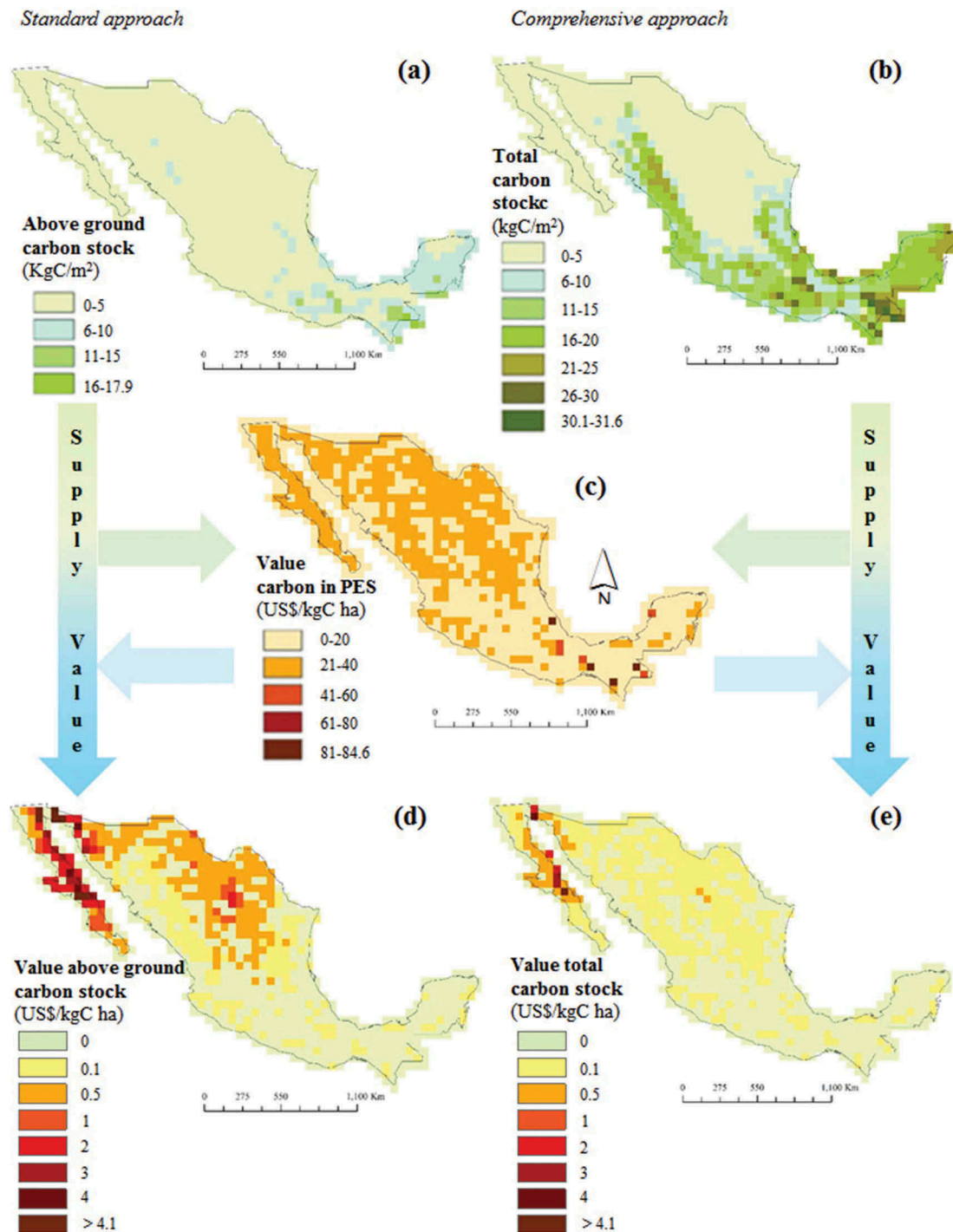


Figure 5. Standard and comprehensive approaches to modelling C stock for Mexico.

