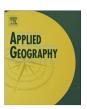
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Redistribution of forest biomass in an heterogeneous environment of subtropical Andes undergoing agriculture adjustment



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ARTICLE INFO

Article history: Available online

Keywords: Aboveground carbon Forest regrowth Forest degradation Forest redistribution Subtropical Andes

ABSTRACT

Estimations of the carbon stored in the above-ground biomass are important from traditional, ecological and forestry to contemporary climate and land-use change perspectives. Carbon sequestration and storage is reduced by deforestation and degradation and enhanced by forest regrowth and expansion. Recent studies show that forests are experiencing redistribution at different scales. Regions with steep topographical gradients simultaneously experience these four processes, upon which the final carbon balance in forests depends, but large scale patterns of above-ground carbon changes within forests have generally been overlooked. We developed above-ground carbon maps for 2000 and 2012 in a heterogeneous environment of subtropical Andes to a) explore the patterns of change in relation to biophysical variables and forests types and b) calculate the relative contribution of within forest carbon change and of forest expansion/deforestation to total above-ground carbon balance. Above-ground carbon trends showed spatial variation: biomass losses occurred in dry forests at low-mid elevations, while gains were restricted to higher elevation forests. Within forest changes implied larger changes in carbon stocks (+361976 Mg C) and in an opposite direction than deforestation and reforestation (-56750.16 Mg C), and determined an overall stability in terms of above-ground carbon for the study period. These contrasting patterns of above-ground change may be representative of larger heterogeneous regions such as tropical and subtropical Andes, and highlight the need of explicitly accounting for within forests change in current carbon regional balances.

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Introduction

Forests have an important role in the global and regional carbon cycles and are valued globally for carbon sequestration "services" (Pan et al., 2011). The carbon stored in the above-ground living biomass of trees is typically one of the largest pools in Neotropical forests, and the most directly impacted by deforestation and degradation (Gibbs et al., 2007). The above-ground carbon balance of a region depends on the organic C accumulation rate within the system, which is mostly controlled by inter-annual climatic variability (Zhang et al., 2013) and by land cover change (Liu, Loveland, & Kurtz, 2004); in particular, changes in forest area (deforestation and reforestation). In addition, changes in biomass that occur within forested areas (degradation and regrowth, to which we refer

as "within forest change") could be relevant to determine the carbon balance of a region. Forest degradation is a human-induced change which affects negatively the structure and functions of forests, leading to alterations in the overall supply of benefits these landscapes provide, such as carbon storage, habitat for biodiversity and climate and water regulation (Asner et al., 2005). The word 'degradation' usually implies relatively subtle and gradual changes in comparison with deforestation, which occurs even when an area is not reclassified into a non-forested land cover category (Sasaki & Putz, 2009). Here, we use the term "forest regrowth" to refer to the opposite process, namely structure enhancement within existing forests, which could be the result of the reduction in the severity or periodicity of disturbances associated with human forest uses. Most analyses of carbon dynamics in the tropics focus on changes resulting from changes in forest area (forest expansion and, more often, deforestation), even when forest structure can change substantially without changes in forest area, for example, as a result of firewood harvesting and grazing (Grainger, 1999; Houghton, 2005; Torrella & Adámoli, 2005), natural succession or recovery from past

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disturbances (Grau et al., 2004). Reforestation and natural forest regrowth have become important components of land use change, particularly in the last century, both worldwide and in Latin America and the Caribbean (Aide et al., 2013; Hansen et al., 2013), and they can imply opportunities for carbon sequestration in forests (Culas, 2012). These kind of subtle and gradual changes are more cryptic and generally difficult to assess, but they might involve significant quantities of carbon, especially when they affect large areas (Houghton, 2005; Houghton & Hackler, 1999).

