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RESEARCH ARTICLE

Ecosystem services of regulation and support in Amazonian pioneer fronts: searching for landscape drivers

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Abstract Landscape dynamics result from forestry and farming practices, both of which are expected to have diverse impacts on ecosystem services (ES). In this study, we investigated this general statement for regulating and supporting services via an assessment of ecosystem functions: climate regulation via carbon sequestration in soil and plant biomass, water cycle and soil erosion regulation via water infiltration in soil, and support for primary production via soil chemical quality and water storage. We tested the hypothesis that patterns of land-cover composition and structure significantly alter ES metrics at two different scales. We surveyed 54 farms in two Amazonian regions of Brazil and Colombia and assessed land-cover composition and structure from remote sensing data (farm scale) from 1990 to 2007. Simple and well-established methods were used to characterize soil and vegetation

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from five points in each farm (plot scale). Most ES metrics were significantly correlated with land-use (plot scale) and land-cover (farm scale) classifications; however, spatial variability in inherent soil properties, alone or in interaction with land-use or land-cover changes, contributed greatly to variability in ES metrics. Carbon stock in above-ground plant biomass and water infiltration rate decreased from forest to pasture land covers, whereas soil chemical quality and plant-available water storage capacity increased. Land-cover classifications based on structure metrics explained significantly less ES metric variation than those based on composition metrics. Land-cover composition dynamics explained 45 % ($P < 0.001$) of ES metric variance, 15 % by itself and 30 % in interaction with inherent soil properties. This study describes how ES evolve with landscape changes, specifying the contribution of spatial variability in the physical environment and highlighting trade-offs and synergies among ES.

Keywords Land-use intensity · Soil ecosystem services · Socioeconomic drivers · Agro-ecosystems · Carbon storage · Soil chemical quality · Water infiltration · Trade-offs

Introduction

The Millennium Ecosystem Assessment (2005) drew attention to the degradation and non-sustainable use of ecosystem services (ES) essential for human life. Understanding ecological processes behind ES and measuring them still raise many scientific questions (Carpenter et al. 2006; Bennett et al. 2009). Our ability to design landscapes that sustainably supply multiple ES suffers from a lack of knowledge on the ecological processes behind ES and their responses to land use and global changes (Foley et al. 2005; Carpenter et al. 2009; Turner 2010). The socio-economic and ecological drivers involved in supplying ES, the relations between ES, and the underlying mechanisms are not well known (Kremen and Ostfeld 2005; Nelson et al. 2009; Breure et al. 2012). A better understanding seems critical for preventing undesired trade-offs among different ES, and conversely for benefitting from positive synergies among them (Bennett et al. 2009).

The Amazon region is an exemplary location for addressing these questions (Foley et al. 2007). Highly diverse (Hoorn et al. 2010), the Amazon forest is also considered one of the last reserves of land to sustain increasing human needs for food and other agroforestry products (Foley et al. 2007). Even though agriculture is not the only direct driver of regional development, it remains the main cause of deforestation (Fearnside 2005; Aldrich et al. 2006; Godar et al. 2012). Slash-and-burn agriculture practiced on the pioneer front is progressively replaced by pastures and export crops at later stages (Rodrigues et al. 2009). The patterns and dynamics of land use, however, largely vary, depending primarily on socioeconomic conditions that prevail at local and regional levels.

Even partial deforestation by logging or fire represents an immediate threat to biodiversity (Gibson et al. 2011) and climate (Malhi et al. 2008). The forest ecosystem is resilient (i.e. can maintain its composition and functions) when the seasonal water deficit is moderate (Phillips et al. 2009). However, due to interactions between deforestation, wildfires and drought, it cannot be ruled out that the south and east of the Amazon River basin could be in a transitory state toward a disturbed system, prone to carbon release, which would affect the water and biogeochemical cycles (Davidson et al. 2012). Closely related to a loss of biodiversity, soil degradation in pastures is no less of a concern (Mathieu et al. 2005, 2009), with consequences for water and nutrient cycles and primary production (Markewitz et al. 2004; Martinez and Zinck 2004; Chaves et al. 2008). Faced with a decrease in pasture productivity, smallholders usually abandon the land they cleared to large farms and ultimately continue their migration, thus contributing to the advance of the deforestation front

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(Muchagata and Brown 2003). Other actors search for technical innovations or claim new public-policy incentives, such as compensation mechanisms (e.g. "carbon credits") recommended in negotiations on Reducing Emissions from Deforestation and forest Degradation (REDD) (Hall 2008).

The future of the Amazon region relies on the capacity of ecosystems to bear the perturbations caused by land-use and climate changes and on the implementation of policies to reconcile development and conservation (Betts et al. 2008). To promote the resilience of human-influenced ecosystems and maintain the global benefits supplied by the Amazonian biome, services of support and regulation, provided by ecosystem functions, such as primary production, nutrient recycling, carbon sequestration and water infiltration into the soil, should be sustained.

In this article, we analyze how these services, assessed through functions, evolve with landscape changes along a gradient of land-use intensity. We test the hypothesis that patterns of land-cover composition and configuration significantly alter ES. The ES addressed are climate regulation, via C sequestration in the soil and plant biomass, water cycle regulation and erosion control, via water infiltration in soil, and support for primary production, via soil chemical quality and water storage. Our specific objectives were (1) to assess the relative contributions of successive land-use changes and spatial variations in the physical environment on ES changes at the plot and farm scales, (2) to assess ES at the farm scale using metrics of land-cover composition and/or configuration and their dynamics, and (3) to reveal trade-offs and synergies among ES during landscape transformation, and the ecological processes at stake.

Materials and methods

Study sites

The study was carried out in two Amazonian regions of Colombia (Caquetá Department) and Brazil (Pará State) with distinct colonization histories. Three areas representative of the diversity of smallholder farming systems were selected in both regions along a gradient of deforestation extent and agricultural land-use intensity (Fig. 1).

Little forest cover remains in the Colombian study areas (20–60 km from Florencia, piedmont region of the Andean eastern cordillera) where deforestation began in the 1940s (Table 1). The three areas differed in their management: traditional systems at *Canelos* dedicated mainly to dairy production and extensive cattle ranching on relatively large farms (Table 1) with long-established degraded pastures; silvopastoral systems at *Balcanes* based on legume fodder crops to restore pastures and improve cattle production; and agroforestry systems at *Aguadulce* that combined cocoa, fruit trees and pastures (Arnauld de Sartre et al. 2011). The Brazilian areas (center of Pará State) were more recently colonized and 40–70 % of the initial forest remained in 2007 (Silva Costa et al. 2012). Most colonists of the *Maçaranduba* area abandoned their initial agro-extractivist activities to turn to livestock production due to the dominance of this activity and the exhaustion of wood resources near the city of Marabá, both sources of conflict with neighboring loggers and cattle ranchers. At *Palmares II*, farmers earn revenue from food crops, rather than livestock production, to feed the nearby city of Parauapebas. The *Pacajá* area, an early pioneer front that starts from a trail (*Travessão 338 Sul*) perpendicular to the Trans-Amazonian highway, was divided between annual and perennial (cocoa) crops and livestock production.