(a) Aboveground C stock using the standard approach. (b) Total C stock including carbon in soil and litter using the comprehensive approach. (c) Values of carbon stock considering the price (US\$) per kilogram C per hectare paid per land use and land cover (as equivalent of aboveground C stock) in payments for ESs (PES) conservation schemes in Mexico. (d) Value aboveground C stock using standard approach. (e) Value total C stock using the comprehensive approach. See details in Table 2, Supplementary Materials 2 and Supplementary Materials 3 for PES schemes.

Despite being a very dynamic component of C stocks, the maintenance of this pool is critical to both AGB and soil stock. We found here that litter C contributes an important fraction of overall C stocks, and that its loss can jeopardize the maintenance of other C pools.

Ecosystem C sequestration values obtained with LPJmL were consistent with recent findings on the current and potential contribution of the tropical

forests of the regions studied. The forests studied here are known to be important carbon sinks (Pan et al. 2011; Chazdon et al. 2016). Our ecosystem C sequestration balance estimates could not be validated because no equivalent current data were available for the same period in the three countries.

C uptake is usually estimated on the basis of changes in land use (Kareiva et al. 2011), but

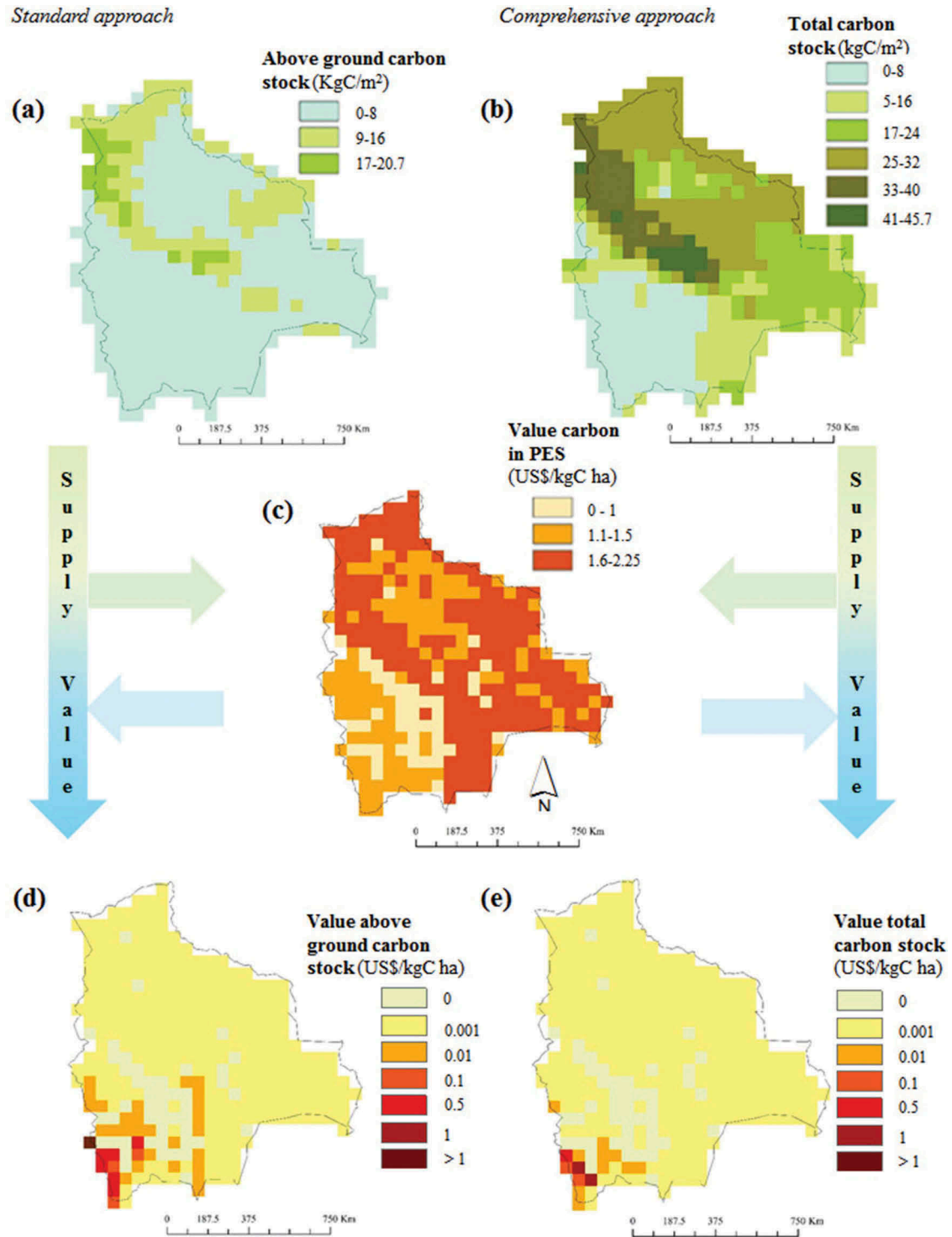


Figure 6. Standard and comprehensive approaches to modelling C stock for Bolivia.

(a) Aboveground C stock using the standard approach. (b) Total C stock including carbon in soil and litter using the comprehensive approach. (c) Values of carbon stock considering the price (US\$) per kilogram C per hectare paid per land use and land cover (as equivalent of aboveground C stock) in payments for ESs (PES) conservation schemes in Bolivia. (d) Value aboveground C stock using standard approach. (e) Value total C stock using the comprehensive approach. See details in Table 2, Supplementary Materials 1 and Supplementary Materials 3 for PES schemes.

ecosystem C sequestration balance is rarely taken into account and most ES models do not take into account the functional C dynamics. Several remote sensing and field-based observational products providing the spatial and temporal coverage of interest are required to evaluate simulated C sequestration and storage, while taking their uncertainty and methodology into

account (Saatchi et al. 2015). One such example is Murray-Tortarolo and collaborators (Murray-Tortarolo et al. 2016) who used remote-sensed data (MODIS), field measurements, flux towers (MTE) and compared them against several DGVMs which estimated C stocks and fluxes in Mexico for period 2000–2005. These results tally with those found here

