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Lost forever? Ecosystem functional changes occurring after agricultural abandonment and forest recovery in the semiarid Chaco forests

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Abstract.

Semiarid forests are worldwide threatened by land use changes, particularly agriculture. However, in some cases, due to particular economic or social processes, agriculture ends and forests may or may not recover to their original state. Using different databases and satellite images integrated into a geographical information system, we located in the central region of the semiarid Chaco forests of Argentina adjacent land use patches of secondary forest (SF), remnant forest (RF) and crops (CP). Using a chronosequence approach, we evaluated changes in the fraction of the photosynthetic active radiation absorbed by the vegetation (FAPAR) between SF and RF and CP, using the enhanced vegetation index (EVI). We evaluated both intra and inter-annual changes in EVI mean (EVI_{mean}), EVI maximum (EVI_{max}), EVI minimum (EVI_{min}), and EVI relative range (EVI_r) as descriptors of FAPAR dynamics and analyzed their changes through time (2000 to 2010) and their relation to rainfall. Secondary forests showed higher seasonality and higher EVI_{mean} values than RF, but differences disappeared as time since agricultural abandonment increased, suggesting that SF

recover their functioning (when compared to RF) after 10 to 15 years. Our results suggest that Chaco's SF have intermediate seasonal patterns in-between RF and CP, as expected by successional theory, and that FAPAR interception by RF appears to be dependent on previous year's precipitation. We found that, although all land uses showed similar precipitation use efficiency (PUE), SF and cropland's productivity were less stable across the years and showed faster increases or decreases compared to RF, depending on precipitation (higher precipitation marginal response-PMR). Our results suggest that at least some aspects of ecosystem functioning can be restored after agricultural abandonment. Future research that combines floristic and structural changes is necessary to fully understand secondary forests regrowth process after agricultural abandonment in the Chaco region.

Keywords: remnant forest, secondary forest, crops, fraction of absorbed photosynthetically active radiation, remote sensing

INTRODUCTION

Semi-arid forests are threatened worldwide (Nichols et al., 2017; Rotenberg, 2011). Agricultural expansion is a major threat in several parts of the world, particularly in South America where the xerophytic forests of the Cerrado and the Chaco experienced one of the world's highest rates of forest loss from 0.5% in Argentina to 4% in Paraguay during 2010 (Baumann et al., 2017; Hansen et al., 2013; Vallejos et al., 2015). Semi-arid forests have an important role as carbon sinks and their conversion to agriculture releases important amounts of CO₂ to the atmosphere (Gasparri et al., 2008; Gasparri & Baldi, 2013), reduces C inputs (Volante et al., 2012) and C stocks (Villarino et al., 2016). In the tropics, secondary forests have been suggested to sequester large amounts of carbon, but limited studies have been performed in semi-arid forests (Bongers et al., 2015) that measure it. Both protecting and restoring semi-arid forests are currently major topics in forest research (Young, 2000).

Forest protection campaigns are often based on the idea of “once cut, forests are lost forever” (<https://www.worldwildlife.org/threats/deforestation>). This statement is effective to persuade the general public on the importance and value of forest conservation but, on the other hand, it discourages restoration practices, either passive or active (Meli et al., 2017; Stanturf et al., 2014). Agricultural abandonment initiates a natural regeneration process of a forest, namely, secondary forest (**SF**). Forest recovery is a complex process that involves structural and functional changes that are compared to a reference situation, such as remnant forests (**RF**) (Chokkalingam & De Jong, 2001). Several authors have pointed out the lack of studies about forest recovery in semi-arid regions and the associated changes in ecosystem services provision (Hayes & Stevens, 2001; Novara et al., 2017). Understanding forest recovery after agricultural abandonment is critical to guide management practices and political decisions aimed at improving forest restoration (Aide et al., 2000; Finegan, 1992; Lugo, 1992).

It has been shown that after a disturbance or repeated disturbances such as agricultural practices, forest ecosystems may or may not recover to their original situation during secondary succession. Walker et al., (2010) and Frazier et al., (2013) suggested that forest recovery after agricultural abandonment depends on three main factors: 1) the type of original ecosystem replaced and the agricultural practices carried out, 2) the length of the secondary succession and 3) the intensity and extent of the disturbance. The success of forest recovery after agricultural abandonment varies among biomes and depends on the structural and functional attributes observed. For example, Jakovac et al., (2015) reported that forests from Central Amazonia did not recover their plant species diversity after intensive cultivation, while Goulden (2011) showed that boreal forests did recover their primary production after fire disturbances, and that such primary production was higher during early years of secondary succession, compared to remnant forest. Forests' recovery after disturbances is related to their resilience, defined as "the capacity of an ecosystem to absorb disturbance and reorganize while undergoing change, so as to retain essentially the same function, structure and identity" (Walker et al., 2004). Recent studies have assessed the resilience of humid tropical forest, but dry forests have been scarcely studied (Jakovac et al., 2015).

The fraction of photosynthetic active radiation absorbed by the vegetation (FAPAR) is a key attribute of ecosystem functioning, since it is tightly related to primary production (Paruelo, 2008). The Monteith's model (1972) states that productivity is the product between the photosynthetic active radiation absorbed by green vegetation (FAPAR) and the radiation use efficiency (RUE). Both FAPAR and primary production are used to assess ecosystem responses to environmental and land use changes (Frazier et al., 2013; Guerschman et al., 2003; Potts et al., 2006; Vassallo et al., 2013). Gross primary production is an important flux of the carbon cycle as it represents the total energy captured by the ecosystem through carbon assimilation during photosynthesis, while FAPAR represents the first step in light interception and therefore constrains primary production (Field et al., 1995). Several vegetation indexes such as the Normalized Difference Vegetation Index (NDVI) or the Enhanced Vegetation Index (EVI) calculated with data

from remote sensors have been used as proxies to assess temporal and spatial patterns of FAPAR and primary production (Baeza et al., 2010; Paruelo & Lauenroth, 1995; Tucker et al., 1985; Volante et al. 2012). Also, Di Bella et al., (2004) showed that vegetation indexes and green tissues' FAPAR are positively and strongly correlated.