In addition, the two regions differ notably in their physical environments. The Caquetá areas lay on Miocene sediments with a relatively flat landscape, whereas Pará areas are situated on granitic or metamorphic crystalline rocks of Paleoproterozoic age, with hilly landscapes of medium roughness at low elevations (maximum 350 m in Brazil vs. 1,100 m in Colombia). Both regions have a humid tropical climate, but the average annual precipitation is about 1,700 mm in Pará and 3,300 mm in Caquetá

Sampling design

This study is based on data collected in 54 farms (nine per area) chosen from an initial set of 304 farms (51 per area; data missing for two farms), from which a classification of farming systems was developed, based on a socio-economic survey (Arnauld de Sartre et al. 2011). Groups of farming systems were separated by cluster hierarchical analysis: farms from

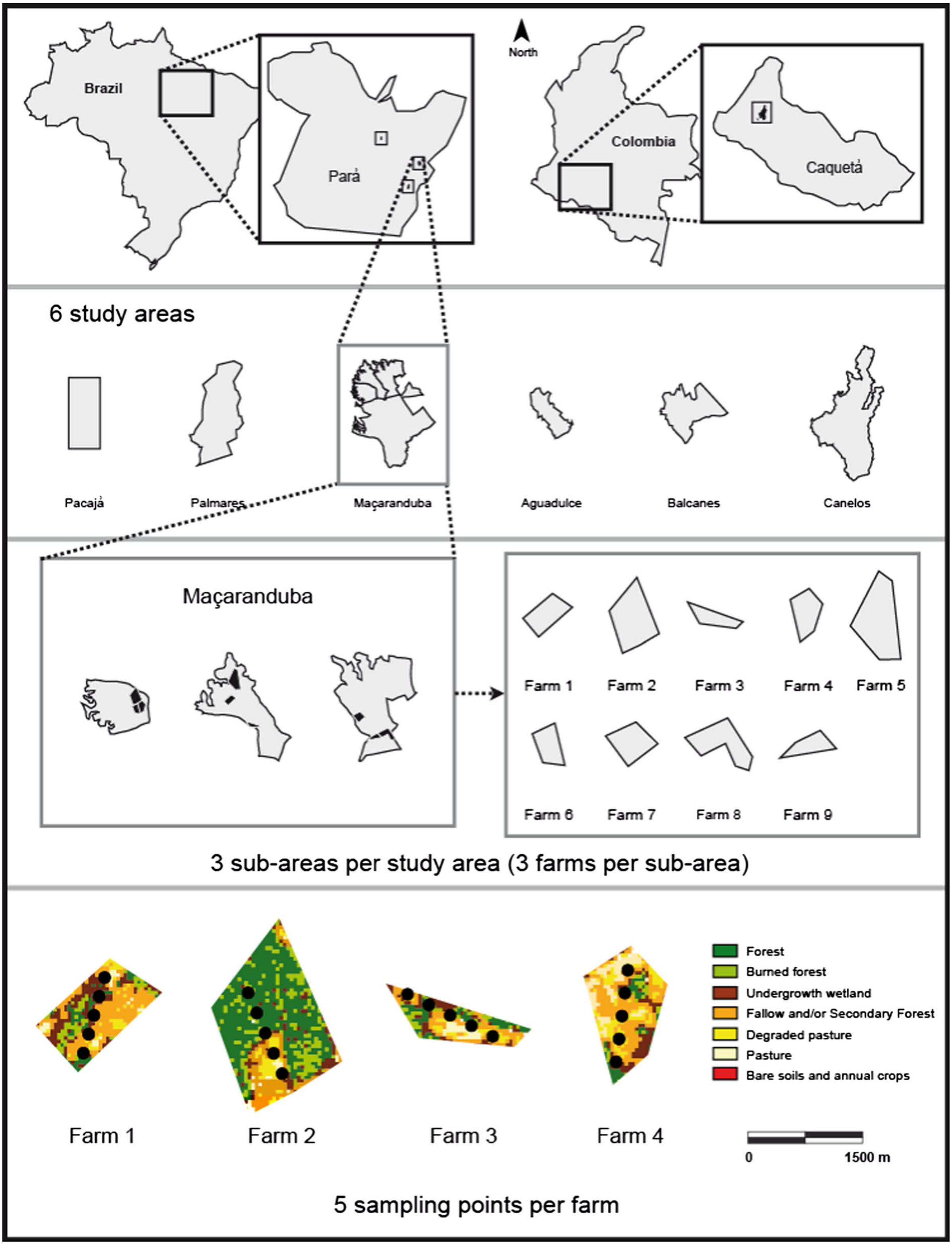


Fig. 1 Location of the study areas and sampling design

Table 1 Geographic location and main characteristics of the study areas

Sites	X (UTM, WGS84) Min Max	Y (UTM, WGS84) Min Max	Colonization start/arrival 50 % current farmers (years)	Average farm size (ha)	Remaining original forest cover in 2007 (%)	Pasture cover in 2007 (%)
Colombia						
Canelos	2,311,340.8	10,168,671.4	1950/1991	184	3	66
	2,320,397.3	10,184,388.2				
Aguadulce	2,324,742.8	10,187,231.1	1950/2000	49	2	39
	2,312,112.4	10,173,341.7				
Balcanes	2,352,560.7	10,178,497.1	1940/2000	65	4	72
	2,335,720.1	10,163,170.7				
Brazil						
Maçaranduba	679,602.5	9,473,375.9	1982/1992	81	39	17
	686,282.9	9,467,677.1				
Pacajá (Trail 338S)	493,585.7	9,582,189.4	1978/1996	82	70	9
	496,152.3	9,591,279.2				
Palmares II	625,263.4	9,343,195.9	1995/1997	25	38	18
	630,403.4	9,352,609.8				

early pioneer fronts deforested 10–20 years ago with mixed production of annual and perennial crops and livestock, and low incomes; similar systems with slightly better incomes; farms with extensive livestock production and the largest incomes; and agroforestry systems established on sites where deforestation began 50–80 years ago, with intermediate incomes.

Each area was divided into three sub-areas, in which three non-adjacent farms were selected to best represent the diversity of the agricultural products, land-cover dynamics and farm size identified by socio-economic and remote-sensing surveys. For each of the 54 farms, five sampling points were spaced equally along a transect corresponding either to the longest diagonal of the farm or a roughly north–south axis (Fig. 1). The distance between points was thus equal to 1/6 of the transect length and varied according to farm area. This approach ensured that the sampling effort of different land uses was proportional to their relative occurrence in each farm. The sampling points were demarcated plots of 50 $\times$ 10 m^2 whose length was perpendicular to the farm sampling transect.

Land-uses description at plot scale

We recorded land uses in the field at the same time that we collected data for ES assessment. Subsequent combination of some of the subcategories identified in the field (e.g. types of perennial crops) allowed each of the 11 land-use categories used for statistical analysis to contain at least 10 observations (Table 2).

