ECOSYSTEMS

Primary Productivity Determinants of Different Land Uses in Humid Subtropical Ecosystems: From Native Forests to Tree Plantations

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ABSTRACT

Land-use changes in forest ecosystems may alter the amount of carbon sequestration. The main objective of this study was to characterize the impact of different land-use practices on structure and functioning of humid subtropical forests that are under severe threat. We emphasize the characterization of canopy photosynthetic activity, assessed by the Enhanced Vegetation Index (EVI), the Leaf Area Index (LAI) and the fraction of Absorbed Photosynthetically Active Radiation (fPAR), using a combination of ground base measurements and remote sensing data on native well-preserved forests, impacted forests by selective logging and pine plantations in NE Argentina. Even though selective timber extraction resulted in a substantial decrease in stand's tree density, EVI values were as high as those from preserved forests. In these forests, an increase in the understory cover appears to compensate the response of stand's EVI to timber extraction. Removal of canopy trees enhances incoming solar radiation, allowing active growth of understory vegetation. The pine plantations exhibited the lowest values of LAI, fPAR and EVI. However, when EVI was normalized by LAI, the pine plantations exhibited the highest EVI/LAI values. Our results suggest that after 15 years of forest recovery from selective timber extraction, photosynthetic capacity was similar to that of preserved forests. Increases in the understory cover may compensate the potential decrease in the canopy photosynthetic activity. Pine plantations resulted in substantially lower productivity as depicted by lower EVI and LAI but exhibited higher growth efficiency than native forests.

Key words: Enhanced Vegetation Index; Leaf Area Index; *Pinus taeda*; Logged forest; MODIS; Understory cover.

HIGHLIGHTS

- Preserved and degraded forests had different structural traits but similar EVI.
- Understory cover explained the homeostatic response of high EVI in degraded forests.
- Pine plantations exhibited highest growth efficiency (EVI/LAI ratio).

INTRODUCTION

Humid subtropical forests without drought seasonality appear to be strong carbon sinks contributing to global carbon forest sequestration (for example, Cristiano and others 2014; Zhang and others 2016). Recent studies in China and Argentina have suggested that these forests assimilate carbon all-year-round with high canopy photosynthetic rates (Tan and others 2012; Yu and others 2014). The subtropical belt is characterized by extensive arid and semiarid ecosystems worldwide; however, in a few regions, such as in the rainfall shadows of the Himalayas and near the subtropical Atlantic coastlines, humid subtropical forests occur (Zhang and others 2016). Compared to tropical rainforests with little climatic seasonality and year-round high temperatures, these forests have a mild cold season that have little impact on productivity, as depicted by high normalized difference vegetation index (NDVI) observed throughout the year, and by high ecosystem net carbon assimilations during winter (Tan and others 2012; Zhang and others 2013; Cristiano and others 2014).

The humid subtropical forests of Argentina correspond to the southern portion of the Atlantic Forest Biome, which extends along the Atlantic coast of Brazil and southeastern Paraguay. Just 100 years ago the Atlantic Forest was the second most extensive forest ecosystem in the Neotropics after the Amazonian forests. However, unlike the Amazonian forests, about 93% of the original cover of the tropical Atlantic Forest has been lost due to human activities during the last decades. Only small fragments remain in Brazil and Paraguay, while the largest continuous subtropical stands persist in NE Argentina (Galindo-Leal and Gusmão-Câmara 2003). Most of the remaining native forest stands in Argentina had experienced some degree of intervention by selective timber extraction of trees with high commercial value. The most well-preserved forests are mainly located in national, provincial parks and private reserves. Many of the humid subtropical forest stands in Argentina have been replaced recently by fast-growth tree plantations, mainly of *Pinus* species, for cellulose pulp and wood production (Izquierdo and others 2008).

Forests are characterized by a functional separation of carbon storage between longed-lived woody biomass fraction and a rapidly turning over photosynthetically active leaf fractions. Despite the relatively small biomass fraction, leaves are the major components determining the carbon, water and energy exchange with the atmosphere (Castro-Izaguirre and others 2016). The leaf area of forest stands leaves can be quantified by the Leaf Area Index (LAI); a dimensionless structural–functional index defined as the projected area of leaves per unit of ground surface area (Bonan 2015). Leaf Area Index and its seasonal variations determine the amount and quality of irradiance distribution inside forest stands (Hardwick and others 2015). Under closed canopy forests, diffuse radiation predominates in the understory, punctuated by direct radiation from sun flecks. Human activities, such as selective timber extraction and afforestations, modify light regimes and forests composition and structure, altering light regimes inside forests as well (Paula and others 2011; Berenguer and others 2014; Rutishauser and others 2016). The formation of larger canopy gaps during selective logging of large trees increases direct irradiance reaching the understory, affecting tree regeneration and growth, and enhancing understory growth, particularly of lianas and bamboo (Campanello and others 2016). Previous studies carried out in these same forests showed that the high values of LAI exhibited by the native forests allow them to maintain high NDVI values throughout the year, whereas pine plantations, on the other hand, have lower NDVI values, as well as lower LAI than native forests (Cristiano and others 2014). Studies on temporal dynamics of LAI are still lacking in subtropical forests and it is essential for the understanding of hydrological and biogeochemical cycles.