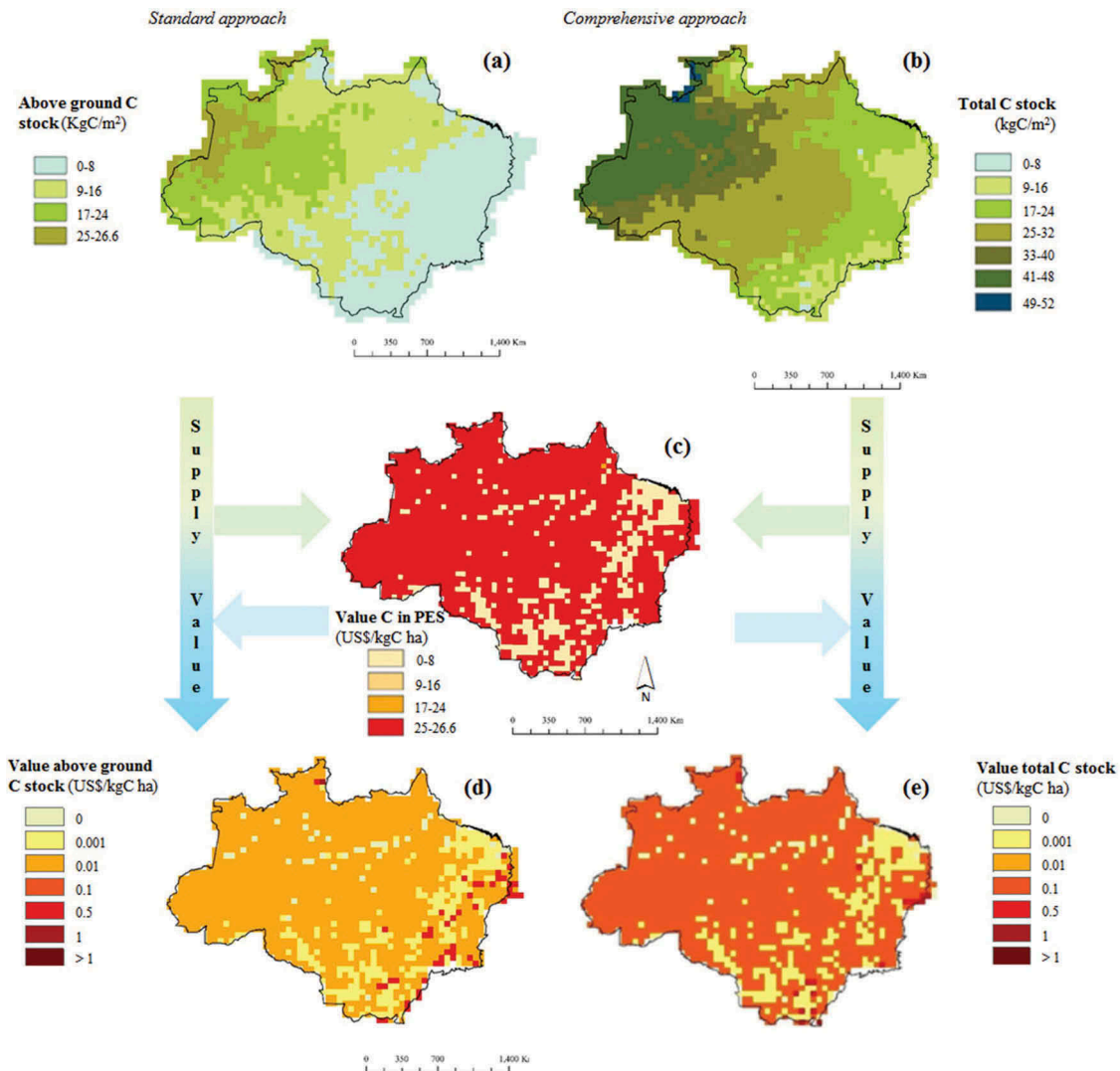


Figure 7. Standard and comprehensive approaches to modelling C stock for Brazilian Amazon.

(a) Aboveground C stock using the standard approach. (b) Total C stock including carbon in soil and litter using the comprehensive approach. (c) Values of carbon stock considering the price (US\$) per kilogram C per hectare paid per land use and land cover (as equivalent of aboveground C stock) in payments for ESs (PES) conservation schemes in Brazilian Amazon. (d) Value aboveground C stock using standard approach. (e) Value total C stock using the comprehensive approach. See details in Table 2, Supplementary Materials 1 and Supplementary Materials 3 for PES schemes.

and show the usefulness of DGVMs such as LPJmL. The use of a multi-model ensemble, for instance, has frequently been used to overcome the limitations of individual models design (Bagstad et al. 2013; Grêt-Regamey et al. 2017).

LPJmL provided information on heterotrophic respiration, fire and biomass harvest which are usually not included in ES assessment, although estimates of these carbon fluxes would be mandatory in any biogeochemistry carbon balance analysis.

Modelling total C stock and ecosystem C sequestration balance of ES with LPJmL also provides a unique opportunity for modelling and mapping the different components of these ESs for the future by using process-based models at national-to-global scales. Incorporating DGVMs such as LPJmL in ES assessments provides consistently simulated data

which can be used for carbon, as shown here, but potentially also for water-related ESs.

DGVMs need to be taken into account when the goal is to communicate simulation results to policy-makers. Yet, the LPJmL specifically, and DGVMs in general, still have uncertainties to describe the ecosystem processes which may affect the carbon stock and flux estimates and thus the error propagation to ES assessment models. Current estimations of heterotrophic respiration imply the decay of timber-forest products as dead organic material remaining in the ecosystem, and include simulations of some levels of deforestation. Although the LPJmL model also simulates the build-up of a slow carbon pool in the soil, this can be regarded as a slow decay of wood products. Knowing the model concept and underlying assumptions would also