Landscape analyses at farm scale

Most of the detailed analytical methods are available in Oszwald et al. (2011). We retain below those aspects necessary to understand the land-cover classifications used in our study. We used remote-sensing data to characterize land-cover dynamics of the 54 farms. We used Landsat TM and ETM + images (30-m spatial resolution, spectral recording adapted to land-cover identification) taken during the dry seasons of 1990, 1994, 1998, 2002 and 2007. Radiometric and atmospheric corrections were applied to the satellite data set with the 5S model (Kergomard 2000). Field validation measurements were taken during the dry season of 2007 and 2008 to build a supervised land-cover classification system with a maximum-likelihood algorithm, which was linked to the spectral signature of each of the land-cover units (Fig. 2).

The supervised classification was performed on the 2007 Landsat TM image. Spectral signatures enabled reconstitution of past land covers from prior images (1990, 1994, 1998, and 2002). At each date, the land cover of each farm was described using 10 composition metrics (relative proportions of the total farm area

Table 2 Land uses recorded in the field in Brazilian and Colombian study areas at the time that data were collected for ecosystem service (ES) metric assessment from a total of 270 points (plots), and number of points in each land-use class and country

Land-use classes	Number of points	
	Brazil	Colombia
Preserved forests	15 (14)	0
Exploited forests	24 (21)	0
Burned forests	10	0
Annual crops (rice, cassava or maize)	14	0
Fallows (secondary forests in abandoned croplands)	17	0
Cleaned pastures	18 (17)	64
Invaded pastures	17	9 (8)
Mixed pastures (pastures with native and silvopastoral systems)	3	19
Perennial crops (cocoa, rubber-tree plantations or agro-forestry systems)	4	24 (22)
Secondary young forests in abandoned pastures	6	4
Secondary old forests in abandoned pastures	7 (6)	15 (14)

Numbers in parentheses indicate the number of plots after eliminating 10 outlier points (extreme values of ES metrics or inherent soil property)

of the 10 land-cover units presented in Fig. 2) and nine structure metrics, both of composition and configuration (Lausch and Herzog 2002): land-cover area (farm area in ha), patch diversity (richness and Shannon diversity, evenness and dominance indices of patches), mean patch density (m ha^{-1}), edge density (m ha^{-1}), and fractal structures (perimeter/area ratio, mean shape index).

These metrics were used to constitute 3-D matrices in which farms were characterized by their land-cover composition and structure at the five dates of the Landsat TM images. Analysis of these matrices with normalized principal component analysis (PCA) and ACT-STATIS method (Lavit et al. 1994) provided four indicators described below (Fig. 2).

The composition indicator clearly separated farms with a predominance of forest (values close to 1) from farms with a high proportion of agricultural land covers (values close to 0). The structure indicator emphasized differences in land-cover organization among farms, from farms in which land-cover mosaic had high shape complexity in forest patches (values close to 1) to others having large agricultural patches (values close to 0); intermediate values were associated with farms having high complexity in secondary vegetation patches. The "composition dynamics" indicator distinguished forested farms that had experienced little or no deforestation since 1990 (values close to 1) from farms with a homogeneous agricultural landscape since at least 1990 (values close to 0); intermediate values were a function of the intensity (i.e. importance and rapidity) of land-cover changes between 1990 and 2007. The "structure dynamics" indicator assessed the temporal change in land-cover organization and distinguished farms having experienced recent deforestation with little forest fragmentation (values close to 1) from farms where deforestation occurred in the 1990s followed by an intense transformation of forest to agriculture (intermediate values), and finally farms with a homogeneous agricultural landscape (values close to 0).

Ecosystem service assessment

Five ES metrics (indicators) were estimated: (1) C stock in aboveground plant (bush and tree) biomass and (2) C stock of the 0–30 cm soil horizon (climate regulation service); (3) water infiltration rate into the soil (water cycle and soil erosion regulation services); (4) a soil chemical quality index and (5) soil storage capacity of plant-available water of the 0–10 cm soil horizon (primary production support service). These ES metrics were estimated at the plot scale from vegetation and soil characteristics measured at all points (Table 3) and at the farm scale by calculating the mean values of the five sampling points within a farm. For the last four metrics, four soil pits regularly spaced 10 m apart were dug in the middle of each 50 × 10 m^2 plot.

Measurements and data collection took place in 2008 during 4 months (April–July) of the rainy season in each country. Well-established and relatively simple methods, described next, were used to characterize a total of 270 points.

C stock in plant biomass

Aboveground dry plant biomass of trees [BT: diameter at breast height (dbh) ≥10 cm] and bushes (BB: dbh