Information provided by remote sensing can be highly valuable for understanding the spatial and temporal dynamics of carbon cycling. The Enhanced Vegetation Index (EVI) is a spectral index similar to NDVI, and is being increasingly used in ecosystem studies because it is closely related to LAI, to the amount of green biomass and chlorophyll content in leaves and to the fraction of Photosynthetically Active Radiation absorbed by the vegetation (fPAR) and thus to primary productivity through CO_2 assimilation (Huete and others 1997; Huete and others 2002; Xiao and others 2006; Doughty and Goulden 2008; Galvão and others 2011; Muraoka and others 2013). However, unlike

temperate or dry forests, information on remote sensing, mainly EVI, applied to humid subtropical forests is very limited (Xiao and others 2005; Garbulsky and others 2010).

The main objective of this study was to characterize the impact of different land-use practices on components of the primary productivity using a surrogate of photosynthetic activity, such as LAI and EVI, of humid subtropical forests in northern Misiones, Argentina. Native well-preserved forests, degraded forests by selective logging and pine plantations of low tree density were studied using field measurements of forest structure and functioning as well as remote sensing data. In this study, forest degradation will be considered as those changes that affect the characteristics of forests, related to the structure or functioning that impact their capacity to provide ecosystem services (Simula 2009; Thompson and others 2013). We emphasize the field characterization of structural and functional properties of forests stands such as aboveground biomass, basal area, LAI, understory cover and EVI and their temporal dynamic for a two-year period. It was hypothesized that removal of native trees leaving the rest of the forest partially intact decreases the stand level carbon assimilation by lowering leaf biomass and photosynthetic activity, while pine plantations are expected to have as much or even higher photosynthetic rates than native forests.

MATERIALS AND METHODS

Study Area

Field measurements of stand structure and functional ecosystem variables were done in *Pinus taeda* plantations and in two native humid subtropical forests, one within the Iguazú National Park and the other one within the Puerto Península Provincial Park, Misiones Province, NE Argentina (26°25 S, 54°37 W, Figure 1). All the native forests occurring in the study area have had some type of commercial forestry intervention (extraction of large trees). In 1928, forested lands from Iguazú department were used to develop the Iguazú National Park, in 1934, considered the most preserved native forest in the province of Misiones, and to the National Forestry Reserve, in 1949, now Puerto Península Provincial Park. From 1949 to 1998, in this last Reserve, selective logging activities were carried out intermittently and at different logging intensities, with some stands being overexploited. The Puerto Peninsula Provincial Park was established in 2004 and remained under exploitation

until that date, when extraction activities were not carried on until today (Hernández and others 2010). The pine plantation belongs to a certified timber company, Pindó S.A. It was planted during 2001 with an initial tree density of 1600 individuals per hectare. The plantation was subject to wood production management practices, and control of weeds and pests were done during the first years until 2005. Annual pruning was carried out during 2004-2006. In 2007, 2010 and 2015, thinning brought tree density to 800, 400 and 170 individuals per hectare, respectively. At the time of this study, pines were 15–18 years old, when final tree density was achieved.

Mean annual rainfall in the area is about 2000 mm and is evenly distributed throughout the year. Although there is not a dry season, some climatic anomalies can occur such as a decrease in precipitation during few weeks triggering short-term drought effects. The mean annual temperature is 21 °C, with monthly means of 25 °C in January and 15 °C in July, representing the warmest and coldest months of the year, respectively. The number of days with temperatures below 0 °C ranges from 0 to 9 in winter, and thus frost seldom occurs; maintaining temperatures favorable for growth during most of the year (Gatti and others 2008). Air temperature below 0 °C occurs mostly in topographic depressions where air inversions can occur. Relative air humidity is high throughout the year with mean monthly values ranging from 73 to 85%. Monthly wind speed at 10 m above the soil surface ranges from 5.3 up to 78 km h^{-1}, with an average wind speed of 6.8 km h^{-1}. Soils are derived from basaltic rocks containing high concentration of Fe, Al and Si, and include Alfisols, Molisols and Inceptisols (Moretti and de Rau 2019).

Field Measurements

Using Google Earth, homogeneous continuous areas larger than 1 ha were randomly selected for preserved native forest stands ($n = 3$), partially degraded native forest stands by selective logging ($n = 3$) and tree plantations of *P. taeda* ($n = 3$). In each one of these ecosystem types, three 90×90 m plots were permanently established (Figure 1). Selected sites were located more than 50 m away from roads and exhibited a homogeneous cover beyond the limits of each plot, extending to the limit of the corresponding pixel. Ecosystem types were defined using thematic maps (Merenson and others 2001; Gibbs and others 2007; UMSEF 2019), Google Earth, and field
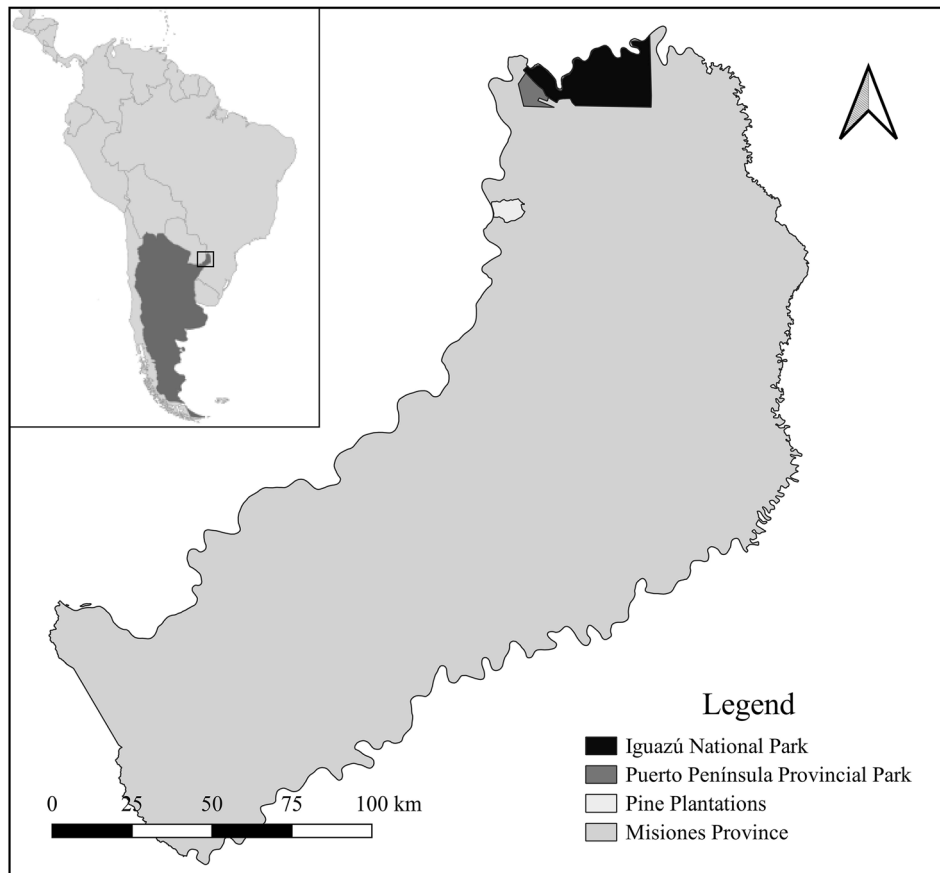
Figure 1. Location of the study sites in Misiones province, Argentina.