Globally, there are important regional differences in carbon sequestration potential among different forest types (Pan et al., 2011), because topography, soil types and water availability affect forest functions, composition and structure (Houghton, 2012). In general, dry forests store less biomass and exhibit lower net primary productivity than moist forests due to their lower structural complexity, lower trees height and slower successional rates, associated to more limited environmental conditions, particularly water availability (Ewel, 1977; Murphy & Lugo, 1986). But also, they are located nearby highly populated areas and tend to be more commonly cleared for agriculture and livestock ranching. The combination of slower successional rates and more intense human impact makes them typically more degraded (Murphy & Lugo, 1986). While moist forests are also threatened by deforestation and degradation in different regions, they often occur at high elevations and slopes, and some of them have recovered in many regions of Latin America (Aide et al., 2013). In addition, their net primary productivity is usually higher, which, coupled with lower human pressure and faster growth rates could derive in positive consequences over aboveground biomass balance. Recent studies have shown a common pattern of forests redistribution in Latin America, where montane forests tend to be re-growing while lowland dry forests either have been severely degraded in the past or experience present day degradation and deforestation (e.g. Aide et al. 2013; Grau, Gasparri, & Aide, 2005). A particular case of this redistribution pattern is our study area, which covers most part of a subtropical watershed in Argentina (Nanni & Grau, 2014).

Above-ground biomass (AGB) can be used as a measure of forest degradation and regrowth since it depends on the number of trees, their size, and wood density (Asner, 2009). The generation of above-ground biomass maps through time allows assessing the main mechanisms that control the spatial distribution of the carbon stored in forests (Above-ground carbon, AGC). Typically, biomass maps combine spectral information derived from remote sensors and field-based AGB sampling to develop statistical models of AGB distribution at different scales and locations, such as the Amazon basin (Saatchi et al., 2007), Africa (Baccini et al., 2008), dry woodlands of North America (Dahlin, Asner, Field, Christopher B., 2012), and dry Chaco forests of Argentina (Gasparri et al., 2010; Gasparri & Baldi, 2013). However, these studies are usually limited to one particular date. Since forested areas undergoing change can be extensive, detailed spatially explicit models or analyses of AGB change through time are key to assess regional changes in carbon stocks and to link these changes to specific forests types, but they are rare (e.g., Pan et al., 2011).

Northwestern Argentina is representative of the environmental heterogeneity and the demographic and socioeconomic processes that have led to forests redistribution in Southern Andean Yungas, including deforestation in lowlands and reforestation in montane lands, reduction of subsistence cattle and rural outmigration (Aráoz & Grau, 2010; Gasparri & Grau. 2009). Its steep biophysical gradients determine the existence of different types of forests and land uses interactions, from woodland extraction and extensive cattle ranching in rural areas to urbanization and intensive agriculture practises in dry forests and piedmonts, and regrowth in more distant, moist forests (Izquierdo & Grau, 2009; Gutierrez Angonese

& Grau 2014; Nanni & Grau, 2014). Trancas department in Tucumán province (2,88,000 ha, Fig. A) includes the key socioeconomic processes and ecosystem types characteristics of northwestern Argentina, thus it allows quantifying forest carbon trends in relation to forest types and redistribution representative of regional-scale changes.

In this area, we elaborated maps of Above-ground carbon stocks for 2000 and 2012 in order to a) explore temporal and spatial patterns of carbon and their association with altitude and forest types, and b) compare the magnitude and direction of changes in AGC stocks derived from degradation-regrowth (within forests) with changes derived from land conversion (i.e. deforestation and reforestation). We finally discuss the implications of our results for the conservation of different forests types and forest carbon stocks in tropical and subtropical Andes ecosystems.

Materials and methods

Study area

Our study was carried out in the department of Trancas, Tucumán, Argentina (Fig. A). The department (288000 ha) includes most of the Tapia-Trancas watershed, a semi-arid tectonic basin limited by the Cumbres Calchaquies range in the west and Medina mountain range in the east; spanning over an altitudinal range from 700 to 4500 masl. Such a steep topographic gradient results in wide ranges of temperature and rainfall; from 300 to 600 mm/year and 18 °C in the lowlands to 600–800 mm of annual rainfall in the midelevation mountain slopes: and <0 °C of mean annual temperature at the top of the Cumbres Calchaquies. As a consequence, the area includes three main ecoregions: (1) dry Chaco forests occupy the central lowlands and eastern mountain slopes; (2) Yungas humid montane forests are located in the east slopes of the Cumbres Calchaquies (approximately between 1000 and 2500 masl in the central-western belt of the study area), and (3) High elevation grasslands, above 2500-2700 masl in the west side of the basin (Fig. A). The entire region has experienced a consistent increase in rainfall between 1950 and 2000 (Minetti & Lamelas, 1995) and a slight increase in temperature between 1990 and 2013 (EEAOC).