Several traits derived from the seasonal dynamics of EVI and NDVI are used to capture and resume the amount and seasonality of light interception, such as: annual integral, relative range and maximum or minimum values of the vegetation index during the year (Alcaraz, Paruelo & Cabello, 2006; Paruelo et al., 2001). Studies using vegetation indexes have shown strong changes in FAPAR when natural ecosystems are replaced by agricultural systems, but less have studied their recovery during secondary succession (Pettorelli et al., 2005). Observations of NDVI or EVI along chronosequences can be used to study FAPAR dynamics across SF of different ages and compare them to adjacent RF (Quesada et al., 2009; Wagner et al, 2011). At landscape level, comparing NDVI or EVI time series in adjacent land uses (i.e. remnant forests, crops and secondary forests) permit to quantify changes in light interception in different land uses.

Precipitation is a major driver of FAPAR and primary production in semiarid ecosystems (Cleverly et al., 2013). In xeric ecosystems annual precipitation is usually positively correlated to primary productivity, though human activities may alter such relationship (Le Houerou, 1984; Noy-Meir, 1973). A global analysis comparing natural forests and crops showed differences in the relation between productivity and water availability (Baldi et al., 2016). The ratio between NDVI (used as a surrogate of primary production) and precipitation is a measure of precipitation use efficiency (PUE) (Verón et al., 2006). Both PUE and the precipitation marginal response (PMR), which describes the sensitivity of primary production to inter-annual changes in precipitation, are used to assess ecosystem changes after disturbances and degradation processes (Verón & Paruelo, 2010). Primary Production is not only influenced by current year precipitation but also by past events, reflecting legacies or ecosystem “memory” (Wiegand et al., 2004). Such memory can be altered by land use changes and also during secondary succession (Paruelo et al., 2005). Assessing

variations in the relationship between precipitation and primary production or FAPAR, may signal potential changes in the resilience of both natural and altered ecosystems.

In this article we analyzed changes in FAPAR (estimated using EVI) of secondary forests (SF) resulting from agricultural abandonment with different successional ages in the semiarid Chaco Region. Using a chronosequence approach, we tested EVI differences between SF, remnant forest (RF) and surrounding croplands (CP), in three different sub-regions of the Semiarid Chaco: the North Juramento (NJ), the Juramento Interfluve (IJ) and the South Juramento (SJ). We hypothesized that SF have different seasonal patterns and higher light interception than RF due to the distinct species and life forms present in early stages of the secondary succession. However, we expect that these differences disappear in late successional stages due to the convergence of structural characteristics of SF and RF. In contrast, CP is expected to have the lowest FAPAR and the highest seasonality, due to the predominance of annual vegetation (growing mostly during summer). In addition, we expect annual FAPAR variations in both types of forest to be related with previous year's precipitation, while cropland's FAPAR will be more dependent on annual precipitation, due to deeper rooting depth's in forests compared to annual crops that will also result in higher PUE and PMR in RF, intermediate in SF and lower in CP.

MATERIALS AND METHODS

The study Region

The study area was located in the semiarid portion of Argentinean Chaco Region where mean annual precipitation varies from 500 to 1000 millimeters (http://climayagua.inta.gob.ar/estad%C3%ADsticas_de_precipitaciones) and mean annual temperature varies from 19 °C to 24 °C (Bucher, 1982) (Figure 1). The Western Chaco region has a semiarid climate, with the greatest water stress occurring during summer (from December to March) (Bucher, 1982). The typical forest of the region is characterized by semi-deciduous and

drought tolerant species known as "quebrachal" (Digilio & Legname, 1966; Legname, 1982; Morello & Adamoli, 1968; Tortorelli, 1956). The dominant community of the semiarid Chaco forests consists of a woody upper stratum, dominated by *Schinopsis lorentzii*, *Aspidosperma quebracho-blanco* (with other important trees such as: *Prosopis Kuntzei*, *Ziziphus mistol*, *Caesalpinia paraguayensi*, *Cercidium praerox*) and a low shrub and herbaceous stratum (Cabrera, 1971). Our study area specifically includes two geomorphologic units: deposits of the Juramento River and Juramento-Dulce Interfluvium (Redaf, 1999) (Figure 1).

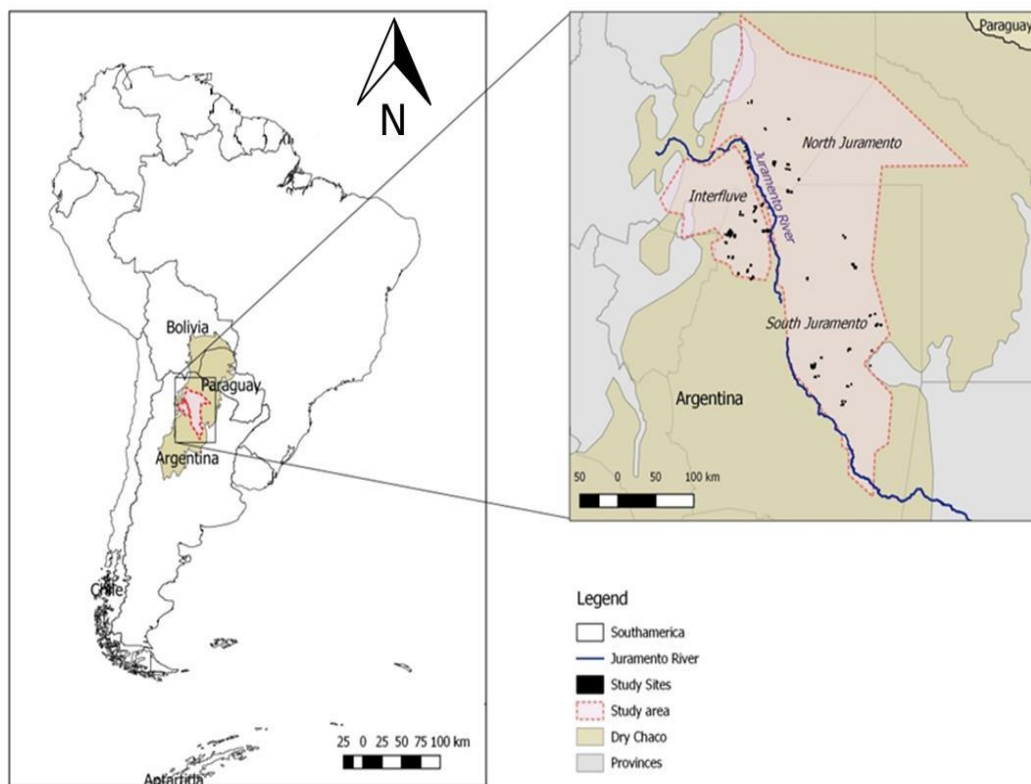


Figure 1. Location of the study sites in the Chaco region of Argentina, showing the three sub-regions studied: the South Juramento River (SJ), the North Juramento River (NJ), and the Juramento-Dulce Interfluvium (IJ). The large red polygon on the right delimits the studied area.