observations. Within each plot, two 10x50 m transects were located and trees were identified to the species level. Diameter at 1.3 m above ground level (DBH) for every individual with DBH larger than 10 cm was measured. Structural variables measurements such as basal area, tree density, tree diversity and aboveground biomass were estimated. Tree diversity was assessed by the Shannon Winner diversity index, estimated as $H' = -\sum p_i \ln p_i$, where p_i is the proportion of every species in each plot (Magurran 2013). Aboveground biomass of native forests was estimated for each individual tree (ABtree) using allometric equations based on DBH and wood density for moist forest stands according to Chave and others (2005). Wood density for each species was taken from Atencia (2003) and wood density for several species was contrasted with our own data obtained in previous studies (Rodriguez 2015) (Linear fit forced to the intercept of the y-axes, slope: 0.90 ± 0.04; $R^2 = 0.98$; $F = 482.13$; $p < 0.0001$). Aboveground biomass in pine plantations was estimated using regional prediction models of

aboveground biomass of *P. taeda* in Misiones (Fassola and others 2010).

Leaf Area Index (LAI), the fraction of photosynthetically active radiation absorbed by the vegetation (fPAR) and understory cover were monitored seasonally. The LAI and fPAR were estimated with a nondestructive method by measuring the incoming light below the canopy and in an open area with the AccuPARLp-80 ceptometer (Decagon Devices, Pullman, WA, USA) held at one meter height above ground along a 50 m transect, taking a point every ten meters (6 points in total, Figure 2) (Cristiano and others 2014). LAI estimates from this device are based on radiative transfer models, whereas the fPAR was estimated as the fraction of absorbed incoming radiation as (PARi − PARt)/PARi, where PARt and PARi are transmitted and incoming PAR measurements done with the AccuPARLp-80 ceptometer, respectively. Understory cover was estimated through the point-intercept method in a 50 m transect, taking a point every five meters (10 points in total, Figure 2). In each point, absence or presence of understory vegetation (including leaves and stems)
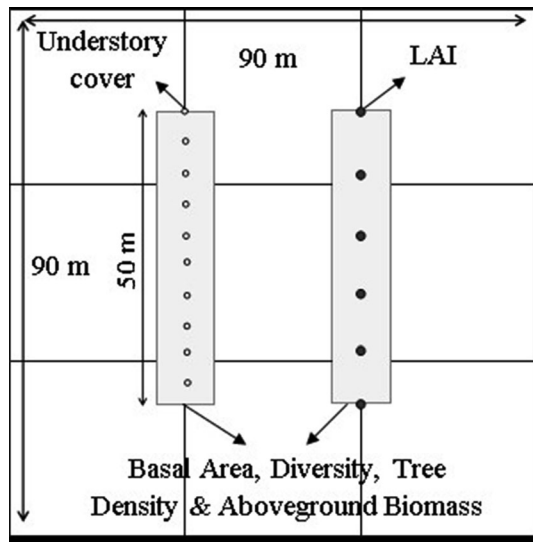
Figure 2. Layout of each of the three permanent plots installed in each ecosystem type (well-preserved forests, degraded forests and pine plantations) used to measure structural and functional traits: basal area, tree density, tree species diversity, aboveground biomass, understory cover, leaf area index (LAI) and the fraction of photosynthetically active radiation absorbed by the vegetation (fPAR). The two 50 m long transects were used to measure basal area, tree density and tree species diversity. In one of the two 50 m long transect LAI and fPAR were measured in 6 permanent points.

was recorded using a measuring stick across six 0.5 m intervals, between ground level and 3 meters high. LAI and fPAR measurements were done in May, August, November 2017, February, May, August, December 2018 and February 2019. Understory cover was measured seasonally during 1 year in May, August, December 2018 and February 2019.