Dry Chaco Forests in lowlands (between 700 and 1000 masl) are dominated by Aspidosperma quebracho-blanco, Caesalpinia paraguanensis, Acacia spp. and Geoffrea decorticans. Between 1200 and 2000 masl, Yungas humid forests dominate, with species such as Juglans australis, Parapiptadenia excelsa, Anadenanthera colubrina, Myrcianthes mato, Zanthoxylum coco and Ruprechtia laxiflora. A transitional belt between Dry Chaco and more humid forests (1000—1200 masl) is characterized by the presence of both types of vegetation, and it is here where most villages are located (Garrido, 2005). As altitude increases, diverse Yungas forests are replaced by monospecific stands of Alnus acuminata patches of forests within a grassland matrix dominated by the genus Festuca (between 1700 and 2700 masl). Selective forest logging takes place along most of the forests in the study area and it is in general for local firewood consumption (pers. obs).

Land-cover change in the study area included processes of both forest recovery and deforestation, with *A. acuminata* monospecific forests expanding over steep highlands above 1700 masl and agriculture expanding over lowland irrigated areas, as a result of the interaction between agriculture modernization, demographic trends and the existence of complex topographic gradients. Although net forest change over the last two decades represented less than 1%, forests redistribution affected 7% of forested lands (Nanni & Grau, 2014). As a result of agriculture modernization, subsistence livestock experienced reductions in the last two decades (Censo Nacional Agropecuario, 2002) while market-oriented

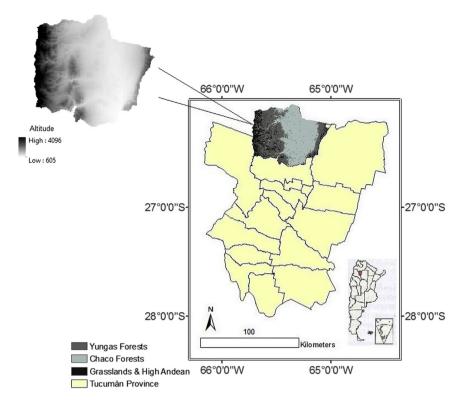


Fig. A. Relative location of the study area within the province limits; including its altitude gradient and main ecoregions.

cattle increased in almost 50% from 2000 to 2012 (Observatorio Ganadero, 2013).

ABG field based estimates

Field sampling was conducted between May, 2012 and May 2013. Twenty samples were distributed along the whole study area in order to encompass the different types of forests that characterize the region: Dry Chaco Forests (n=5), Transitional Forests (n=4) and Yungas forests at different altitudinal ranges (n=11) (Table 1). Samples consisted in 100×100 m quadrats with a set of circular plots in each of their vertexes (Gasparri & Baldi, 2013). Plots

were divided in two concentric circles: in the minor or inner circle (area $= 500 \text{ m}^2$), all stems with a diameter at breast height (DBH) > 10 cm were recorded; while in the major circle (1000 m^2) only stems with DBH > 20 cm were recorded. The DBH 10 cm size limit includes all the species of the top and mid-canopy layers, and the major individuals of the understory (SAyDS, 2004), which on average account for 64% of forests biomass (Brown & Lugo, 1984).

For all stems sampled, the species identity was recorded. The data of each sample was then analyzed in order to estimate AGB for each cluster using global allometric equations developed for different kind of forests (Chave et al., 2005), based on DBH and wood density of the species. Wood density was obtained from the

Table 1

Altitude, Richness (S), Forest type (FT), Dominant sp. (D.sp, i.e. species which account for >50& BA), Basal area (BA), above-ground biomass (AGB) and above-ground carbon (AGC) for the 20 field sites.