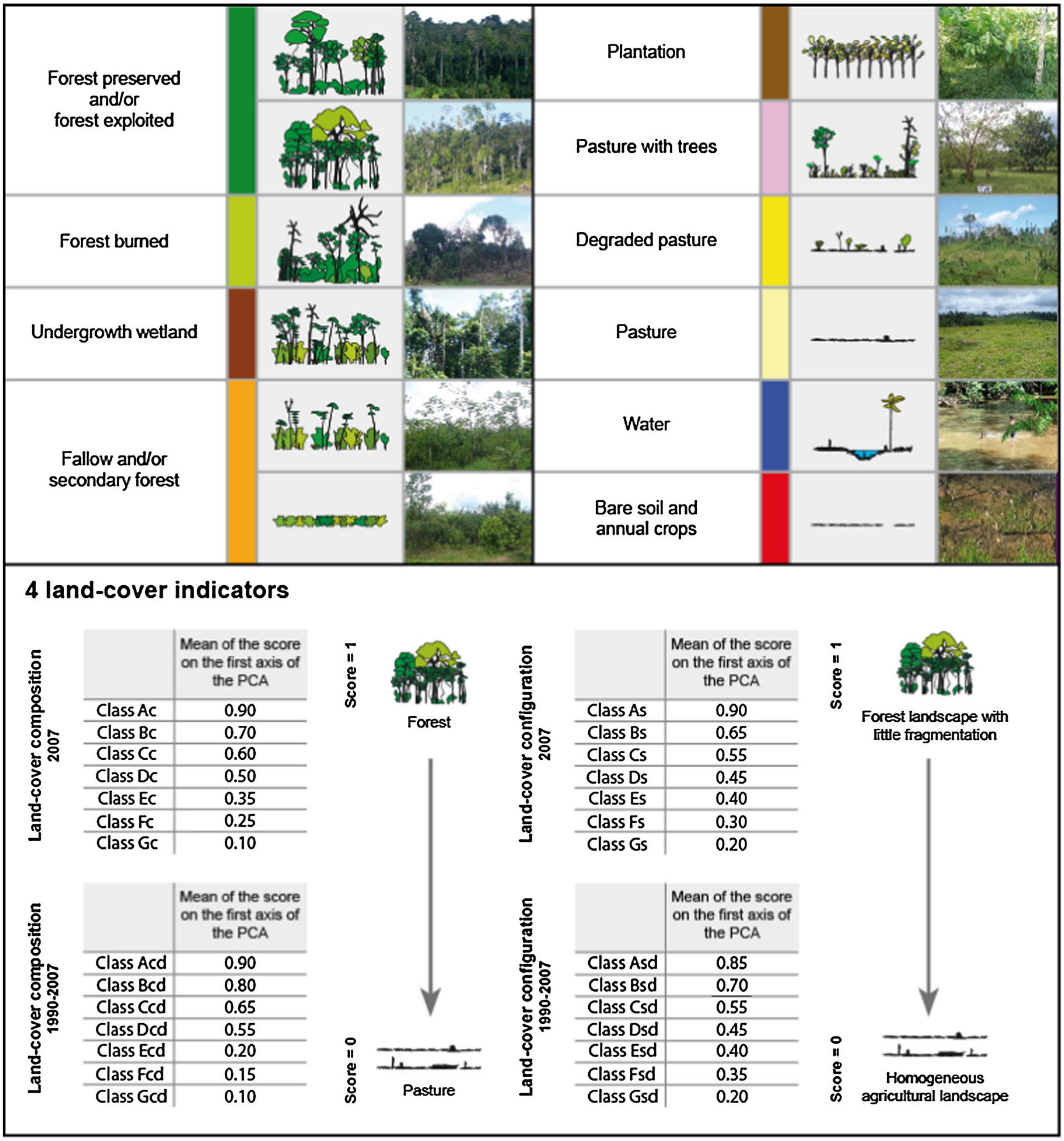


Fig. 2 Land-cover units distinguished from remote sensing analysis (Landsat TM spectral signature, images of 1990, 1994, 1998, 2002 and 2007) and field validation (2007 and 2008). Landscape metrics: four landscape indicators describing land-cover composition and structure in 2007 and dynamics of land-cover composition and structure between 1990 and 2007

<10 cm and height >2 m) was estimated by applying allometric equations provided for forests (Higuchi et al. 1998; Gerwing 2002) and fallows (Nelson et al. 1999) after identifying species and measuring the diameter and height of individuals on plots of 50×10 m^2 and 50×5 m^2, respectively, and the water content at 70 °C of corresponding biomass aliquots (all individuals with dbh ≤ 5 cm), otherwise

Table 3 Ecosystem service (ES) metrics estimated in this study and soil or plant characteristics measured for the estimation of each ES metric

ES metric	Unit	Soil and plant variables
C stock in plant biomass	Mg ha^{-1}	Aboveground dry plant biomass of trees (BT) and bushes (BB)
C stock in soil	Mg ha^{-1}	Bulk density (ρ_b) and total C content at 0–10, 10–20 and 20–30 cm depths
Water infiltration rate into the soil	mm h^{-1}	Infiltration rate (V_i)
Soil chemical quality	0.1–1	Exchangeable Ca^{2+}, Mg^{2+}, K^+ and NH_4^+ and extractable phosphorus (P) contents at 0–10 cm depth
Soil storage capacity (height) of plant-available water	cm	Clay, silt and sand contents, ρ_b, vertical resistance (R_v), C content, pH, cation exchange capacity (CEC) at 0–10 cm depth

Italics indicate inherent soil properties

(dbh >5 cm) applying the factor 0.603 according to Higuchi et al. (1998). In the absence of C analysis of plant samples, a factor of 0.5 was used to estimate C mass in plant biomass (Markewitz et al. 2004).

C stock in soil

Soil total C contents in the 0–30 cm horizon were measured with a CHNS analyzer in three samples from each plot (composites of the 0–10, 10–20 and 20–30 cm depths from the four pits). To calculate C stock, measurements of bulk densities (ρ_b; cylindrical core method, 7 cm diameter) from 0 to 30 cm, separating 0–2, 2–5, 5–10, 10–20 and 20–30 cm depths were repeated in the four pits.

Water infiltration rate into the soil

Applying the infiltration Beerkan test (Labassatère et al. 2006), we calculated the infiltration rate (V_i) of a fixed water volume of 250 cm^3 poured in a simple ring 20 cm in diameter inserted at the soil surface to a depth of about 1 cm. This infiltration test was repeated four times, near the soil pits.

Soil chemical quality index

Particle-size distribution and chemical properties of the 0–10 cm soil horizon were determined on a composite from two pits. The chemical properties performed were pH H_2O, cation exchange capacity (CEC) at soil pH, exchangeable Al^{3+}, Ca^{2+}, Mg^{2+} and K^+, exchangeable NH_4^+ and extractable phosphorus (P, Mehlich 'double acid' extraction method in 0.05 M HCl and 0.0125 M H_2SO_4 solutions) using standard methods (Pansu and Gautheyrou 2006). A soil chemical quality index was determined from normalized PCA of soil chemical properties (Velasquez et al. 2007); this index considered only the variables that contribute to soil chemical fertility: exchangeable Ca^{2+}, Mg^{2+}, K^+ and NH_4^+ and extractable P.

Soil storage capacity of plant-available water

More time consuming, measurements of soil water retention at different water potentials followed a specific sampling protocol: cores with undisturbed structure (cylinders of 100 cm^3) from the 0 to 10 cm horizon (four replicates) were taken from one of the five points in each farm, chosen so that the main land-use types were sampled in each area proportionally to their occurrence. From laboratory measurements with a pressure-plate apparatus (Pansu and Gautheyrou 2006) for 27 points (108 cores) in each country, multiple linear regression models (Pachepsky and Rawls 2004) were generated to estimate, from the simplest soil variables measured at all points (clay, silt and sand contents, bulk densities (ρ_b), vertical resistance (R_v) of the superficial horizon measured with a cone penetrometer, pH, CEC and C content), the water retention capacities at different water potentials. We then calculated plant-available water capacity as the water volume drained between matrix potentials of −30 kPa and −16 MPa.

We aimed to separate the variability in soil ES explained by transformation of the landscape into arable fields from the variability due to the soil diversity in the landscape, which is related to the nature of the geological substrate or other pedogenetic factors. To this end, we distinguished dynamic or manageable versus inherent soil properties, as defined by Robinson et al. (2009) and Dominati et al. (2010). Among the soil properties used to calculate soil ES metrics (Table 3), clay, silt and sand contents, and, to a lesser degree, CEC are related to the mineral composition of the soil and thus inherent, because they have little sensitivity to land-use changes. In contrast, all the other characteristics, related to soil structure (ρ_b, R_v, V_i) or its organic and chemical compositions (C, pH, Al^{3+}, Ca^{2+}, Mg^{2+}, K^+, $NH_4{}^+$, P) react more dynamically to farming practices that influence the soil. Like ES metrics, clay, silt and sand contents, and CEC values were averaged over each farm.

Statistical analyses of landscape effects on ES metrics

Variability in ES metrics was analyzed (1) at each point (i.e. the plot scale) as a function of the land use observed at the time of measurement and (2) at the farm scale as a function of the classifications derived from the composition and structure of land-cover mosaic.

We performed normalized PCA to account for gradients that separated points and farms according to ES metrics and to inherent soil properties. All metrics and properties were corrected for normal distribution (Shapiro–Wilk's normality test $P > 0.05$). To assess the degree of discrimination of land-use or land-cover categories at the plot and farm scales, we used redundancy analysis (e.g. Borcard et al. 1992). The index characterizing the separation between land-use or land-cover changes (between-class variance) was tested against simulated values obtained after 999 permutations of the rows of the ES metrics table. Finally, we performed partial redundancy analysis to decompose the variation of ES metrics according to the combination of land-use or land-cover categories, inherent soil properties and their interaction. The resulting variances were similarly tested against simulated values obtained after 999 permutations of the rows of the ES metrics table.