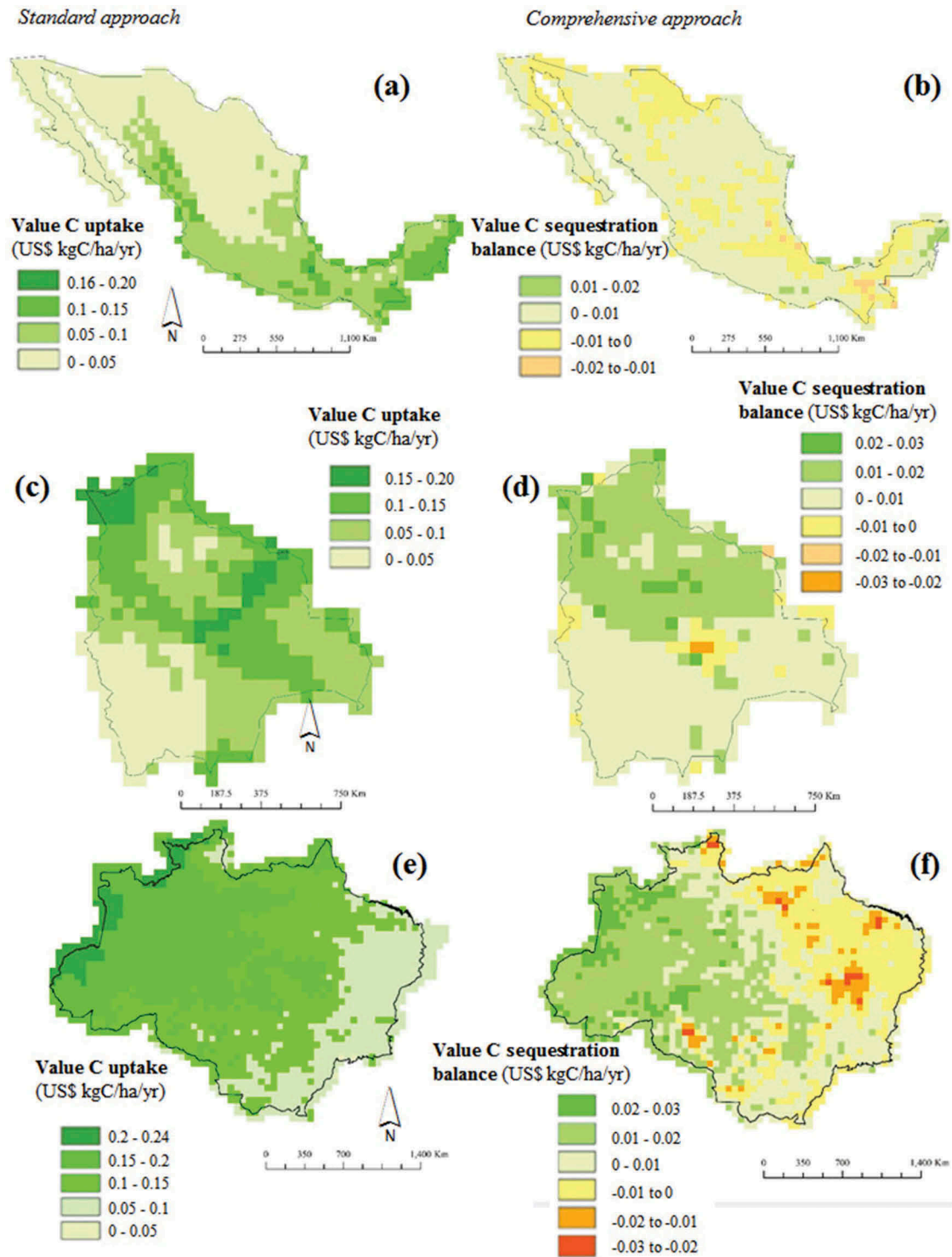


Figure 8. Standard and comprehensive approaches to modelling ecosystem C sequestration balance for Mexico, Bolivia and Brazilian Amazon.

(a) Value C uptake for Mexico using standard approach. (b) Value C sequestration balance for Mexico using comprehensive approach. (c) Value C uptake for Bolivia using standard approach. (d) Value C sequestration balance for Bolivia using comprehensive approach. (e) Value C uptake for Brazilian Amazon using standard approach. (f) Value C sequestration balance for Brazilian Amazon using comprehensive approach.

allow factorial experiments to help explain certain changes in the provision of ESs. These features make such models very useful in assessing the impact of alternative climate change and policy implementation scenarios.

Importance of including soil C in total C stock estimations

Our study highlighted the importance of the areas studied with regard to their contribution to global C stocks. The three countries account for 14.3–22.4% of

the total C stocks of the world (Saatchi et al. 2011; Ciais et al. 2013).