Site	Altitude	S	FT	Sp.	BA (m_2/ha)	AGB (Mg/ha)	AGC (Mg/ha)
1	1569	4	Moist	J. australis, D serratifolia	26.8	228.8	114.4
2	933	11	Dry	C. tala, M. alba, E.contorisiliquum	15.8	109.9	54.95
3	1170	14	Moist	J. australis, T. tipu, A. edulis	17.7	130.6	65.3
4	1174	8	Moist	A. colubrina, P. excelsa, J. australis	36.9	277.2	138.6
5	1183	8	Transitional	J. australis, C. tala	27.1	122	61
6	1190	9	Moist	P. excelsa, P. zapallo, T. tipu	58	306.3	153.15
7	1380	9	Transitional	A. edulis, A. colubrina	15.3	114.1	57.05
8	1245	11	Dry	B. praecox, A. quebrachoblanc, C. tala	23.8	237.3	118.65
9	1087	6	Moist	C. porphyrium, T. tipu	64.1	111.8	55.9
10	1476	5	Transitional	S. bumeloides, F. coco	7.7	62.8	31.4
11	1321	6	Moist	A. edulis, F. coco, P. excelsa	8.13	69.1	34.55
12	1487	2	Moist	T. stans	0.8	13.4	6.7
13	1325	7	Moist	A. edulis, A. aroma	9.5	119.4	59.7
14	927	8	Transitional	L. lucidum, M. alba, A. aroma	60.7	437.2	218.6
15	651	11	Dry	S. humboldtiana, A. aroma	52.28	241.1	120.55
16	620	14	Dry	G. decorticans, S. fasciculatus	12	176.5	88.25
17	933	13	Dry	S. haematospermum, Z. mistol, M. alba	30.3	213.3	106.65
18	1662	11	Moist	A. edulis, D. serratifolia	12	156.9	78.45
19	2003	1	Moist	A. acuminata	13.6	130.9	65.45
20	1406	3	Moist	Pinus sp.	98.95	765.5	382.75

database generated by INTI-CINEMA (2010), which includes data for all species registered in our samples.

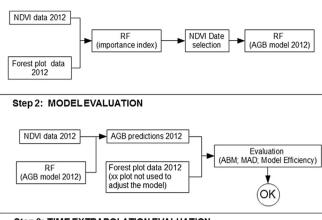
MODIS imagery and AGB mapping

The overall methodology for deriving AGB spatial explicit models for different years within the study area implied a combination of field data with spectral information derived from satellite imagery. Radiation reflectance of the visible and infrared wavelengths is associated to vegetation structure (tree density, height, and basal area); which in turn is ultimately correlated to biomass (Baccini et al., 2004). For AGB modelling we used the MODIS product MOD13Q1 (Collection 5). This product has a spatial resolution of 250 m and it includes the normalized vegetation index (NDVI), with a 16-day compositing scheme that helps eliminate cloudy or unreliable pixels. Prior to generating AGB models, cultivated areas of 2000 and 2012 respectively were excluded by manual digitalization, in order to frame our study to exclusively quantify woodland biomass. We then transformed the generated AGB models to AGC models by dividing their values in two, since biomass carbon stocks are roughly half the total biomass.

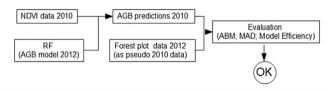
The Random Forest (RF) method (Breiman, 2001) for mapping AGB was applied in this study as an alternative to lineal regressions. Regression Trees analyses have clear advantages over classical statistical methods in that no a priori assumptions about the nature of the relationshipsamong the response and predictor variables are made, allowing the possibility of interactions and nonlinearities among variables (Prasad, Iverson, & Liaw, 2006), Also, these methods provide better insight into the spatial influence of the predictors (Iverson & Prasad, 1998) and therefore have found favor among remote sensing researchers. RF are an ensemble machinelearning method for classification and regression that operate by constructing a multitude of decision trees at training time and outputting the values that are the mode of those output by individual trees. Under the recognition that part of the output error in a single regression tree is due to the specific choice of the training dataset, the training algorithm for RF applies the technique of bootstrap aggregating, or bagging, which consists in the creation of several similar datasets by resampling with replacement, to fit trees to the samples. After training, predictions for unseen samples can be made by averaging the predictions from all the individual regression trees, thus the variance component of the output error is reduced (Breiman, 1996; Liaw & Wiener, 2002). Based on previous studies (Gasparri & Baldi, 2013; Gasparri et al., 2010), we selected NDVI as the independent variables in the AGB modelling process. The whole model development was performed with R software (R Development Core Team, 2005) using the Random Forest package (Liaw & Wiener, 2002).