Excluding the Amazon region, nearly 3.6 million km² of natural vegetation were converted to anthropogenic land uses in South America in the last 100 years (Hansen et al. 2013;

Salazar et al., 2015). In the Dry Chaco Region including Paraguay, Bolivia, and Argentina, 158,000 km² ha of native forests were deforested before 2012 (Vallejos et al., 2015). Considering only the Argentinean portion of the Dry Chaco, 60,000 km² were deforested between 1977 and 2010, and were replaced by annual crops (mainly soybean) and perennial pastures (Paruelo et al., 2011, Piquer-Rodríguez et al., 2015). The expansion of soybean and pastures is driven mainly by the biofuels and food demands, as well as favorable prices and new farming technics (Gasparri et al., 2013; Goldfarb & Zoomers, 2013). Very few areas of the Argentinian portion of semiarid Chaco region have experienced a natural regrowth of previously deforested areas, because agricultural expansion was the major trend in the region from 1977 to 2007 (Volante & Paruelo, 2015). Though uncommon however, some patches of land have indeed been abandoned after cultivation, usually due to specific circumstances associated with social conflicts, such as land tenure or use rights (Volante & Paruelo, 2015; Seghezzo et al., 2017) and have allowed forest to regrow.

Data consolidation and study site selection

Using different databases and satellite images integrated into a geographical information system, we searched in the semiarid Chaco region for adjacent land use patches of secondary forest (SF), crops (CP) and remnant forest (RF). Remnant forests were our reference sites, corresponding to those sites without forest clearings before 2011. Cropped areas included old agricultural patches (up to 37 years under cropping) to relatively recently converted areas (3 years of continuous agriculture). Secondary forest corresponded to areas totally deforested for agricultural production then abandoned and currently undergoing natural forest regrowth. To select these areas, we used a land use change database provided by INTA (Instituto Nacional de Tecnología Agropecuaria) including data from 1976 to 2009 and reported by Volante et al., (2015) and Vallejos et al., (2015). This database provides information on deforestation year, area deforested and crop rotations (pasture or crop species) and includes most of the Argentinean portion of the semiarid Chaco. To complement the database we created an image time-series using Landsat Thematic Mapper (TM)

scenes from 1984 to 2011 (path-rows 229-76, 229-77, 229-78, 229-79, 230-76, 230-77, 230-78, 230-79) . LANDSAT images were obtained from CONAE (Comisión Nacional de Actividades Espaciales, Argentina) and GLOVIS (<http://glovis.usgs.gov/>). We used a soil database from INTA (INTA, 2009) to determine soil types present in each vegetation patch.

We identified 33 sites with adjacent patches of RF, CP and SF (a total of 99 patches) distributed across the region (Figure 1 and Table 1). The patches area was in the range of 25 to 500 ha and all adjacent land uses had the same soil type (INTA, 2009). Therefore, our experimental design included each site as a block with one plot of each land use (RF, CP and SF). Using the INTA database and temporal series of LANDSAT and MODIS images we estimated the time since agricultural abandonment in each SF patch, which varied between 2 and 26 years (Table 1). To verify the age of the secondary forest we used historical LANDSAT images that were visually interpreted to determine the moment in which agricultural paddocks had been abandoned, and we further checked with the same image database for forest secondary development so as to avoid sites that could have set back to agriculture. In addition, we used EVI MODIS data for the period 2000 to 2011 to check for comparable secondary successional patterns. We divided the study region in three sub-regions as they show different average EVI values ($p=0.054$), which were slightly higher in the North Juramento (NJ) compared to Interfluve (IJ) and South Juramento (SJ) (Figure 1).

Sub-regions	Time after agricultural abandonment and forest recovery (years)			Total sites
	<10 years	10-20 years	20-30 years	
NJ	2	2	1	5
IJ	3	10	3	16
SJ	4	7	1	12
Total	9	19	5	33

Table 1. Number of sites studied in each sub-region for different classes of time after agricultural abandonment as determined by photointerpretation.

Estimates of vegetation light interception using remote sensors

For the 99 patches selected, we retrieved composited values of the Enhanced Vegetation Index (EVI) from MODIS to use as a proxy of FAPAR. We used time-series of h12v11 scenes from MODIS Terra satellite (Mod13q1 product), filtered and interpolated including data from 2000 to 2011. This product is distributed by Land Processes Distributed Active Archive Center (LPDAAC), has a temporal resolution of 16 days and a pixel size of approximately $250\text{ m} \times 250\text{ m}$. Each of these image products are maximum value composites (MVC); in other words, mosaics formed by the highest daily values of each pixel during the 16-day period. EVI images were filtered in order to discard clouds, shades, aerosols in the atmosphere, using the QA band (with quality information) of product MOD13Q1. Poor quality pixels were scarce in the time series, but were replaced with the average value of EVI of the immediately previous and later date, when present. For the same period (2000-2011), we obtained time-series of mean annual precipitation from a monthly data product of the TRMM satellite (Tropical Rainfall Measuring Mission) with a spatial resolution of $0.25^\circ \times 0.25^\circ$.

We compared seasonal and annual dynamics of EVI in adjacent land uses (SF, CP and RF), in conjunction with precipitation patterns. In the semiarid region, rainfall occurs from mid spring to late summer and determines the growing season of natural vegetation (from October to March) (Morello et al., 2012; Tiedeman et al., 2012; Bucher 1982). Therefore, soybean and maize are sown from late spring to early summer (Houspanossian et al., 2016). EVI MODIS time series were integrated annually, from August to July of the next year, rather than using the calendar year to more effectively capture the growing season of the study area. For CP and SF patches, we only included EVI values retrieved during years under cropping or during secondary succession. To better characterize the seasonal dynamics of the different land uses we estimated the mean EVI (EVI_{mean}), the maximum EVI (EVI_{max}), the minimum EVI (EVI_{min}) and the relative range (EVI_{rr}), following Paruelo et al. (2008). We related the mean annual EVI with values of mean annual precipitation for

each site, and estimated correlations and lag-correlations (one and two years) between both variables. We calculated the precipitation use efficiency (PUE) as the ratio of annual EVI_{mean} and annual precipitation, and the precipitation marginal response (PMR) as the slope of the linear regression between EVI_{mean} and annual precipitation (Verón et al., 2006).