At the plot scale, boxplots and Kruskal–Wallis rank-sum tests were also used to assess single effects of land use on each ES metric. Normalized PCA performed on inherent soil properties yielded three successive uncorrelated gradients (PCA axes) that were used in subsequent modeling. We then performed Gaussian general linear modeling (GLM) on each ES metric using the form: ES metric[i] $\sim$ x1 + x2 + x3 + x1:z1 + x2:z1 + x3:z1, with x1, x2 and x3 as the first three axis plot scores respectively and z1 as the land-use categories. For model selection, we used the Akaike's Information Criterion (AICc) and, as suggested by Burnham and Anderson (2002: p. 71), focused on the differences in AICc for the first three models. The statistical significance of model parameters was estimated by analysis of deviance (validated by F tests) between a null model (no effect) and a model that included one or more explanatory variables. Analysis of deviance also allowed us to calculate the proportion of deviance explained by explanatory variables (i.e. an index of the contribution of the variable to the ES metric variation).

Statistics and graphical outputs were computed with the ade4 (Dray and Dufour 2007), MulIn (Barton 2012) and vegan libraries (Oksanen et al. 2013) implemented in R freeware (R Core Team 2013).

Results

ES variation at the plot scale

The statistical analyses were performed on 260 points after eliminating 10 points with extreme values for certain variables (Table 2): six points from Brazil with the highest values of C stock in plant biomass (two points) or soil chemical quality index (two points) or the lowest clay contents (two points) and four points from Colombia with the highest values of water infiltration rate into the soil.

The first two axes of a PCA performed on the ES metrics accounted for 59 % of the total variance. The first PCA axis (39 % of total variance) contrasted primary forests (preserved, exploited and burned) and pastures, whereas the second PCA axis tended to oppose annual crops and secondary forests (Fig. 3a, b). Land-use classification (Table 2) explained 36 % (i.e. between-class variance; $P < 0.001$) of the total variance in ES. Primary forests were associated with higher plant biomass C stock and water infiltration rates. In contrast, higher plant-available water capacity and soil chemical quality were observed in pastures.

Principal component analysis performed on soil texture (clay, silt) and CEC revealed a similar separation of land uses along the first axis (63 % of total variance), contrasting in particular unburned primary forests and pastures (Fig. 3c, d). Land-use classification explained 35 % ($P < 0.001$) of the total

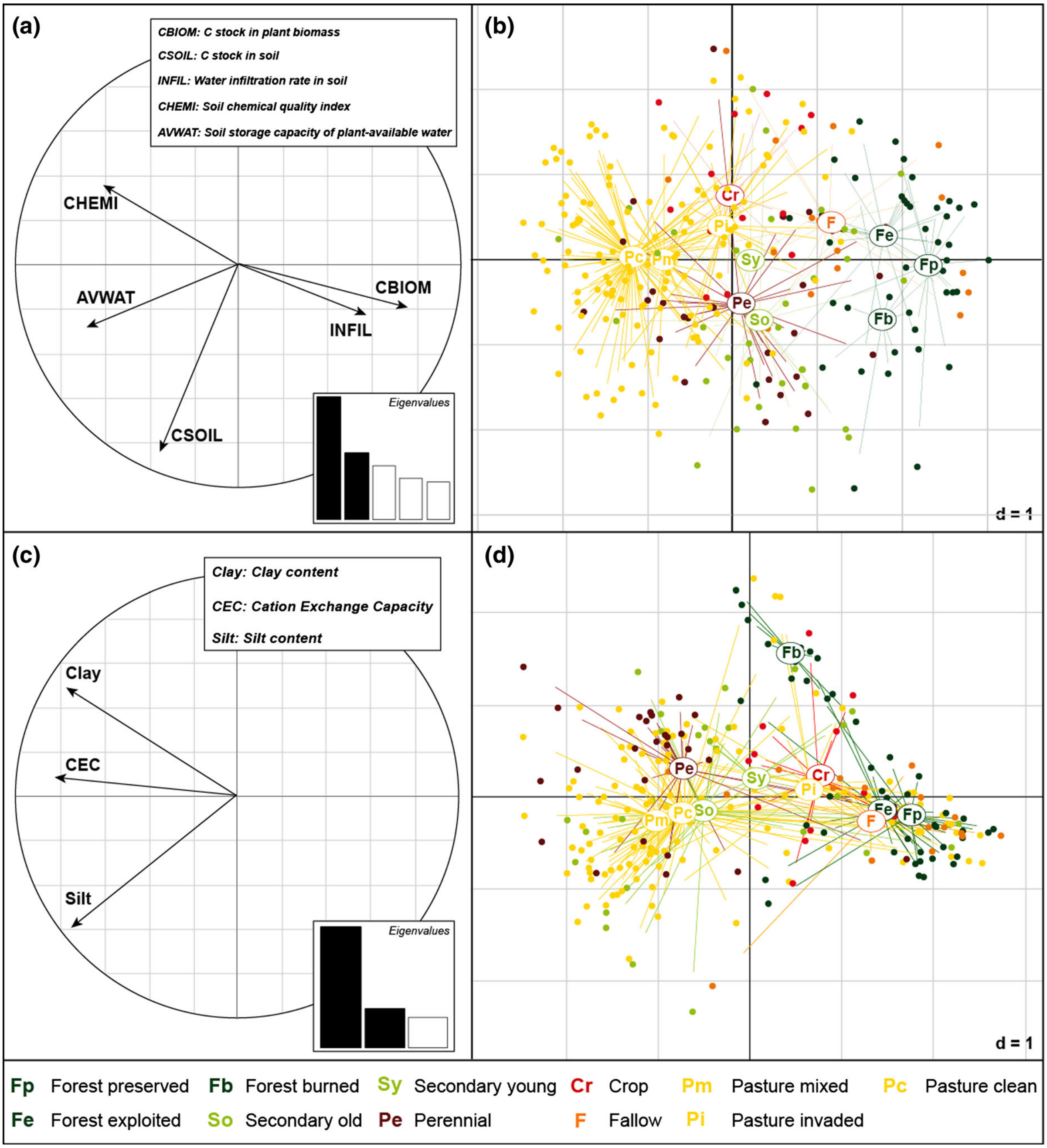


Fig. 3 Results of normalized principal component analysis (PCA) performed on the five ecosystem service metrics (**a**, **b**) and inherent soil properties (**c**, **d**) at the plot scale. **a**, **c** Correlation of variables with the first-two PCA axes (each arrow points in the direction of highest value for a given variable); the inset shows the distribution of variance among PCA axes. **b**, **d** Associated PCA factorial map showing plots grouped by land-use classes ($R^2 = 0.339$, $P < 0.001$) and by inherent soil properties ($R^2 = 0.347$, $P < 0.001$)

variance in inherent soil properties. Primary forests were associated with soils having a lower CEC, less clay and little silt. Since land use had little or no impact on these inherent soil properties, PCA highlighted differences in soils among sites, which can be mainly attributed to the geological substrates. The

Table 4 Redundancy analysis (RDA) variation partitioning of ecosystem services at the plot scale according to land use, inherent soil properties and their interaction

	Variance	R^2	% of total explainable
Total explainable	2.298^{***}	0.460	100
Inherent soil properties	0.603^{***}	0.121	26
Land use	0.848^{***}	0.170	37
Land use × inherent soil properties	0.847^{nt}	0.169	37

*** Simulated $P < 0.001$ for the RDA permutation tests

^{nt} Not testable

crystalline nature and age of rocks of the Brazilian Shield has favored the formation of sandy rather than clayey and loamy soils; the clay fraction of these soils is composed only of kaolinite and metal oxides with low CEC, unlike soils developed on more recent sedimentary formations of the Andean piedmont.