The use of RF to prepare the AGB maps included four steps (Fig. B): 1) selection of NDVI useful dates: 2) model evaluation: 3) model capacity of time extrapolation and 4) AGB mapping. In order to choose the most useful NDVI dates, we tested all the NDVI data collected by MODIS during the sampling period (May 2012-May 2013, 28 dates) with RF importance index (Breiman, 2001) for each independent variable (i.e., different dates). Although RF method includes an internal validation through the exclusion of about 37% of the data ("out-of-bag data") in each bootstrap resample (Breiman, 1996), we still evaluated the overall model performance through three criteria: a-mean difference between observed and predicted values (average model bias, AMB), which represents the error of a set of predictions; b-mean absolute difference between observed and predicted values (MAD), which indicates the average error associated with a single prediction (a specific pixel) and c-the efficiency of the model (analogous to R²) which compares predictions directly to observed data (Vanclay, 2004). After the

Step 1: NDVI DATE SELECTION



Step 3: TIME EXTRAPOLATION EVALUATION



Step 4: AGB MAPPING

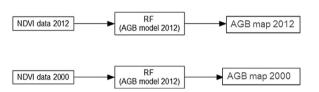


Fig. B. Scheme of AGB modelling proceedings, from data collection to AGB mapping.

evaluation, we fitted a predictive RF model setting to adjust 1000 trees with the 20 samples taken in the field and the NDVI values for the selected dates of year 2012. Since we aimed to develop a 2000 AGB map, we tested the model capability of predicting AGB of previous years. We used the 2012 fitted model to predict the biomass in the year 2010 (i.e., using remote sensing data of year 2010) and we contrasted the predicted biomass values of 2010 with 2012 field data, assuming no major changes in plots biomass occurred between these years. For the evaluation of both predicted and measured values we used the three criteria described above. Additionally, we evaluated the confidence of our biomass mapping extrapolation in time proceeding by using MODIS MOD17A3 product, which provides annual continuous estimates of NPP for the 2000–2010 period. This product produces gross primary production of vegetation every day, and sums to net primary production, essentially vegetation growth, at the end of the year (Zhao et al., 2006). The sum of 2000-2010 NPP values at a given pixel is thus the carbon accumulated by growth, and should approximate C gain values produced by our models. To also account for 2010–2012 and cover the whole study period, we added 2000–2012 mean NPP multiplied by two to the calculation. We then performed Pearson correlation tests between C accumulation derived from 2000 to 2012 NPP sum and our C gains estimates.

We estimated changes in the above-ground carbon pool of the study area by considering changes both in forest area and changes within forests. For the former, we digitized crops and pastures for 2000 and 2012 in Landsat TM images in order to derive deforestation rates within the period. Since we could not directly estimate reforestation rates, we used 1986–2006 deforestation/

reforestation ratios (Nanni & Grau, 2014) to approximate reforestation values. We then calculated C change due to land conversion by multiplying changes in forest area by C regional mean, and estimated within AGC change for 2000–2012 (gross 2000–2012C change -land conversion C change).

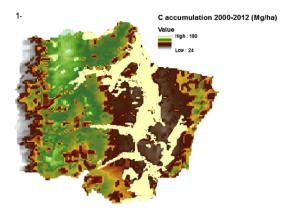
To estimate within forest changes, we applied GIS raster calculator tools and developed a 2000–2012 C change map for the study area (i.e., the difference in estimated C between the two maps). In order to be conservative and to only account for the pixels that have undoubtedly changed between 2000 and 2012, C change values which ranged within the average model bias (15% to account for both models bias) were considered as unchanged between 2000 and 2012. This allowed us to identify sites of forest regrowth and degradation, as well as unchanged sites. To explore the spatial patterns of C change, we used a Digital Elevation Model (Jarvis, Reuter, Nelson, Guevara, 2008) and derived altitude (which encompasses other biophysical factors such as annual rainfall, radiation, temperature and forest species composition). We performed linear regressions models with AGC gains and losses as the dependent variables and altitude as the independent variable.