Statistical Analyses

To compare the overall effects of land uses on EVI dynamics we used a general mixed effects model, considering land use (SF, RF and CP) and sub-region (IJ, SJ and NJ) as fixed effects and blocks and years as random effects. In addition, to assess monthly differences between land uses we performed an analysis of variance (ANOVA) for each month and attribute (mean EVI_{mean} , EVI_{max} , EVI_{min} , EVU_{rr}) within each sub-region (NJ, IJ and SJ). The factors in this analysis were site and land use, while year was used as a covariate. ANOVA comparisons between land uses were used for each year of the EVI time-series from 2000 to 2011. As with MODIS EVI, we observed annual growing season considering from August of one year to July of the following one. We also calculated the inter-annual variation coefficient for the EVI series from 2000 to 2011, for each land use type and sub-region. Pearson's correlations analyses were performed to evaluate the relationship between precipitation and EVI_{mean} , both at annual and monthly time steps, including possibly-lagged relationships. Finally, to assess differences between land uses in PUE and PMR we performed an analysis of variance (ANOVA) for all sub-regions. We used ANOVA with Tukey comparisons at $p < 0.05$ to test for significant differences between land uses for each month (figures 4 and 5), and for the complete study period (figures 3 and 6), and denoted no significant differences (ns). All statistical analyses were conducted using R software (www.R-project.org/) and INFostat package (www.infostat.com.ar).

RESULTS

Secondary forests (SF) showed higher seasonality and higher EVI_{mean} values than remnant forest (RF), but differences disappeared approximately ten years after agricultural abandonment (Figure 2 and 3). Croplands (CP) tended to have the lowest EVI_{mean} values compared to both forests types. EVI_{mean} differences between land use types were small, but significant in all sub-regions (Figure 3). Secondary forests presented higher EVI_{max} and lower EVI_{min} values and therefore, a higher relative range (EVI_{rr}) compared to RF, while CP showed the highest EVI_{max} and the lowest EVI_{min} values and thus, the highest EVI_{rr} compared to both forest ecosystems (Figure 3). Overall, SF with more than ten to fifteen years of abandonment reached similar EVI_{mean} , EVI_{max} , EVI_{min} and EVI_{rr} values as compared to RF.

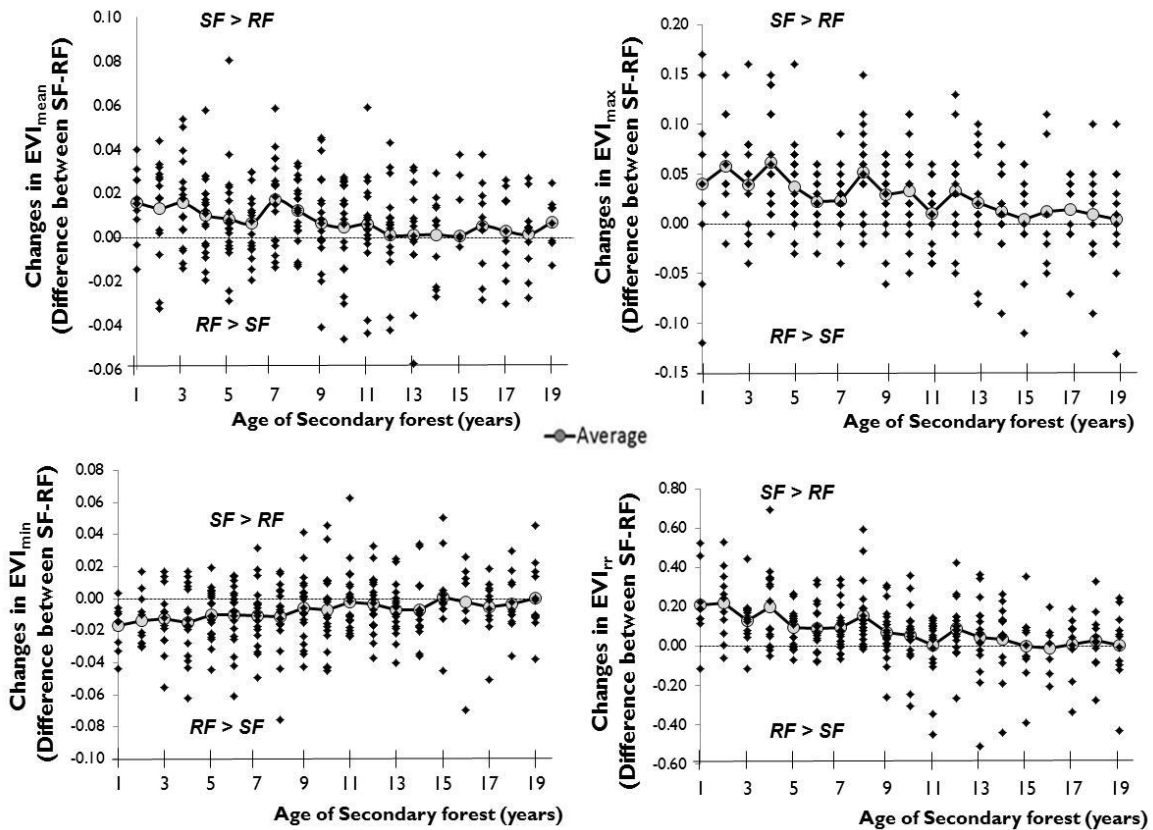


Figure 2

Figure 2. Changes in EVI_{mean} , EVI_{max} , EVI_{min} and EVI_{rr} between paired sites of secondary forest

(SF) and remnant forest (RF) in relation to the age of the secondary forest (e.g. time after agricultural abandonment).