Remote Sensing data

The Terra MODIS sensor (Moderate Resolution Imaging Spectroradiometer) is a 36-band spectroradiometer that measures visible and infrared radiation from 0.4 to 14.5 μm. The individual spectral bands have different spatial and temporal resolutions. The measurements made by the MODIS sensor yield data used to develop different products, for example, vegetation indices, productivity estimates, land surface cover, evapotranspiration, fire occurrence (Running and others 1994), atmospherically corrected to eliminate water vapor, clouds, heavy aerosols, and cloud shadows. The MOD13Q1 v 6.0 (Didan 2015) product, from Terra-MODIS, provides information on vegetation indices, specifically NDVI and EVI. The EVI index was

developed for minimizing atmospheric effect using the difference between de blue and red reflectance as:

$$EVI = G \frac{NIR - R}{NIR + C_1 R - C_2 B + L}$$

where NIR, R and B are surface reflectance in the near-infrared, red and blue bands (centered at 469, 645 and 858 nm in MODIS sensor, respectively), L is the canopy background adjustment for correcting differential NIR and R radiant transfer through canopy, C_1 and C_2 are the coefficients for aerosol resistance, correcting influences in the red band with the blue one, and G is a scaling factor. Coefficients in MODIS EVI algorithm are $L = 1$, $C_1 = 6$, $C_2 = 7.5$ and $G = 2.5$ (Didan 2015). The MOD13Q1 product has a spatial resolution of 250 m and a temporal resolution of 16 days and is projected on a sinusoidal 10° grid, where the globe is divided for production and distribution purposes into 36 tiles along the east–west axis, and 18 tiles along the north–south axis each approximately of 10° × 10° (Myneni and others 2002). In this study, the h13v11 tile was used. Dates were selected so they were the closest to the field measurements dates (January 17, June 26, September 09, December 03, 2017 and February 18, May 09, July 17 and December 03 2018). All images were provided by the Instituto de Clima y Agua (ICYA), Instituto Nacional de Tecnología Agropecuaria (INTA). The EVI data were extracted from the corresponding pixel for each plot. The geographical coordinates of the center of each site (pixel) are included in Table 1. The sites selected had the same soil type and topography (200–300 masl.).

Data Analysis

Differences in structural variables (Diversity, Tree density, Basal area and Aboveground Biomass) were analyzed with a one-way ANOVA with three levels (ecosystem types). Variances were modeled allowing for different variances per site so that assumptions of normality and homoscedasticity were met. Multiple comparisons across ecosystem types were made using Tukey contrasts based on $\alpha = 0.05$.

The seasonal values of LAI, fPAR and EVI were analyzed using general linear models of repeated measures over time, where first-order temporal autocorrelation (considering one-time step) for each plot was modeled. In turn, variance was modeled to allow different variances per ecosystem. For fPAR, a Log-it transformation of the data was performed to normalize its distribution (Baum

Table 1. Central Geographic Coordinates of Each Three Pixels Used to Characterize the MOD13Q1 (EVI) MODIS Product in Each Ecosystem Type

Ecosystem type	MOD13Q1 (EVI)	
	Latitude (S)	Longitude (W)
Preserved forest	− 25.708985	− 54.469237
	− 25.688155	− 54.483818
	− 25.688155	− 54.465071
Degraded forest	− 25.725649	− 54.548391
	− 25.727732	− 54.544225
	− 25.727732	− 54.546308
Pine plantation	− 26.077676	− 54.592134
	− 26.077676	− 54.600466
	− 26.077676	− 54.602549

The pixels correspond to the field permanent plots.

2008). For each season EVI was normalized by plot LAI, considered to be an estimate of growth efficiency (Waring and others 2016) and differences among seasons and ecosystems were also evaluated trough general linear models of repeated measures over time. In each case, model selection was based on the Akaike Information Criteria (AIC) (Akaike 1974). A cross-correlation analysis between EVI and field LAI was carried out for each plot. For variables that change across time, cross-correlation is an important measure, indicating statistical dependencies between two variables taken at a certain time interval (Kohn 2006). This was carried out for each plot and differences among ecosystems in cross-correlation coefficients for each lag were evaluated with a two-factor ANOVA.

In each plot, coverage of understory vegetation by point interception was used to estimate understory cover for each season from soil surface up to three meters height. A two-way ANOVA was performed to assess the differences between ecosystems and seasons. Differences between ecosystems in understory vertical distribution were analyzed using a generalized linear model for quasi-binomial variable, in order to meet the assumption of non-dispersion. Linear relationships between the understory cover integral and field LAI and EVI and were done for each ecosystem type. All analyses were done using R language in RStudio software (R Core Team 2013, RStudio Team 2015).

RESULTS

Both preserved and degraded native forests exhibited similar structural attributes, but although no significant statistical estimates were observed, the tree density and basal area tended to be lower in the degraded forests compared to the preserved forests (Table 2). Native forests basal area and aboveground biomass were higher than that of pine plantations ($F_6 = 3.74$, $p < 0.1$, $F_6 = 2262$, $p < 0.05$). Tree density in the preserved native forest was the highest, and in the pine plantations, the lowest ($F_6 = 11.07$, $p < 0.05$). Degraded native forests exhibited inter mediate values, with lower values of structural variables than preserved native forests (Table 2). They also exhibited almost a 10% less evergreen species than preserved native forests, with a mean abundance of 78% of evergreen species, 19% of deciduous species and 0.03% of brevi-deciduous species in preserved native forests and of 70% evergreen species, 28% deciduous species and 0.02% of brevi-deciduous species in degraded native forests.