Results

Based on RF Importance index, the selected dates to map AGB were July 11th and July 27th, 2012. The statistics of the model fitted for 2012 showed a 46.7% of variation explained. The predictions evaluation showed a mean predicted versus a mean observed deviation of 8.2% and an average absolute deviation for a single prediction of 2.2%. Prediction capacity of the model for other years. assessed by model evaluation for 2010, showed an averaged model bias (predicted versus observed) of 7.1% and an average absolute deviation of 0.1.9%, with 40% of AGB variation explained. The assessment of time extrapolation uncertainties through the comparison of C gains derived from our model and the NPP-derived accumulated C showed that estimates of C gains were positively and strongly correlated with NPP derived C accumulation (r = 0.55, p < 0.0001; Fig. C1,2). Modelled C gains reached higher values than NPP-derived accumulated C in 2012, consistently with the underestimation of forest carbon in 2000 map. Also, low modelled C gains (around 50-100 Mg/ha) were given higher NPP derived C values, but this could be due to the fact that NPP only accounts for growth, thus, it is always cumulative and does not capture degradation processes that may have occurred either gradually (e.g. fuelwood extraction) or abruptly (e.g. fire) within the study period. Additionally, predicted-observed plots for both years (Fig. D4) showed that the 2012 model presents a good prediction capacity, while the 2010 model seems to underestimate predicted values.

AGC values in field samples ranged from 6.7 to 218.63 Mg/ha (including higher values of 382.76 Mg/ha in pine plantations, which occupy a negligible area, Table 1), showing a high variation between different types of forests within the study area. AGC maps capture that variation with a range from 0 to 250 Mg C/ha, a mean of 77.5 Mg C/ha for the region and a total carbon stock of 23,17,893 Mg C in 2000; and a regional mean of 89.15 Mg C/ha and a total carbon stored in forests of 23,57,471.5 Mg C in 2012 (Fig. D1,2). Biomass carbon was higher in Yungas montane forests and decreased both towards Chaco dry forests and highlands of grass and *A. acuminata* forests patches, although the lowest values were found in transitional, mid-elevation forests (Fig. D).

Between 2000 and 2012 the study area remained rather stable in modelled AGC, with a positive balance of 305225.84 or +1.3% Mg C, which falls within the average model error but illustrates approaches zero carbon changes. This apparent stability resulted from strong geographic patterns of C gains and losses (Fig. D3): while in the central lowlands C remained stable, the belt of transitional



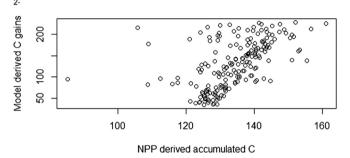


Fig. C. NPP derived 2000–2012 C accumulation (Mg C/ha) (1) and NPP derived C accumulation vs. modelled AGC gains plot (2).

forests towards the west of the study area experienced the most important reductions in C, with higher increases occurring almost exclusively in Yungas montane forests.

Elevation was positively correlated with C gains ($R^2=24$, p<0.0001, Fig. E1), but not to C loses ($R^2=0.05$, p=0.11, Fig. E2). Dry Chaco forests between 600 and 900-masl remained comparatively stable. C losses were notoriously restricted to the range between 1000 and 1300 m.a.sl, while gains increased linearly from 1200 to 1700 masl (Fig. E1). In sum, C trends were segregated spatially and involved different forests types, losses restricted to transitional forests and gains dominating in moister forests at higher altitudes.

Deforestation rate for 2000–2012 was 251.62 ha/year, while our estimates of reforestation rate were 198.78 ha/year, implying a net forest conversion rate of -52.84 ha/year and C change due to forests conversion of -56750.16 Mg C. Changes within forests, on the other hand, resulted in a positive balance of 361976 Mg C.

Discussion

The development of temporal carbon maps is key for understanding changes in the carbon stored by forests, one of the largest carbon sinks and sources worldwide (Houghton., 2005). However, the contribution of within forest AGC change to biomass carbon balance has generally been overlooked. This study shows that non-parametric methods (i.e., Random Forests) seem to be adequate for modelling broad AGC changes through time in heterogeneous regions such as Neotropical Andes, where abrupt and contrasting gradients of biophysical conditions and forests types allow for a better adjustment of predicted to observed values. By generating maps of change between two dates comprising a 12-year period, we obtained accurate estimates of carbon stocks and changes within forests, and we found an overall stability of total carbon stocks in forests between 2000 and 2012 within the study area.