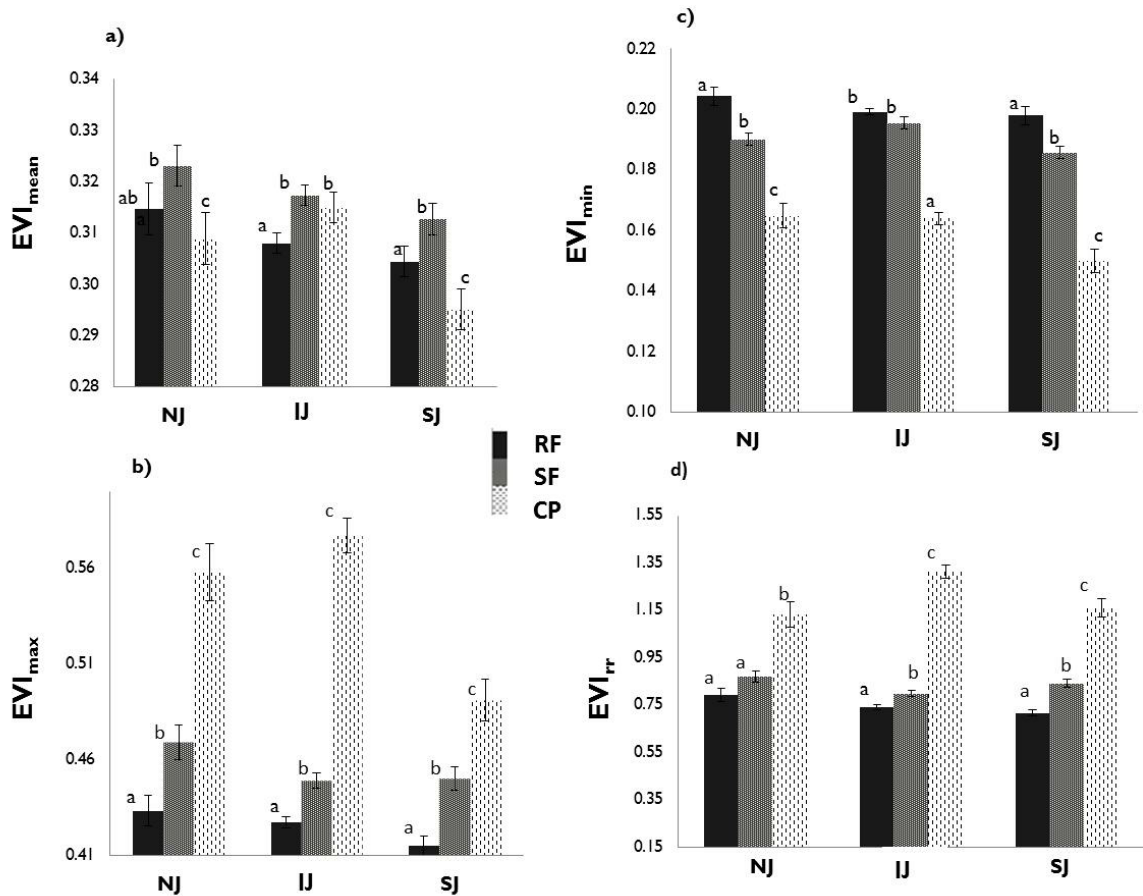


Figure 3. Differences in mean annual functional attributes of light interception dynamics (described by EVI_{mean} , EVI_{min} , EVI_{max} , EVI_{r}) of remnant forest (RF), secondary forests (SF) and croplands (CP), in the three sub-regions studied: NJ, IJ and SJ. Different letters indicate significant differences between land use classes in Tukey post-hoc analyses ($p < 0.05$, $n=5$ for NJ, $n=16$ for IJ and $n=12$ for SJ). Vertical thin bars show standard errors.

Intra-annual EVI_{mean} variations differed between land uses, though all of them showed a similar seasonal pattern following rain distribution. Overall, SF tended to maintain higher EVI_{mean} values compared to RF during the peak of the growing season, while CP presented several distinct patterns

from both forest types (see temporal patterns in Figure 4). While both forest types had their EVI_{max} occurring around December, crops had their EVI_{max} occurring between February and March, depending on the sub-region. In addition, CP showed a shorter and delayed growing season compared to SF and RF, though the date of the EVI_{min} was similar (June to August) for all land uses (Figure 4). Monthly EVI values of CP were significantly lower than that of forests during the start of the rainy season (October-November and December, Figure 4).

Sub-region	Land use	Precipitation	One year lag	Two year lag
NJ	RF	0.13 (0.37)	0.25 (0.08)	0.20 (0.20)
	SF	0.17 (0.22)	0.22 (0.14)	0.11 (0.48)
	CP	0.42 (0.01)	-0.01 (0.94)	0.11 (0.54)
IJ	RF	0.02 (0.84)	0.19 (0.02)	-0.0025 (0.98)
	SF	-0.01 (0.90)	0.07 (0.41)	-0.06 (0.48)
	CP	0.35 (<0.001)	0.11 (0.19)	-0.04 (0.67)
SJ	RF	0.18 (0.05)	0.20 (0.04)	0.32 (<0.001)
	SF	0.31 (<0.001)	0.21 (0.04)	0.18 (0.09)
	CP	0.42 (<0.001)	0.21 (0.04)	-0.07 (0.50)

Table 2. Pearson correlation coefficients between EVI_{mean} and precipitation during the same year, the previous year and two years before (p values are shown between brackets). Values in bold denote statistically significant correlation coefficients. RF is remnant forest, SF is secondary forest and CP is croplands.