We showed that by not including C stocks in soils, governments and global assessments are underestimating total C stock and balances, especially in the tropics. Large amounts of carbon are stored in permafrost, boreal forest, tropical wetlands and peatlands, which are ecosystems particularly vulnerable to warming and land-use change (Ciais et al. 2013), but the three countries studied here contribute between 7.9% and 12.6% of global soil C (Ciais et al. 2013); soil C levels were particularly high for Mexico (58%).

Discrepancies in aboveground C stocks between the different data sources for the different countries can be explained by the approaches used. LPJmL groups species into major PFTs and agglomerates landscape mosaics into large grid cells of 50 × 50 km (Sitch et al. 2003; Bondeau et al. 2007). It also depends on the model approach used to simulate stem mortality (Johnson et al. 2016). The discrepancies were slightly those relative to field estimates, which are the most precise, but they only apply to a small fraction of the land and hardly consider the variation across and within landscapes (Poorter et al. 2015).

The methodological differences scale up when total C stocks of a country are aggregated. Overcoming the discrepancies between locally measured C stocks, knowing how they scale up to larger geographical units, such as a country or biome, and knowing which ecosystem processes play a role at the larger scale would help to reduce uncertainties associated with the C stock estimation.

Importance of assessing ecosystem C sequestration balance and including heterotrophic respiration

Our data agree with findings that considered Mexico, Bolivia and the Brazilian Amazon as important and large C sinks (Gloor et al. 2012; Murray-Tortarolo et al. 2016). This is one of a few studies for Bolivia in which all the components of C uptake and C release have been quantified for the entire country using a process-based approach (Gloor et al. 2012; Seiler et al. 2015). Our results confirm the studies conducted for Mexico (Murray-Tortarolo et al. 2016) and in Bolivia and the Brazilian Amazon (Gloor et al. 2012).

Our results highlight the importance of including heterotrophic respiration as a basic ecosystem process for assessing C sequestration as an ES. Simulation of changes in carbon stocks and fluxes could become increasingly more important if changes in tree mortality are thought to be a potential effect of climate change and could reduce the ability of tropical forests to act as C sinks (Brienen et al. 2015).

Implications for national programmes targeting C stocks

Our findings indicate that payments for ES schemes may be underestimating total C stocks as they only take into account aboveground carbon and do not include soil carbon and litter (Engel et al. 2008). The payments made under PES schemes, however, are not usually based on estimation of C stock. Mexico, for example, currently does not have a payment for carbon scheme, but PES payments for water and biodiversity are made on the basis of the estimated opportunity costs to farmers of not clearing the forest to grow crops. Under REDD+, payments to farmers will be on the basis of input/investment costs for improved management, although the country will claim international compensation on the basis of performance against a national deforestation baseline. Many other payments for ecosystem schemes, particularly in the voluntary carbon market, are based on the principle of additionality: payments to farmers and communities are for increases in stock (sequestration) or decreased rates of loss, not total C stock.

This exercise serves to demonstrate that if PES payment schemes for conservation of stocks were to be made on the basis of existing C levels, they would underpay for the real C stocking services if they ignore soil carbon. This is important in the light of the fact that, e.g. in the humid topics of Mexico, forests hold large C stocks for which incentives for conservation through payments for ES often do not reflect the real opportunity costs of conversion of these forests to other uses, particularly given the recent changes to legislation to promote mining, tourism and agricultural development as well as the national campaign against hunger (<http://normatecambiental.org>). In Bolivia, the areas with the highest C stock correspond to protected areas and indigenous territories (Fig. S8 in S5 Appendix). Threats to the loss of such C stocks include recent decrees to allow the exploitation of hydrocarbons and the construction of hydroelectric plants within such areas, poor forest management, pressures to reduce poverty of forest dwellers, despite Bolivia's commitments to international climate change agreements (Bodansky 2010). In the Brazilian Amazon, a large variance in C stocks is given by abiotic factors such as increasing precipitation, topographical conditions and humidity, as well as by anthropic factors like land-use conditions (e.g. decreasing land-use intensification from east to west), and least by the types of conservation units or tenure). Yet payment systems are currently based on the latter characteristics rather than the former, and so incentives do not reflect the important biophysical factors that determine carbon stocks.

