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Argentinian Yungas Forest Fragmentation: Effects on Aboveground Biomass, Microclimate and Carbon Storage

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Abstract

The Argentinian Yungas ecosystem, the more extensive of the two richest biodiversity ecoregions of the country, is subject to rapid deforestation and fragmentation. Because these fragments are the future biodiversity reserves of this ecosystem, it was interesting to know if they constitute small-scale replicas of the forest from which they were detached. Our objective was to characterise the fragments and compare them with sectors of continuous forest by studying the aboveground tree biomass (for the five most representative forest species), microclimate (three variables) and edaphic factors (three) as a function of distance from forest edge at 15, 25, 50, 100 and 200 meters. We selected two size categories for fragments: 5 - 10 ha and 100 - 150 ha, located in the lower Yungas forest (LYF). We did sampling during the dry and wet seasons. As a result, in the larger fragments, the distance exerts a significant effect on the records of the microclimate and edaphic variables, gradually modifying them from the edge to the interior (up to at least 100 meters). The variations are more evident in the wet season. Solar radiation and relative humidity were two of the factors with greater response (Spearman $r = -0.89$; $p < 0.001$ and $r = 0.58$; $p < 0.001$, in the dry season, respectively). The microclimate of small fragments does not depend on the edge distance, but it is actually sunnier, drier and hotter than that of the forest. The soil has also lost organic carbon and humidity. These changes are accompanied by a lower AGB in the fragments with respect to the forest (6% and 60% of 162 ± 26.02 $t \cdot ha^{-1}$, for small and big fragments, respectively). The five species studied show less density and trees of reduced dimensions (lower dbh and height). Fast-growing pioneer plant species and disturbance-loving lianas accompany them. Edge plant composition presents notorious changes in the bigger fragments.

Biomass and ecosystem processes such as carbon cycling, which have been modified into fragments, both are directly associated with the structure and functioning in LYF remnants. The human and animal intervention detected in the area could be interacting synergistically with the microclimate and biological changes observed and potentiate the effects of degradation in the fragments, creating conditions of greater threat to LYF's biodiversity. However, the management of the LYF ecosystem within an adequate land use scheme could conserve and even encourage the recovery of the fragments ensuring a natural legacy of great importance for the country. Financing opportunities and globally assumed responsibilities in the context of climate change could constitute a favorable framework for the implementation of strategies to safeguard these forests.

Keywords

Biogeochemical Carbon Cycle, Biomass, Carbon Sequestration, Edge Effects, Microclimate Changes

1. Introduction

Moist mountain forests are disappearing rapidly because of fire, selective logging and clear-cutting, and the remainder area is divided into fragments which are not only separated from each other, but which often are very small (Achard et al., 2002; FAO, 2015). The smallest and most isolated forest patches with the most regular shapes and those found near to roads are highly vulnerable to degradation, which affects the structure of the ecosystem (Newman et al., 2014). Many ecosystem functions, including hydrology and biochemical cycling, can be altered (Baccini et al., 2017). These fragments are often unable to support viable populations and deleterious edge effects—ecological changes associated with the abrupt, artificial edges of forest fragments—can also rise sharply in intensity (Baker et al., 2016). The world's largest and longest-running experimental investigations, the Biological Dynamics of Forest Fragments Project (BDFFP), spanning an area of ~1000 km^2 in central Amazonia, has been evaluating the effects of fragmentation on rainforest biodiversity and ecological processes for almost 40 years (Laurance et al., 2017). Studies have determined that some animal species are more vulnerable to fragmentation (e.g. narrow ecological tolerances, Gascon et al., 1999), and that the most vulnerable plants are those demonstrating high sensitivity to edge effects (Laurance et al., 2006a) and/or needing animal assistance for pollination and seed dispersal (Cramer et al., 2007). Indeed, they have clearly identified how the edges of fragments lead to microclimatic changes (Kapos, 1989), increase tree mortality (Laurance et al., 2006b) and alter carbon-storage dynamics (Laurance et al., 2017). The loss of biodiversity can be the ultimate consequence of fragmentation (Ferraz et al., 2003; Gibson et al., 2011).