As expected, the variability in ES thus resulted from a variety of factors, including inherent soil properties, land use and their interaction. Partial redundancy analysis demonstrated that these three effects explained 46 % of the total variance in ES, mostly due to land use and the interaction between land use and inherent soil properties (37 % of the explainable variance each) (Table 4).

General linear modeling performed on each of the five ES metrics separately highlighted the high contribution of inherent soil properties to the explained deviance; the effect of interaction between them and land use was reduced or negligible (Table 5). The effects of inherent soil properties were higher on chemical quality and even higher on plant-available water capacity, since the relations between water potential and water content from which the latter metric was estimated largely depend on soil texture. Land use, whether alone or in interaction, had a much lower impact, especially on soil plant-available water capacity. A low effect of inherent soil properties was sometimes compensated by a higher land-use effect, as for C stock in plant biomass and water infiltration rate (Table 5).

Boxplots of the ES metrics as a function of the 11 land-use categories showed a high within-category variance (Fig. 4). For soil C stock and soil plant-available water storage capacity, significant trends among land use (Kruskal–Wallis test; $P < 0.001$ for

Table 5 Deviance decomposition obtained from GLM performed at the plot scale between each ecosystem service (ES) metric and land-use categories and inherent soil properties (values correspond to percentage of deviance explained)

Ecosystem service metrics	Land use	Inherent soil properties	Interaction
C stock in soil	–	22.8^{***}	–
C stock in plant biomass	52.6^{***}	12.2^{***}	–
Water infiltration rate in soil	22.4^{***}	10.7^{***}	–
Soil storage capacity of plant-available water	4.3^{**}	52.8^{***}	4.2^{**}
Soil chemical quality	4.2^{*}	41.3^{***}	–

The GLM of each ES metric has the form: ES metric[i] $\sim$ x1 + x2 + x3 + x1:z1 + x2:z1 + x3:z1, with x1, x2 and x3 as the first three axis plot scores, respectively, of the normalized principal component analysis performed on inherent soil properties, and z1 as the land-use categories

*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$

all ES metrics) throughout the succession primary forest–crops–pastures–plantations–secondary forest were driven by inherent soil properties (Table 5). In contrast, water infiltration rate, which depends on land use, was significantly lower in the three pasture categories.

ES variation at the farm scale

Principal component analysis performed on the ES metrics averaged for each farm again revealed the importance of C stock in plant biomass, as well as soil plant-available water capacity, in separating farms along the first axis (44 % of total variance; Fig. 5a). Unlike for the plot-scale analysis, water infiltration rate did not co-vary with these metrics.

Between-class analysis showed that the classification of land-cover composition in 2007 explained 35 % ($P < 0.001$) of the total ES variance. The first PCA axis identified a gradient of anthropogenic pressure, which contrasted two sets of farms, each containing three classes that did not differ greatly, even though they were differentiated by the landscape analysis (Fig. 5c). Thus, the set of classes Ac, Bc and Cc, associated with higher C stock in plant biomass (Fig. 5a), included Brazilian farms in which primary forest still represented 45–98 % of the farm area (2007 composition indicator between 1 and 0.6). In contrast, the set of classes Ec, Fc and Gc showed higher soil

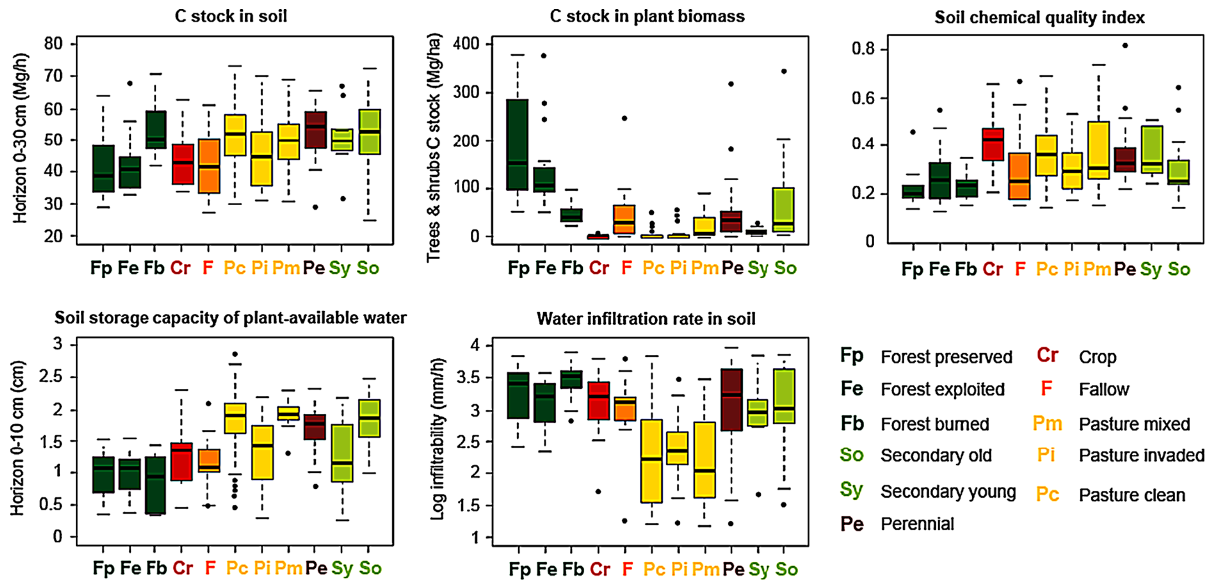


Fig. 4 Boxplots of the ecosystem service metrics as a function of the 11 land-use categories