Implications for global markets and funds targeting C sequestration

The revelation that heterotrophic respiration associated with the decay of organic matter has not been included in the past in payments schemes for C sequestration and the evidence that overall sequestration has been overestimated and that payments may even have been made to areas that are net emitters, has profound implications for the design and implementation of future payment schemes. The use of a more comprehensive approach to ecosystem C sequestration modelling would shift the focus to not only promoting the uptake of carbon by ensuring that vegetation remains productive, but to also ensuring that carbon is not lost from dead organic material, i.e. through explicitly incorporating measures for soil carbon management.

Our results suggest that large parts of the areas studied might not be in fact generating additional C through sequestration. Areas where emissions from heterotrophic respiration appear to exceed uptake need to be carefully checked, considering novel estimations as Greenhouse gases Observing Satellite (GOSAT) available more recently. Greater awareness is needed that a positive change in biomass does not automatically contribute to a positive ecosystem C sequestration balance, mainly considering the strong impact of emissions by heterotrophic respiration.

Our findings also show that further emphasis needs to be placed on the processes that lead to C emissions in order to truly assess the ecosystem-level contribution of tropical forests to climate change mitigation. Accounting for the actual components of C uptake and C release is not only relevant for estimating C balance, but would also provide a more realistic assessment for carbon markets and a better estimation of the real contribution of such schemes to mitigating climate change. Markets, particularly in the voluntary carbon sector, have been driven by data on changes in aboveground C stocks from which ecosystem C sequestration balance has been derived. Such a partial assessment of C sequestration could compromise the achievement of C sequestration targets and the integrity of current carbon credit systems.

The comprehensive approach described here can quickly advance policy design and implementation

The stock and sequestration ESs models produced by LPJmL can provide a cost-effective source of national-level information for the design of climate mitigation policies. This is especially true for the case of accounting for C in soil and litter (Lal 2004) and for C emissions from heterotrophic respiration, fire and crops. With improved LULC information on forest degradation, selective logging and land

abandonment, DGVMs such as LPJmL could be improved to separate carbon fluxes arising from each of these processes and reduce error propagation, avoid double-accounting, and thus reduce uncertainties in the valuation of the respective ESs. Yet given the rough resolution of the models (50×50 km), other data sources will be needed to improve model evaluation and for cross-checking data consistency, such as LIDAR (LIght Detection And Ranging) for refining soil C stock data (Asner et al. 2014) and MODIS (Potter et al. 2009) for refining NPP information. Given high-resolution spatio-temporal climate data sets, DGVMs such as LPJmL could be applied at higher resolution levels for the benefit of ES assessment and for testing alternative policy options.

In this paper, we chose to average 20 years of data (1981–2000) for which robust information on climate is available to provide very sound messages to support policy design and implementation. The approach suggested here may be refined using more recent information to create alternative future scenarios, which in turn may be applied in the design and implementation of climate mitigation policies.

Conclusions

In this work, we show that modelling carbon stock and carbon sequestration using DGVMs such as LPJmL provides a unique opportunity to include and assess the ecosystem components relevant to inform policy design and implementation.

The application of LPJmL allowed us to determine that Mexico, Bolivia and the Brazilian Amazon have large total C stocks including those in soil and litter, which are largely unaccounted for C assessments for policy and payment schemes. As a consequence, prices per ton of carbon currently being paid in Payments for Ecosystem Service conservation schemes are up to 500 times lower than those obtained using more comprehensive ES approach.

We also found that emissions from heterotrophic respiration of organic material offset a large proportion of the carbon gained through growth of living matter, and that standard approaches to modelling carbon sequestration that omit this process largely overestimate C sequestration balance. This means that funds, markets and decision-makers are inadvertently overestimating up to 100 times the carbon that they think they are saving and that a large fraction of the studied areas (up to 33%) considered today as sinks are actually net emitters.

Process-based ESs models that incorporate crucial ecological processes are needed to support policy design on the ESs valuation.

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