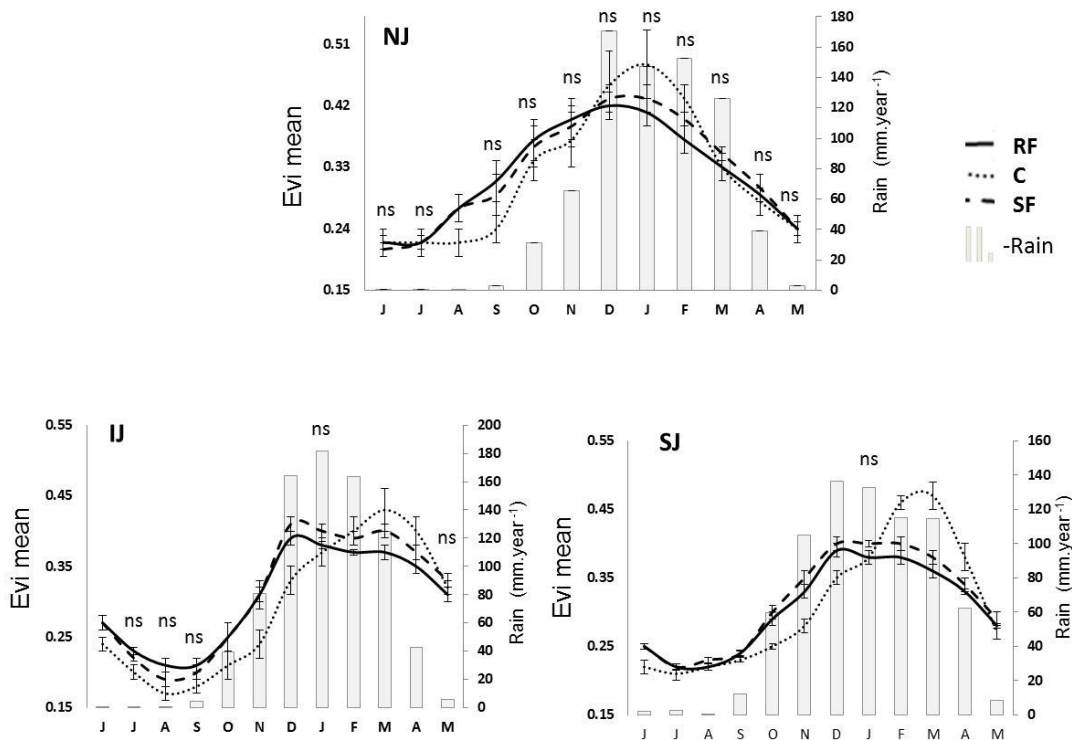


Figure 4

Figure 4. Monthly variations in precipitation (grey bars) and seasonal changes in monthly EVI_{mean} values of crops (CP), remnant forest (RF) and secondary forests (SF) in North Juramento River (NJ), Juramento-Dulce Interfluvium (IJ) and South Juramento River (SJ). Data is average for the 10 years studied (2000 to 2010). Non-significant differences between land use classes for each month, estimated in Tuckey post-hoc analyses ($p < 0.05$, $n=5$ for NJ, $n=16$ for IJ and $n=12$ for SJ) are indicated with “ns”. Vertical thin bars show standard errors.

Inter-annual changes in EVI_{mean} for all land uses followed annual precipitation anomalies, but correlations were stronger for CP than for both forest types (Figure 5). Inter-annual EVI_{mean} changes were smaller in SF and RF compared to CP in the three sub-regions studied, particularly in drier-than-average and wetter-than-average years, when differences among land uses were usually statistically significant (Figure 5). Therefore, EVI_{mean} values showed a closer association with

annual precipitation records for crops than for both forest types, while annual EVI_{mean} changes in RF were significantly associated with rainfall occurrence in the previous year in all sub-regions (Table 2). Associations between EVI_{mean} and precipitation were stronger in the SJ sub-region (the driest), where all land uses showed correlations with both current and one or two previous year precipitations (except for CP with two previous year precipitation). Also, CP showed a greater inter-annual EVI_{mean} coefficient of variation than both type of forests (CV 0.11, 0.09 and 0.09 for CP, SF and RF, respectively, average of the three sub-regions). The PUE was similar for all land uses, but crops had a higher PMR, in accordance with their higher responses to annual rainfall. Finally, we observed a common but unexpected negative trend over the years in EVI_{mean} values for all land uses and in the three sub-regions studied (Figure 5).

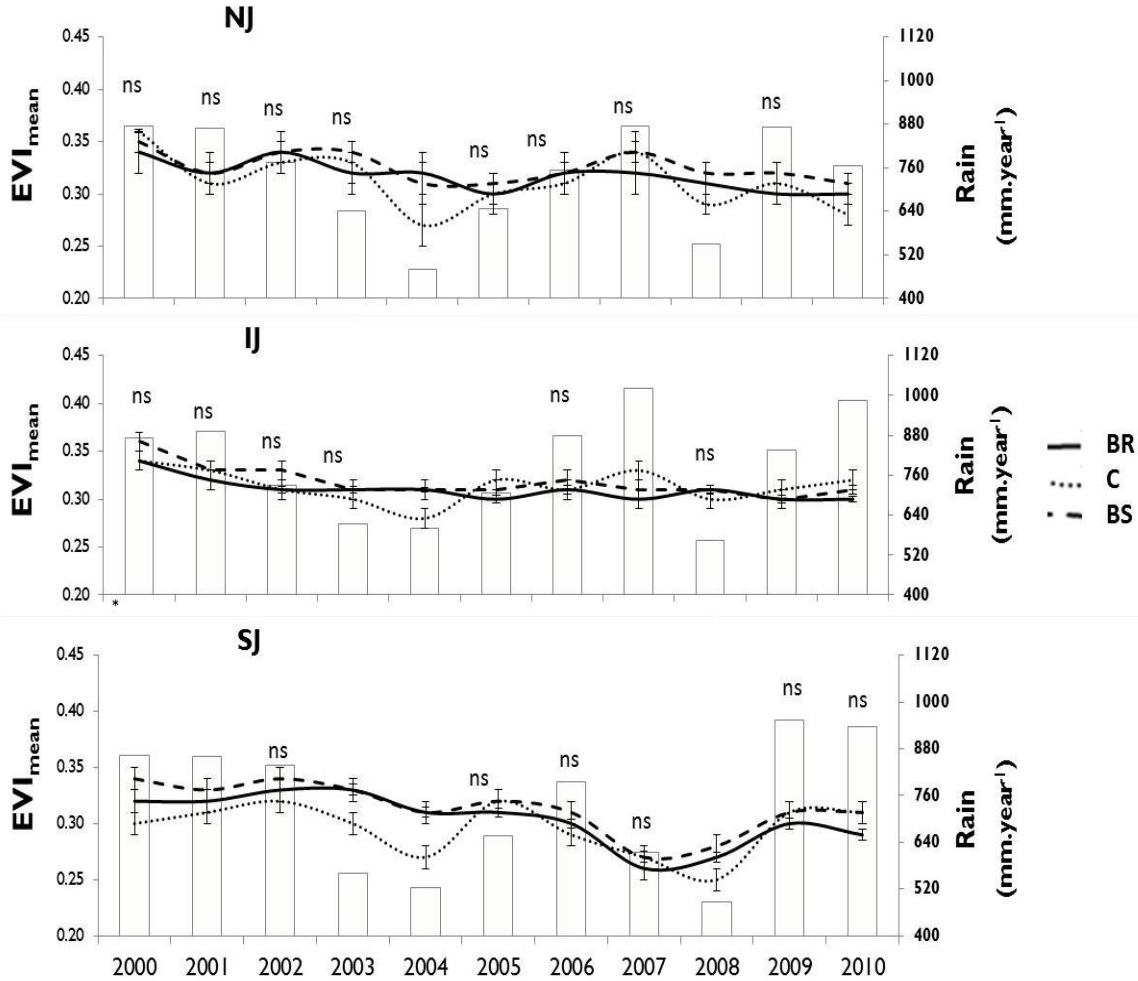


Figure 5. Annual variations in precipitation (grey bars) and in the enhanced vegetation index (EVI) of crops (CP), remnant forest (RF) and secondary forests (SF) for the three sub-regions studied (NJ, IJ and SJ). Each year ranges from August to July of the following year. Non-significant differences between land use classes for each year, estimated in Tuckey post-hoc analysis ($p < 0.05$, $n=5$ for NJ, $n=16$ for IJ and $n=12$ for SJ) are indicated with “ns”. Vertical thin bars show standard errors.