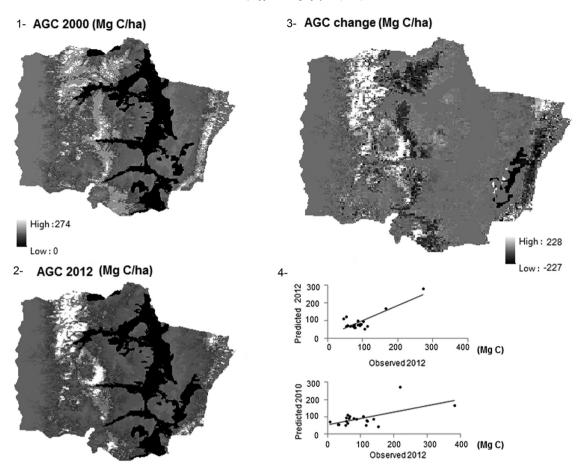


Fig. D. AGC models for 2000 (1) and 2012 (2), and AGC change map (3); evaluation plots of 2012 predicted values vs. 2012 observed values and 2010 predicted vs. 2012 observed values (4).

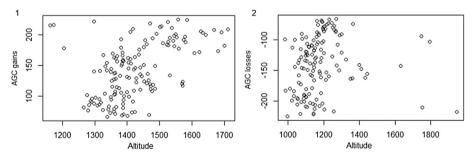


Fig. E. AGC gains (1) and loses (2) as a function of elevation.

Despite high forest heterogeneity and a consequent wide range of AGC values, predicted AGC values for the region concurred with those reported in literature for comparable forests ecosystems, with AGC ranging from 24 to 106 Mg C/ha in dry forests (Gasparri & Baldi, 2013) and rising up to 100–300 Mg C in moister forests (200–400 Mg C/ha in San Javier Yungas subtropical forests, Grau et al., 2010).

Despite an underestimation of AGC when extrapolated in time, generated models were reliable and allowed an accurate prediction of forest C gains and losses patterns and magnitudes. In our study, the four components of AGC change (deforestation, expansion; degradation, regrowth) implied important magnitudes of C fluxes. However, within forests dynamics played a more significant role over these patterns, involving larger quantities of

carbon and thus reversing the negative trends derived from land conversion. Within forests trends in our study area were consistent with results from permanent plots in tropical forests of Amazonia, where mature forests sites have accumulated substantial amounts of biomass, exceeding loses from tree death (Phillips et al., 1998). However, our results contrast with regional estimates of losses derived from degradation, which have generally been low compared to those from deforestation (5% for the world humid tropics, Achard et al., 2004; 25–42% for tropical Asia, Houghton & Hackler, 1999). Moreover, degradation could play an even larger role in the count, since AGC is underestimated in the 2000 model. Thus, our findings strongly suggest the need of inclusion of within forests change in large scale forest carbon assessments, since they can be decisive in the overall carbon

balance, especially in heterogeneous regions where often, different trends coexist.

The comparatively larger influence of within forests changes over carbon fluxes can be explained through the reduction of deforestation rates for the time frame analyzed, compared to rates for the past two decades (512.15 ha/year for the 1986-2006 period vs. 251.62 ha/year for 2000–2012 period). This may imply that the watershed is reaching a stabilization stage in terms of its land use. as are many regions worldwide (Mather & Needle, 1998; Redo et al., 2012). Agriculture adjustment, which led to the redistribution of forests within the study area (Nanni & Grau, 2014) may also be promoting these changes within forests, since the reduction of extensive livestock due to population out-migration or to the shift towards different kind of economic activities may be lessening the pressure over forests. However, given that biomass recovery after disturbances can take several decades to reach mature forest values (Aide et al., 2000; Grau et al. 1997), stabilization of within forest changes can lag for long after stabilization of land cover. Areas with steep topographic gradients that limit agriculture expansion, such as Neotropical Andes in South America, will likely exhibit positive AGC balances (Culas, 2012) both as a consequence of forest expansion into abandoned marginal agriculture lands and of secondary succession and regrowth of areas previously degraded by extensive grazing and firewood harvest; but the relative importance of the later process would become comparatively more important in time.