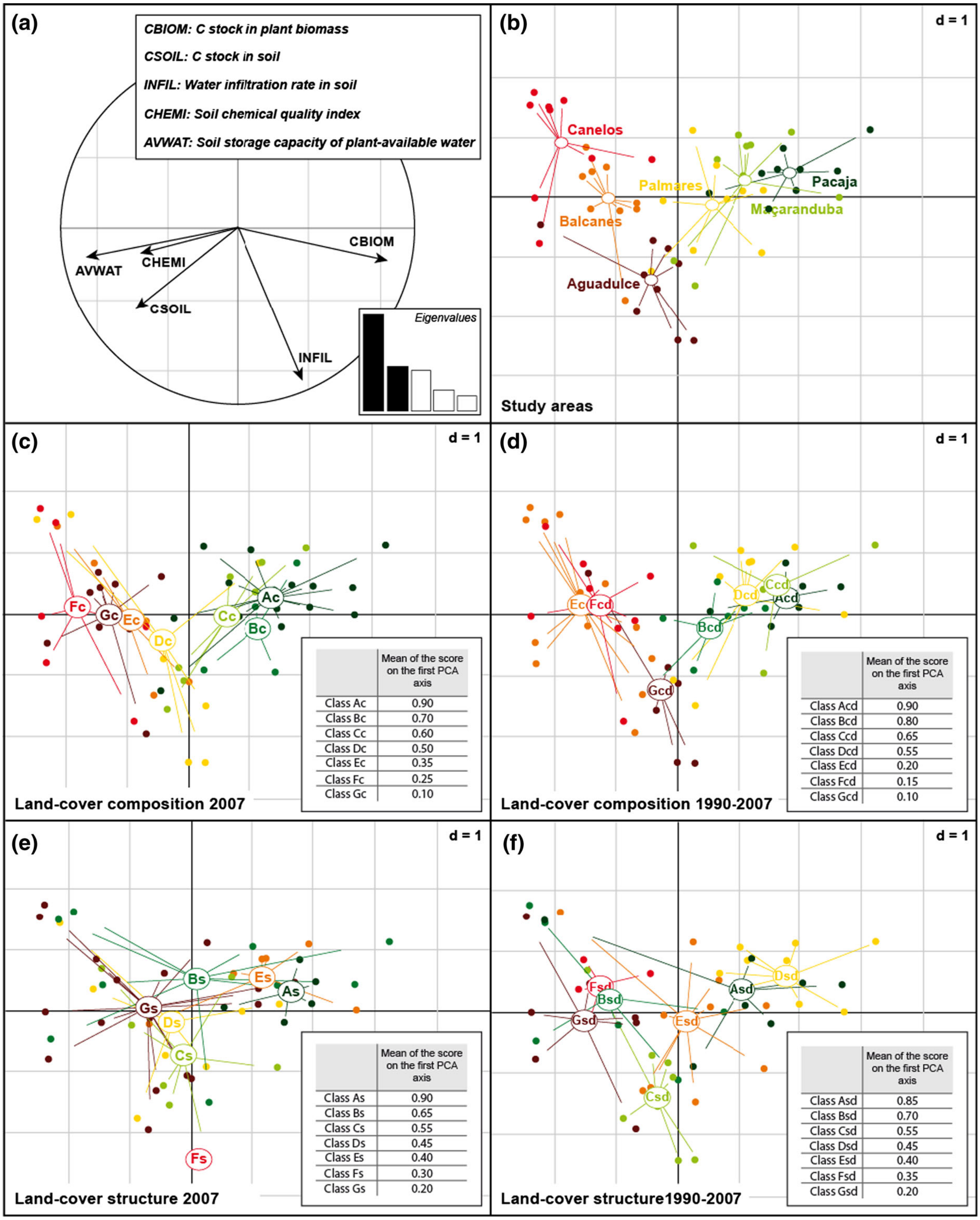
plant-available water storage capacity and chemical quality (Fig. 5a). This set included Colombian farms whose landscape was intensely impacted by agriculture (2007 composition indicator between 0 and 0.35), characterized by pasture or perennial-crop and fallow or secondary forest land covers. Class Dc, in the middle of the PCA plot (Fig. 5c), grouped farms of *Maçaranduba* and *Aguadulce* areas (Fig. 5b) with a transition landscape between those found in each of the two sets identified above.

Classification based on the land-cover composition dynamics from 1990 to 2007 explained most of the ES variance (45 %, $P < 0.001$) and distinguished three sets of farms (Fig. 5d). The first set was composed of farms of Brazilian areas with remaining primary forest. Classes Acd, Bcd, Ccd and Dcd of this first set (composition dynamics indicator between 1 and 0.5) are distinguished by the intensity of primary forest clearing between 1990 and 2007. The second set of classes, Ecd and Fcd (composition dynamics indicator between 0.2 and 0), was dominated by Colombian farms with an agricultural landscape, where fallow or secondary land covers appeared between 1990 and 2007. The third set corresponded to some farms (class Gcd) whose landscape changed little or not at all, dominated by a homogeneous agricultural landscape since 1990 (pasture or perennial crops).

Classification based on the land-cover structure measured in 2007 (Fig. 5e) only explained 23 % of total ES metric variance ($P < 0.001$). Classification of land-cover structure dynamics explained 29 % of total ES metric variance ($P < 0.001$) and distinguished two sets of farm classes along the first PCA axis (Fig. 5f, classes not in order of land-cover structure dynamics indicator). Classes Asd, Csd, Dsd, and Esd were characterized by little forest fragmentation due to recent deforestation, or a very heterogeneous and dynamic landscape with a high relative importance of woody vegetation (primary or secondary forest and perennial crops). Classes Bsd, Fsd, and Gsd were characterized by a homogenous and stable agricultural landscape or low patch diversity in a recent silvopastoral system (*Balcanes* area).

Finally, partial redundancy analysis demonstrated that among the classifications, land-cover composition dynamics explained most of the ES metric variance

Fig. 5 Results of a normalized principal component analysis ► (PCA) performed on the five ecosystem service metrics at the farm scale. **a** Correlation of ES metrics with the first two PCA axes (each arrow points in the direction of highest value for a given metric); the inset shows the distribution of variance among PCA axes (i.e. eigenvalues). Associated PCA factorial maps showing farms grouped according to: **b** study area; **c** land-cover composition in 2007 ($R^2 = 0.354$, $P < 0.001$); **d** land-cover composition dynamics from 1990 to 2007 ($R^2 = 0.451$, $P < 0.001$); **e** land-cover structure in 2007 ($R^2 = 0.225$, $P < 0.001$); and **f** land-cover structure dynamics from 1990 to 2007 ($R^2 = 0.287$, $P < 0.001$)



(45 %, $P < 0.001$) at the farm scale, both by itself (26 % of the explained variance) and in interaction with inherent soil properties (53 % of the explained variance) (Table 6). Land-cover structure dynamics explained 29 % of the ES metric variance ($P < 0.01$), by itself and in interaction with inherent soil properties

Table 6 Redundancy analysis (RDA) variation partitioning of ecosystem service metrics at the farm scale according to land-cover indicators and inherent soil properties

	Variance	R^2	% of total explainable
Land-cover composition in 2007			
Total explainable	2.537^{***}	0.507	100
Inherent soil properties	0.767^{***}	0.153	30
Landscape	0.409^{ns}	0.082	16
Landscape × inherent soil properties	1.360^{nt}	0.272	54
Land-cover composition dynamics			
Total explainable	2.872^{***}	0.574	100
Inherent soil properties	0.616^{***}	0.123	21
Landscape	0.745^{***}	0.149	26
Landscape × inherent soil properties	1.512^{nt}	0.302	53
Land-cover structure in 2007			
Total explainable	2.592^{***}	0.518	100
Inherent soil properties	1.469^{***}	0.294	57
Landscape	0.465^{ns}	0.093	18
Landscape × inherent soil properties	0.659^{nt}	0.132	25
Land-cover structure dynamics			
Total explainable	2.631^{***}	0.526	100
Inherent soil properties	1.195^{***}	0.239	45
Landscape	0.503^{**}	0.101	19
Landscape × inherent soil properties	0.932^{nt}	0.186	35

*** Simulated $P < 0.001$ for the RDA permutation tests; ** simulated $P < 0.01$

^{ns} Not significant ($P > 0.05$)

^{nt} Not testable

(19 and 35 % of the explained variance, respectively). In contrast, both land-cover composition and structure measured in 2007 had little predictive ability, essentially due to interaction and a non-significant pure effect. The inherent soil properties pure effect was significant regardless of the land-cover classification considered and higher with those based on structure (Table 6).