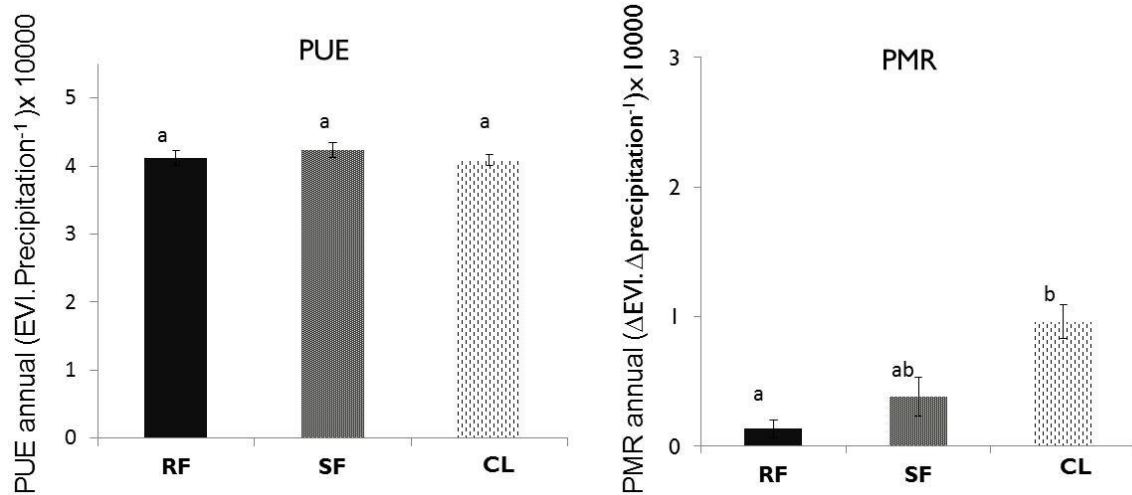


Figure 6. Annual estimates of PUE (Precipitation Use Efficiency) and PMR (Precipitation Marginal Response) for RF, CP and SF. Different letters indicate significant differences between land use classes in Tuckey post-hoc analysis ($p < 0.05$, $n = 5$ for NJ, $n = 16$ for IJ and $n = 12$ for SJ). Vertical thin bars show standard errors.

DISCUSSION

We found that SF had greater photosynthetically active radiation absorption than RF and CP, which is in accordance with other studies performed in boreal regions (Goulden et al., 2011, Stoy et al., 2008). This supports successional theories that suggest that light interception is higher during the initial stages after disturbance than in established mature forests (Odum, 1969) and constitutes novel evidence in the less-studied semiarid forests (Goetz et al., 2012; Iwata et al., 2013). According to the Monteith's model (1972), FAPAR is one component used to estimate gross primary productivity changes. In addition to using FAPAR, other studies use RUE to characterize secondary forests dynamics, the second component of Monteith's model (Quesada et al., 2009).

Garbulsky et al., (2010) found that RUE is around 0.8 to 1.3 g of C.MJ⁻¹ of APAR in semiarid forests and crops, respectively. As EVI is a proxy of FAPAR and crops have greater RUE than forest, higher productivity values are expected in croplands. In that sense, there is evidence that crop productivity is higher than that of forests (10 Mgha⁻¹ y⁻¹ vs. 6 Mgha⁻¹ y⁻¹) when the identity of crop and moisture gradients is considered (Murray et al., 2016). However, we must be careful with estimates of productivity that do not consider root partition and the presence of senescent material (Paruelo, 2008). In SF, RUE is expected to change throughout the succession as a result of the replacement of species with different functional attributes, and this can be estimated using the remote sensor indexes such as PRI (Photochemical Reflectance Index) (Garbulsky et al., 2013; Peñuelas et al., 2011). Additionally, it would be interesting to address structural attributes of forests as well, because during secondary forest development, some over-story trees may not form a completely closed canopy. Furthermore, the presence of grass and shrubs may also contribute to EVI values obtained from a site, rather than just tree canopy (Swanson et al., 2011).

Changes in seasonal patterns of light interception or EVI has been observed worldwide when native forest are replaced by croplands (Baldi et al., 2014; Guerschman et al., 2003; Paruelo et al. 2001; Volante et al., 2012). Our results show that SF of the Chaco has intermediate values between RF and croplands in the attributes describing seasonality. Paruelo et al., (2016) showed that the level of provision of ecosystem services related to carbon gains and water regulation increased as EVI mean increased and seasonality decreased. In that way, successional changes operating in the SF would reflect an increase in the provision of regulation ES as compared to croplands (sensu MEA, 2005). When all parameters were observed together (integral of EVI, intra-annual curve, and EVI extreme values), the time needed to recover a SF to a similar functioning to that of a RF, was approximately ten years of abandonment. In coincidence with our study, other authors also found a rapid increase in productivity during the first 15 years following abandonment in tropical secondary forest, accompanied by quick accumulation of biomass and nutrients in leaves and roots (Guariguata & Ostertag, 2001). Other studies in the semiarid Chaco region quantified the

importance of tree above and belowground biomass, as well as their contribution to local estimates of carbon sequestration and offset of greenhouse gas emissions (Iglesias et al., 2012; Manrique et al., 2011). In Argentina, restoring degraded areas through secondary forest succession is considered a key opportunity for climate change mitigation (SAyDS, 2015). Rotenberg et al., (2011) showed that semiarid forests can play a critical role in the climate system due to their cooling effect at global scale and their substantial carbon sequestration.

The differences in intra-annual variation of light interception and EVI in forests and crops can have ecohydrological implications. As in other works, forests show higher light interception values during part of the growing season from September to March (Zerda & Tiedemann, 2010), while crops have a short and sharp growing season coincident with precipitation events (Clark et al., 2010). Land cover changes in which dry forests are transformed into croplands, affect the seasonal dynamics of water by increasing deep drainage, recharge and reducing evapotranspiration (Calder, 1998; Zhang et al., 2001). In addition, crops water supply decouples from evapotranspiration, whereas this process is coupled in dry forests. Unlike crops, forests have fluctuations in the water table during the year because their roots consume water, thus avoiding its rise to surface (Giménez et al., 2016). On the other hand, forests make recharge low, storing chlorides in the soil profile and preventing them from reaching the surface and salinizing the soil (Amdan et al., 2013; Marchesini et al., 2017). Therefore, SF derived from forest regrowth after agricultural abandonment could probably regulate the water table ascent and avoid soil salinization, in a similar manner as RF.