The preserved and degraded native forests exhibited similar LAI dynamics with the lowest values occurring during the cold season (6.69 ± 0.45 and 5.71 ± 0.50, respectively) (Figure 3A). Pine plantation LAI was significantly lower than native forests LAI, and it exhibited also lower seasonal variations, with values between 4.24 ± 0.52 and 5.53 ± 0.49 ($F = 2.78$; $p = 0.0115$) (Figure 3A). The fPAR in both preserved and degraded native forests showed small seasonal variations, and it remained high throughout the year, ranging from 0.90 to 0.98. Pine plantations showed the lowest fPAR values as well as a different seasonal dynamic, with minimum values during the spring ($F = 2.12$; $p = 0.049$) (Figure 3B). Contrary to LAI, pine plantations showed the least variability in fPAR, followed by preserved native forests and, lastly, degraded native forests. The seasonal EVI variations showed significant differences among ecosystem

Table 2. Mean ± Standard Error of Tree Diversity, Tree Density, Basal Area and Aboveground Biomass in the Three Types of Ecosystems

	Preserved native forest	Degraded native forest	Pine plantation
Diversity H′	3.48 ± 0.136 A	3.17 ± 0.192 A	–
Tree density (trees ha^{-1})	407 ± 57 A	313 ± 70 A	170 ± 61 B
Basal area (m^2 ha^{-1})	24.6 ± 2.82 A	21.02 ± 4.52 A	15.95 ± 3.28 B
Aboveground biomass (tn ha^{-1})	312.46 ± 38.2 A	252.42 ± 58.3 A	85.34 ± 39.3 B

Different letters indicate significant differences (p < 0.05) among them.

types ($F = 5.177$; $p < 0.001$). Native forests exhibited similar EVI values during winter (0.48 ± 0.01 for both preserved and degraded forests), whereas pine plantations exhibited a minimum in autumn (0.43 ± 0.03), both during the cold season (Figure 3C). Maximum values, on the contrary, were different for each ecosystem type. Preserved native forests exhibited a maximum during the summer (0.70 ± 0.014), while in the degraded native forests spring values were the highest (0.71 ± 0.01). Pine plantations maximum was observed during the summer, although no differences between seasons were found for this ecosystem. Intra-annual variation in EVI was higher in preserved and degraded native forests (variation coefficient of 16.44% and 17.94%, respectively) than in pine plantation (12.83%).

Field LAI and fPAR and remote sensing EVI values were lowest for the pine plantations compared to both native forests. However, when EVI was normalized by LAI, pine plantations exhibited the highest values compared to native forests, and seasonal dynamics appeared to be similar for all ecosystem types (Figure 4).

The understory vegetation was significantly different across ecosystems ($F = 12.69$; $p < 0.001$). Degraded native forests and pine plantations showed an increase in understory cover of 38% and 40%, respectively, compared to preserved native forests. There were no significant differences among seasons ($F = 0.69$; $p = 0.57$), although there was a trend toward greater understory cover during the fall in all three ecosystems. The vertical distribution of understory vegetation showed differences across ecosystems ($\chi^2 = 267.54$; $p < 0.001$). From one meter high, both degraded native forests and forest plantations exhibited a greater coverage than preserved native forests. Although this pattern was observed through all heights, in the first intervals the understory cover was largest in forest plantations than both native forests, while at heights greater than 2 m, the greatest coverage was observed in degraded native forests (Figures 3C and

5). LAI was negatively correlated with understory cover only in the degraded native forests ($R^2 = 0.47$; $F = 10.61$; $p = 0.009$), whereas no relation was found in preserved native forests and pine plantations ($F = 2.78$; $p = 0.13$ and $F = 0.69$; $p = 0.43$, respectively) (Figure 6).

Cross-correlation analysis showed different responses of EVI to LAI among seasons and ecosystems ($F = 3.61$; $p < 0.0001$). Differences were found in almost every lag considered. However, all three ecosystem types exhibited the highest positive correlation at lag 0; meaning correlation between variables is highest within each season. Also, all three ecosystems showed the highest negative correlation at lags 2 and − 2, meaning EVI was also negatively correlated with LAI values from two seasons before (Figure 7).

DISCUSSION

Total leaf area is one of the determinants of energy and water vapor fluxes between vegetation and atmosphere. Changes in forest structure can alter leaf area and light regimes in forests stands, modifying carbon sequestration and other processes such as decomposition and soil evaporation. Understanding how leaf area index (LAI) dynamics are modified under different land-use types is crucial for understanding energy, carbon and water fluxes between the land surface and the atmosphere (De Kauwe and others 2011; Rautiainen and others 2011). In this study, LAI changed seasonally and among forest ecosystems from around 6 to 9 in native forests and from 3.5 to 6 in pine plantations. Contrary to expectations, both preserved and degraded native forests exhibited similar LAI values, whereas the pine plantations exhibited a consistent lower LAI throughout the year. In native forests, LAI decreased during the cold season when incident radiation is lower and several species drop their leaves. Despite this decline in LAI, the fraction of absorbed radiation (fPAR) remained high during the whole year (higher than 95% of
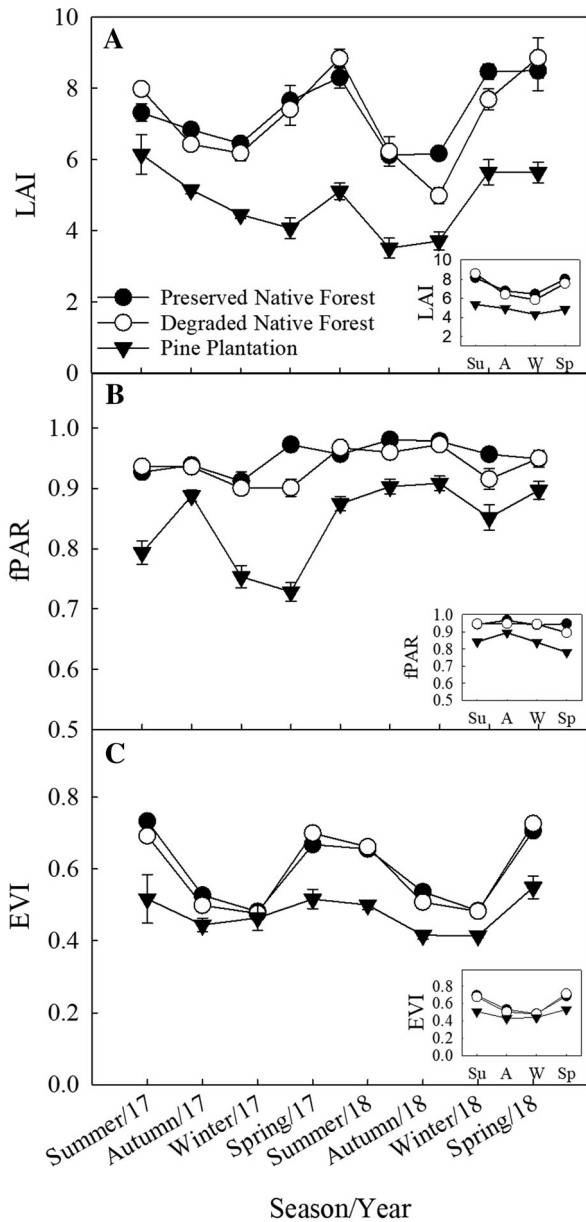
Figure 3. Seasonal mean ± standard error of **A** field leaf area index (LAI), **B** fraction of photosynthetically active radiation absorbed by the vegetation (fPAR) and **C** MODIS enhanced vegetation index (EVI) in three ecosystem types. Insets correspond to the seasonal dynamics of LAI, fPAR and EVI predicted values by the selected models.