AGC gains and losses were spatially segregated, and altitude had an influence on patterns of change, possibly as a result of the interaction of both land use and biophysical factors. C gains became more consistent at 1200 masl and were a dominant trend from 1300 masl up, restricted almost exclusively to moist, montane forests. In addition to changes in land use and related changes in disturbance regimes (e.g. fire, Aráoz & Grau, 2008), forest growth could be favoured by the increase in rainfall recorded during the past decades (Minetti & Lamelas, 1995). Higher rainfall enhances both woody encroachment over non-forest grasslands and forest growth, and therefore promotes carbon gains through forests expansion and within forests. Also, moist forests exhibit high NPP values (Fig. D1), which coupled with their increasing biomass carbon, may translate in good opportunities for the watershed aboveground carbon storage. The altitudinal range between 100 and 1200 masl experienced substantial C losses. This elevation range comprises forests with relatively high NPP values but subjected to fuelwood extraction and extensive livestock activity, and therefore, their degradation may negatively affect regional carbon balance. The apparent AGC stability of dry forests in lowlands, on the other hand, may be the result of intensive past degradation, since their NPP values were considerably low. These complex interactions between biophysical features, forest types and human uses result in carbon stocks redistribution within the watershed, from drier and flatter to steeper, moister areas. This pattern of redistribution has been shown at different scales (Hansen et al., 2013; Nanni & Grau, 2014; Redo et al., 2012), including one recent analysis of global terrestrial biomass (Liu et al., 2015) showing that 2002-2013 AGC loses due to tropical deforestation are compensated by increasing AGC in boreal and temperate forests. However, studies have focused on land conversion, without accounting for within forest biomass trends.

While many areas exhibit a clear dominance of a particular land cover trend (deforestation, forest expansion, degradation or regrowth), mountainous, environmental contrasting regions such as Neotropical Andes are subjected to the simultaneous occurrence of different aspects of land use change. In these regions, different processes characterize distinct types of forest; thus yielding antagonistic costs and opportunities in terms of carbon and other

ecosystem services, and these redistribution patterns are consistent at larger scales of analysis (Liu et al., 2015). In this sense, both the generation of remote sensing methods and permanent plots networks that accurately estimate cryptic but significant processes such as degradation and regrowth; and the understanding of AGC spatial and temporal variability are critical for regional carbon policy development concerning carbon emission reductions, such as REDD+. In this work, we used remote sensing data and RF to estimate current (2012) and past (2000) AGC. We submitted the models to a simple but robust validation method; and reduced the uncertainties in change estimates by considering only changes larges than error. The documented broad changes found were reliable and consistent with changes in land use within the area (Nanni & Grau, 2014), showing patterns of association with biophysical variables related to agriculture adjustment, such as elevation. Based on this, we believe our results are an initial but robust and promising approximation of the relative importance of within forests AGC dynamics over regional carbon balance, and can be used as a general orientation of forests carbon budget patterns in Andean regions. Also, they highlight the need of developing more accurate methods to estimate regional carbon fluxes derived from forest degradation and regrowth.

Conclusions

The combination of field sampling and spectral information through non-parametric statistical methods is adequate for developing accurate, AGC temporal models, particularly in heterogeneous landscapes resulting from steep environmental gradients. To our knowledge, this study constitutes the first spatial local-scale explicit assessment of forest carbon changes in a subtropical region undergoing a process of land use/cover redistribution comparatively more important than net forest cover change. Within forest changes in carbon stocks proved to yield higher amounts of C than changes derived from land conversion, and thus can have a major and usually unassessed influence over regional carbon balance. These contrasting trends among different components of AGC change and over forests with different composition and land uses highlight the need of further examining current carbon regional balances, and explicitly accounting for within forests change in AGC assessments. The comparatively larger influence of within forest processes over carbon stocks might be a relatively common situation of regions in which land conversion rates have slowed down or become stabilized, and which exhibit topographical constrains to forests degradation and deforestation (e.g. Neotropical Andes of South-America). In these heterogeneous regions, it is also likely that degradation and growth processes are restricted to specific types of forests, where conservation efforts should be focused.

Acknowledgments

We thank Ceballos, S., Lizardo, G., Loto, D. and Schaaf, A. for their assistance in the field, and School N° 385 in Rearte, Trancas, for providing lodging during the field work. This research is funded by Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) PhD scholarship and by Rufford Small Grants for Nature Conservation for the first author's PhD project "land use change and ecosystem services provision in a subtropical watershed".

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