Light interception anomalies have been associated with precipitation and land use changes that have altered natural vegetation functioning in northern Argentina (Baldi et al., 2008; Paruelo et al., 2004). In our work, light interception by remnant forests, which often present deciduous species that sprout before the beginning of the rainy season, was related to previous year precipitation, suggesting a “carry over” or memory effect in the semiarid Chaco forests (Fabricante et al., 2009). Other studies have also found a linear relationship between crops FAPAR with current year precipitation, in agreement with our findings (Huber et al., 2011). The forest’s memory may be

related with the capacity of trees to use moisture stored at greater depths within the soil that can buffer water deficit and may explain the low correlation of forest EVI_{mean} values with current year precipitation (Camberlin et al., 2007). Crops showed a higher coefficient of variation for EVI values than forests, being strongly linked to precipitation anomalies, whereas forests seem to be more resilient to climatic fluctuations (Volante et al., 2012). Accordingly, crop productivity responded faster to increases or decreases in precipitation, and had higher PMR compared to SF or RF, though PUE of all land uses was similar (Knapp et al., 2008; Lin, 2011; Verón & Paruelo, 2010).

Our study suggests that ecosystem functioning may be restored (with passive restoration) in SF after agricultural abandonment, and ecosystem services provided by RF could potentially recover (Scott & Morgan, 2012). In the Chaco region, SF are usually considered “degraded” or “unproductive”, because dominant life forms are shrubs and there is usually low tree abundance (Adamoli et al., 1990; Cardozo et al., 2011). However, plant species change, soil carbon recovery and other key aspects of ecosystem structure and function have been scarcely studied. Opposite to this perception, our results show that SF has a greater interception of photosynthetically active radiation than RF and CP, in accordance with Sánchez-Azofeifa (2009). Still, we have only explored functional aspects of carbon gains and light interception, but other compositional and structural attributes need to be considered to have a more complete characterization of the successional process. A comprehensive study of SF that considers both ecological and socio-economic aspects would allow the design of more accurate forest recovery strategies with passive or active methods. It would also present the opportunity to restore several ecosystems services provided by forests, such as forage value, energetic use, climate regulation, mellific use, water retention, carbon sequestration, fruits for consumption, medicinal compounds, among others (Benayas et al., 2007; Cáceres et al., 2015). This information will be valuable for reconciling different perceptions among local stakeholders regarding land use planning and decision making in the region (Seghezzo et al., 2011). Finally, there are still unsolved questions regarding landscape structure and resilience (size, shape and distance of abandoned patches) as well as the role of

disturbances that affect successional pathways, all which remain up to this day as research challenges.

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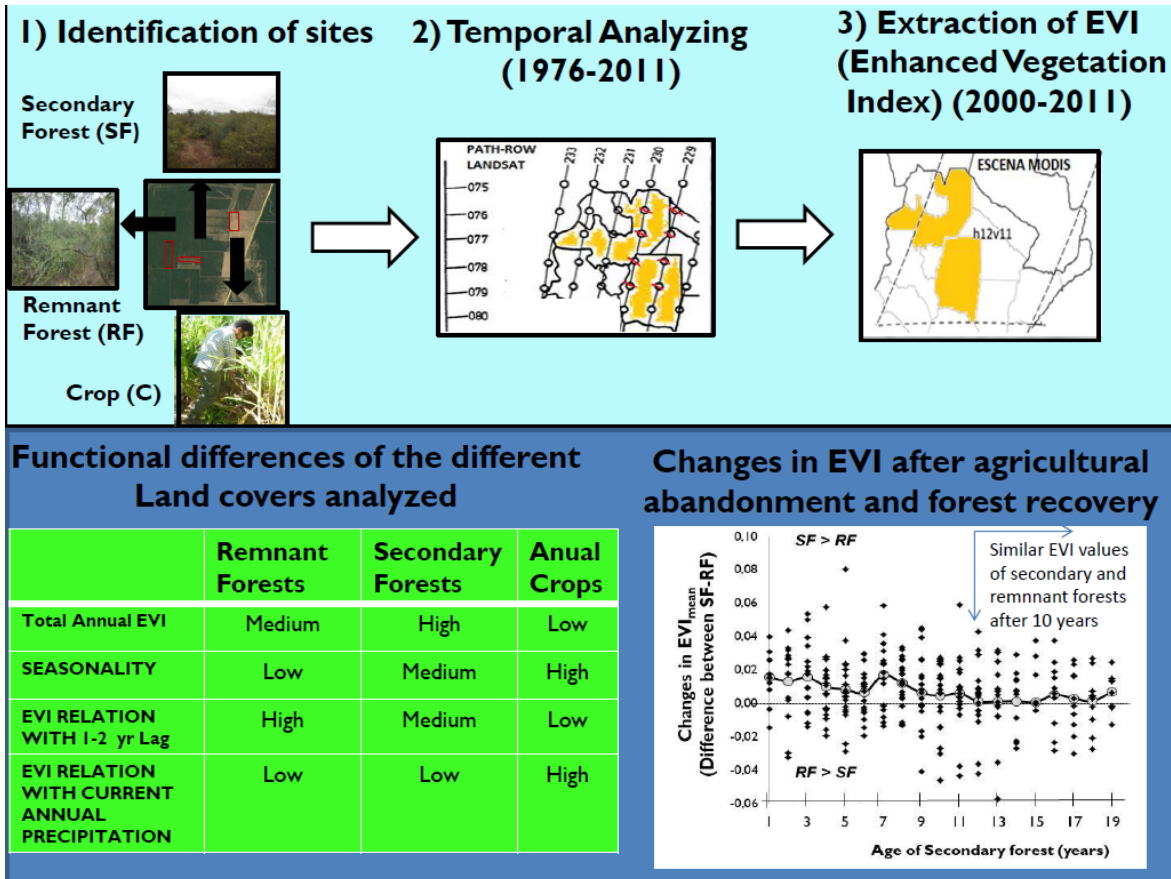
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Graphical Abstract



Highlight

Young secondary forests had higher EVI and greater seasonality than remnant forests

Secondary forests recovered their functioning 15 years after agricultural abandonment

Productivity of remnant forests depended on previous years' precipitation

Secondary forest and cropland's productivities depends on annual precipitation

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