Figure 4. Seasonal mean ± standard error of enhanced vegetation index (EVI) normalized by field leaf area index (LAI), a surrogate of light use efficiency for each ecosystem type. Inset corresponds to the seasonal dynamics of EVI LAI^{-1} predicted values by the selected model.

incident solar radiation) suggesting that leaf area is sufficient to capture almost all the incoming solar radiation. Similar patterns of LAI dynamics were found in Amazonian forests, where maximum LAI was observed during the dry season when incident radiation is highest (Myneni and others 2007; Doughty and Goulden 2008).
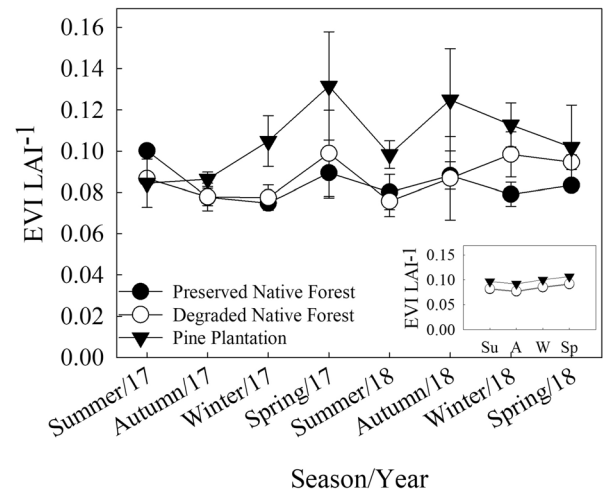
Degraded native forests exhibited a more pronounced seasonal cycle, with higher fPAR variability than in preserved native forests. A high heterogeneity in light regimes inside the canopy implies a combination of high and low fPAR areas. In areas where fPAR is low, air and soil temperatures are high and soil evapotranspiration and respiration increases (Tan and others 2012; Hardwick and others 2015). Degraded native forests exhibited the highest understory vegetation cover, followed by pine plantations and finally by preserved native forests. The higher understory cover in modified forests ecosystems compared to preserved forests indicates a higher amount of light reaching the understory. Furthermore, LAI values were negatively linearly related to changes in understory cover in degraded native forests, while no relation was found for preserved native forests or pine plantations. Lower LAI and fPAR values in the degraded native forests are probably being compensated by the photosynthetic activity of high understory cover and not by the canopy trees leaf chlorophyll dynamics as it was previously suggested by Cristiano and others (2014) for the same subtropical forests and tree plantations. In tree plantations, the understory vegetation is affected by the stand age (Onaindia and Mitxelena 2009; Ritter and others 2018), the frequency and intensity of thinning, the silvicultural practices, such as the control of weeds and pests, and the proximity to a native forest that could act as a seed bank source (Vespa and others 2014). In pine planta-
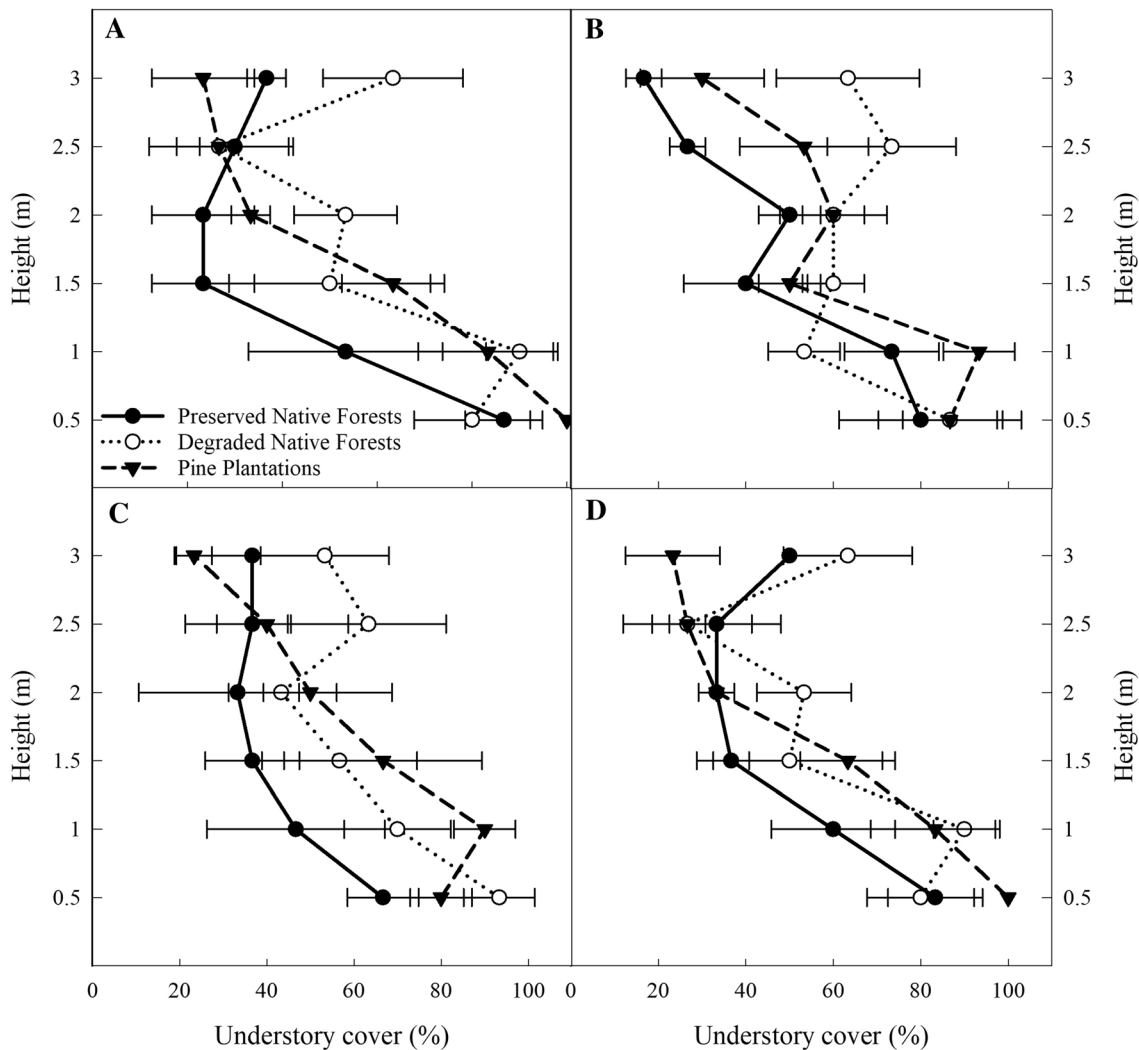
Figure 5. Seasonal mean ± standard error of percentage of understory cover at each height interval across seasons: **A** summer, **B** autumn, **C** winter, **D** spring.