Discussion

Our purpose was to address a set of regulating and supporting ES on which farmers depend for managing the land that they have cleared. We analyzed how these ES evolve with landscape changes along a gradient of land-use intensity. Firstly, the productive capacity of soil, that is, its chemical and physical fertility via nutrient and water cycling, must be maintained, if not improved. Amazonian soils being chemically poor and physically fragile, their fertility must not be degraded by practices inappropriate to the climate and soil conditions. Secondly, these practices must also take care of regulation services of the water cycle to conserve soil and water resources: precipitation must infiltrate into the soil and replenish plant-available water and groundwater instead of running off at the soil surface and increasing the risks of erosion and nutrient leaching upstream and of floods downstream. Finally, compensation mechanisms, such as "carbon credits", recommended in international climate negotiations, assume that carbon stocks in soil and vegetation compartments of agro-ecosystems and their variability in the landscape are well known (Hall 2008).

Our results confirm the important contribution of inherent soil properties to the provision of soil ES and their variability. The diversity of the Amazonian biophysical environments is known (Hoorn et al. 2010). As a result, soils differ at scales from the regional (Quesada et al. 2012) down to the local scale of soil catenas (Fritsch et al. 2007), at which landscape ecology is mostly studied. Soils differ mainly in their depth and composition. We considered easily accessible inherent soil properties (texture, CEC) and measured them in the shallowest layer. These properties explained 30 % of the variance in ES at the plot scale, when taken together (Table 4) and 11–71 % when taken separately (Table 5). Such a contribution was expected for soil ES, and even for C stock in plant biomass, which depends on soil quality (Quesada et al. 2012).

Landscape transformation, however, had a significant impact since about half (46 %) of the total variance in ES at the plot scale was explained jointly by land use, inherent soil properties and their interaction (Table 4). Still a sizeable proportion of variance remained unexplained, aggregating the measurement uncertainty influencing the assessment of ES metrics and the limits of the two classifications considered. Indeed, land-use classification did not include the diversity of farming practices or crop duration. For inherent soil properties, we did not consider, for example, the degree of hydromorphy linked to topographic location. Consequently, using land cover or land use as surrogates of ES to draw maps ignores the large variability in ES metrics according to land use (Fig. 4).

Though within-land-use variability was often high, significant between-land-use variations occurred for all ES metrics (Fig. 4). The metrics least influenced by within-land-use variability and most influenced by land-use changes were C stock in plant biomass and water infiltration rate (Table 4). These metrics were also the most positively correlated to each other and negatively correlated to soil chemical quality (Fig. 3a). This analysis clearly showed synergy between C stock in plant biomass and water infiltration rate, and a trade-off demonstrated by opposite variation between them and soil chemical quality. In contrast, C stock in soil was not explained by land use (Table 4) nor correlated with C stock in plant biomass (Fig. 3a). Thus, the soil does not significantly compensate the loss of C from plant biomass (Desjardins et al. 2004).

The underlying drivers of temporal dynamics of the ES studied are primarily socio-economic. Smallholder farming systems considered in this study comprise specific forestry, cropping, and grazing practices, influenced by access to markets, credit, and technical assistance. These practices affect ecological processes by modifying habitats and relationships between living organisms (Mathieu et al. 2009). In this regard, slash-and-burn agriculture changes chemical soil quality, which is low in the forest, as ashes from the tree biomass are incorporated into the soil. It is well known, however, that the efficient nutrient recycling of biotic processes in tropical rainforest ecosystems compensates for the poor chemical quality of soils (Stark and Jordan 1978). The highest values were thus recorded under annual crops, the result of a trade-off between C stock in plant biomass and chemical soil quality. Next, intense activity by soil organisms in primary forest, in particular soil ecosystem engineers (earthworms, termites and ants), maintains a macroporosity favorable to infiltration and soil aeration (Barros et al. 2001). Under pastures, soils may compact in a few years from livestock trampling, exposure to precipitation, and decreased biodiversity of soil fauna (Mathieu et al. 2009). The soil compaction results in a loss of macroporosity, which may be compensated by a gain in mesoporosity (i.e. medium-sized pores (0.2–15 μm) that store plant-available water), whose highest values were observed in pastures (Fig. 3a, b); however, we showed that this ES metric was more influenced by inherent soil properties than land use (Table 5). The soil changes add to the difficulty of managing weeds and woody regrowth, explaining the decrease in productivity of pastures and finally their abandonment (Mitja et al. 2008). The intermediate position of secondary forests in the analysis of ES metrics, between pastures and primary forests, reveals a partial restoration of physical soil properties, especially infiltration rate (Fig. 3b) (Zimmermann et al. 2006). This physical restoration depends on several factors (pasture duration, grazing practices, composition and structure of the surrounding landscape) that influence the species composition of plant successions and their ability to restore the soil by reactivating processes existing in the forest. The intermediate position of perennial crops also indicates that they degrade soil less than pastures.

Changing the scale does not notably modify the relations among variables, except for C stock in plant biomass and water infiltration rate, which appear less correlated. Averaging the five points in each farm to perform farm-scale analyses may not be the most appropriate approach for these two metrics, which often vary by 2–3 orders of magnitude between forests and pastures.

Landscapes of the pioneer front have changed rapidly in the past 10–20 years, and it is interesting to note that, among the four farm-scale classifications, the one based on land-cover composition dynamics (1990–2007) explained the most variance in ES metrics. The land-cover composition made in 2007 at the time of field data acquisition explained less variance in ES metrics (Table 5). The classifications based on composition separated stable agricultural landscapes from much more dynamic and diverse ones related to the rapid replacement of forest ecosystem by an agrosystem; they contrasted the two dominant landscapes in the two countries. However, most of the farms setting up agroforestry systems (group Gcd; Fig. 5d) separated from the other Colombian farms, especially the extensive cattle farms, involving higher infiltration rates.

Land-cover structure explained less of the variance in ES metrics. It would appear that metrics describing landscape structure (fragmentation, size, shape, connectivity metrics) influence biodiversity (e.g. Fahrig et al. 2011) more than the regulation and supporting

ES studied here via C sequestration in soil and plant biomass, water infiltration and storage in soil and chemical quality of soil, which probably depend on agricultural practices applied locally (on each plot), rather than on the environment of the plots.

Finally, the hypothesis that patterns of land-cover composition alter ES is true in Amazonian pioneer fronts. However, the ES metrics assessed vary in different ways during the transformation of a forest ecosystem into agrosystems, revealing synergies and trade-offs between services. Climate, water cycle and soil erosion regulation services are those most affected by expansion of pastures in the landscape, to the detriment of tree cover (primary and secondary forests, perennial crops), by loss of carbon in biomass and a strong decrease in water infiltration into the soil.

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