tions, enhanced understory cover was not related to a decrease in LAI, as observed in degraded native forests. In these ecosystems, enhanced understory cover is strongly influenced by the higher incoming solar radiation due to the low tree density which was a consequence of management practices (Trentini and others 2017).

The humid subtropical forests maintain high photosynthetic activity during the whole year because of the high proportion of evergreen trees. Evergreen trees may maintain relatively high net carbon assimilation rates even during the cold periods because respiratory losses decline more than gross primary productivity due to the decline in air temperatures (Zhang and others 2013; Di Francescantonio and others 2018). This pattern was observed in East Asian subtropical evergreen forests in China (Zhang and others 2016) as well as in

humid subtropical forests in Argentina (Cristiano and others 2014). Also, both preserved and degraded native forests have abundant lianas, bamboos and palms that can be locally dominant. Moreover, differences in leaf characteristics of these life-forms may affect canopy reflectance and thus EVI values (Gatti and others 2011; Montti and others 2014; Campanello and others 2016). In this study, the EVI changed seasonally in the native forests from 0.4 to 0.76 which represents 36% of the potential variations in the 0–1 range. These EVI values are consistent with the values found for different moist tropical forests of South America, ranging from 0.4 to 0.65 (Xiao and others 2006; Doughty and Goulden 2008; Blundo and others 2018). The photosynthetic capacity of degraded forests exhibited a tendency to decrease when compared to preserved native forests, especially
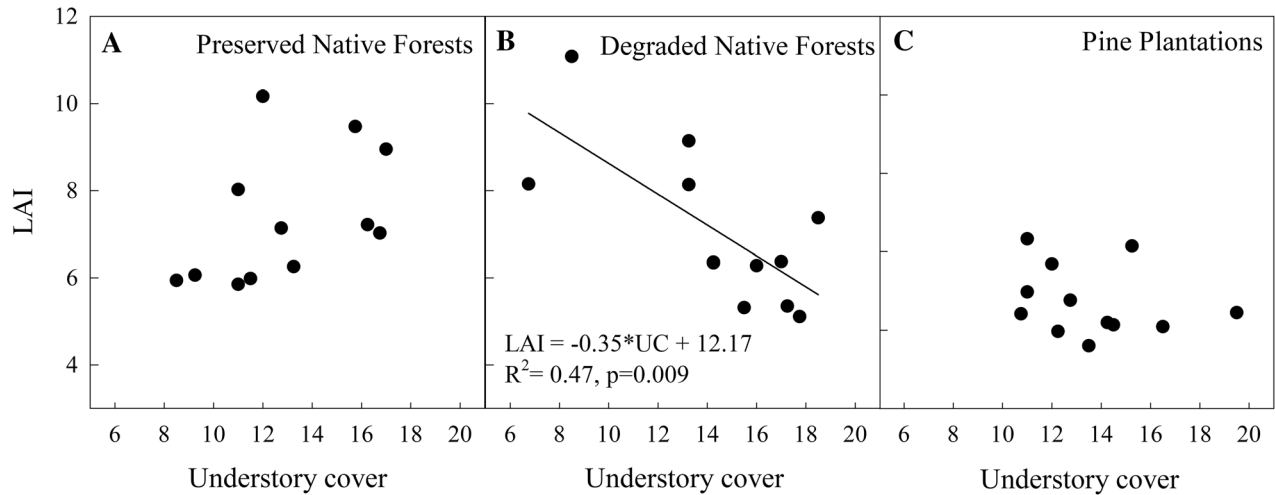
Figure 6. Linear relationships between Leaf Area Index (LAI) field values and Understory cover integral (UC) for each ecosystem type. Linear regression equation, R^2 and p values are indicated when significant relationships were found.
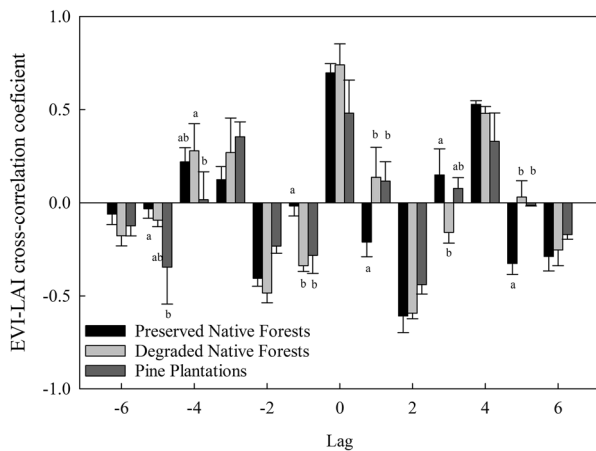

Figure 7. Cross-correlation coefficients between EVI and Field LAI at different lags for each ecosystem type. At each lag, significant differences among ecosystems were indicated with different letters.

during the cold season, while showing no differences during the spring–summer seasons. Cristiano and others (2014) suggested that the photosynthetic activity of this ecosystem during winter could be compensated by an increase in the photosynthetic activity of evergreen trees. Consistent with this hypothesis, degraded native forests had approximately a 10% less evergreen species than preserved native forests, which can explain the decrease in EVI during the cold season.

Contrary to what was expected, the timber extraction resulted in a decrease in the aboveground biomass of trees and basal area of the forest stands (a difference of 60 tn/ha and 3.58 m^2 m^{-2}, respectively, between preserve and degraded native

forests), but it did not have a large impact on EVI, the surrogate of canopy photosynthesis (Xiao and others 2006). Logged forests may exhibit an enhanced primary productivity as a result of increased canopy photosynthesis or by an increase in carbon use efficiency (Riutta and others 2018). The EVI relativized by LAI, an estimate of growth efficiency (productivity per total stand level leaf area (Waring and others 2016)) tended to be higher in degraded than preserved native forests. As it was expected for pine plantations, growth efficiency was substantially higher during the whole year, indicating higher light use efficiency, consistent with selection of high yield species used for the forestry industry. This greater efficiency is partially due to the intrinsic characteristics of the species and its interaction with the environment and, also, because of the silvicultural practices that favors tree growth, such as the control of weed which can reduce competition effects. Lastly, seasonal dynamics among the three types of ecosystems were similar and exhibited an increase during the spring when new leaves are produced (Di Francescantonio and others 2018). Enhancement of carbon uptake has been related to changes in leaf ages in Amazonian forests (Doughty and Goulden 2008), consistent with the phenological pattern observed in this current study.

Vegetation index dynamics (EVI) and its biotic or abiotic determinants have been poorly studied in the subtropical South American forests, and no relations between EVI and climatic or biotic variables were found (Cristiano and others 2014; Fernandes Santana and others 2016; Blundo and others 2018). In this study, EVI temporal variations

were able to reflect the seasonal pattern of canopy activity and exhibited a high correlation coefficient with field LAI measurements, both with the same and previous seasons. Although no differences were found across ecosystems, correlation between EVI and field LAI tended to be higher in native forests than in pine plantations. The same pattern was found at lags 2 and − 2, with native forests exhibiting a higher negative correlation than pine plantations (lag 2 indicates a 6-month period). Native forests appear to be determined by LAI dynamics more than pine plantations. Similar to observations in Amazonian forests (Doughty and Goulden 2008; Galvão and others 2011), changes in EVI dynamics are more related to changes in canopy photosynthetic activity caused by changes in leaf age rather than changes in LAI.

CONCLUSIONS

An important finding of this study is that, after 15 years of recovery from selective timber extraction of canopy trees, stand level photosynthetic activity (EVI) was recovered and thus forest carbon fluxes would not be substantially impacted. Even though selective timber extraction resulted in a decrease in stand basal area, EVI values were as high as those from preserved forests. This homeostatic response of forests to timber extraction is a result of an increase in the abundance of the understory vegetation in the partially degraded forests. We cannot predict what the maximum level of biomass removal and the length of recovery would be necessary before ecosystem carbon fluxes restore the amount of carbon sequestration. When well-preserved or mild harvested forests are replaced by fast-growth plantations such as pines, stand level photosynthetic capacity substantially decreases compared to native forest; however, growth efficiency as depicted by the EVI-LAI ratio is enhanced, reaching maximum values in this ecosystem type.

Compliance with Ethical Standards

Conflict of interest The authors declare they have no conflict of interest.

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