According to a rating created by the Food and Agriculture Organization of the United Nations (FAO, 2015), Argentina is among the top ten countries that most destroy their forests, and the FAO calculates that the loss has amounted to more than 7.5 million hectares from 1990 to 2015. Almost 80% of forest loss has taken place in the northeastern part of the country. The Yungas ecosystem, the more extensive of the two richest biodiversity ecoregions of the country, is considered by the World Wildlife Fund as one of the 200 Global Terrestrial Ecoregions, because effective conservation in these ecoregions would help conserve the most outstanding and representative habitats for biodiversity on this planet (Olson & Dinerstein, 2002). However, there are few Yungas protected areas and is definitely the most threatened ecosystem of the region (Pacheco et al., 2005). A sharp fragmentation process is taking place in the lower Yungas forest (LYF), a sector with very gentle slopes which is most suitable for agriculture. Until 2000, the LYF was partially replaced by sugar plantations, tobacco and commercial afforestation; in more recent years, the expansion of soy has been a major stimulus (Volante et al., 2012).

Current trends show that the LYF will continue to regress and that the relicts of the LYF that have been immersed in an agricultural-urban matrix are those that should be managed in the future. Some studies in the LYF enable us to predict the impacts of the conversion of the forest to other land use. Ripley et al. (2010) claim that forest conversion to livestock grazing use, degrades the soil by the loss of litter cover (40% lower), organic C soil (37.5% lower), total N (34.1% lower), and greater soil penetration resistance compared with the native forest soil. This creates potential for further soil losses from water erosion during monsoon rains. Tosi et al. (2016) found that forest conversion to croplands modified the structure and function of soil microbial communities, and in the short-term (3 - 5 years) agricultural soils exhibited a reduction on microbial biomass (~45%) and ammonification (~67%). Biological studies have observed that, after a year of the creation of logging gaps, short herbs colonize the gaps. Later, exotic grasses vegetation and tall herbs (dispersed through extraction tracks) invade the gaps, which can impede the colonization and development of pioneer trees and natural regeneration. Logging gaps can also affect biological processes that occur in the ecosystem, such as seed dispersal. For example, because arboreal frugivorous birds disperse most tree seeds in tropical and subtropical forests, the low activity of this guild in logging gaps contributes to the low regeneration observed (Zurita & Zuleta, 2009).

Nevertheless, no study has clearly characterized the microclimate and forest structure in LYF fragments with respect to the continuous forest sector, nor the possible microclimatic edge effect when in contact with a different matrix. The question that had guided the present investigation is: are fragments a small-scale replica of the forest from which they were detached? If there are abiotic modifications in the fragments, they could influence the aboveground biomass (forest structure and plant composition) and the flows derived from it that are the support for all the ecological processes that take place there, such as the carbon storage dynamics. The identification and understanding of what happens in the fragments is essential for assessing not only their vulnerability, but also their potential resilience in the face of global climate change and their ability to recover after various perturbations (Laurance et al., 2017). In this context, our objective was to characterize the fragments and to compare them with existing continuous forest sectors, studying the changes in aboveground tree biomass, microclimate and edaphic factors as a function of distance from forest's edge. We are interested in contributing elements for the development of LYF management guidelines within an adequate land use scheme that conserves and even encourages the recovery of fragments, thus ensuring a genetic legacy of great importance for the country. Financing opportunities and globally assumed responsibilities in the context of the current climate change could constitute a favorable framework for the implementation of strategies to safeguard these forests.

2. Materials and Methods

2.1. Study Area

The study area is located in the district of Orán (latitude 23˚20'S, longitude 64˚30'W, elevation 350 - 580 m a.s.l.), Salta province, northwestern Argentina. The Yungas forest that constituted the matrix of the landscape in 1986 retreated and fragmented until in the 2000 it happened to constitute patches on an agricultural matrix. Since 2000 to 2004, the rate of deforestation between Calilegua and Baritu National Parks, increased two-fold from 1000 ha per year and reaching over 3000 ha per year in some areas (Somma, 2006). The increase in the fragmentation and the separation of patches of natural habitat are continuous (Volante et al., 2012). We selected this area (**Figure 1**).

The climate is subtropical with a dry season (in winter). Annual mid-temperature is 21.4˚C. Mid-temperature in summer is 26.5˚C and 14˚C in winter and annual precipitation reaches 600 - 750 mm. The most of the rain is concentrated in summer, between October and April. The original material consists of deposits derived from tertiary rocks such as sandstones, siltstones, claystones and conglomerates, with a lower proportion of Ordovician, Cambrian and Precambrian rocks. According to FAO taxonomy, the dominant soils in the sampled area are Haplic and Luvic Phaeozem. The soil contains 31.8% clay, 45.2% silt and 23% sand. The cation exchange capacity is 19.9 meq. 100-1. Slopes and strong summer rain can lead to erosion that can be accelerated after native vegetation is replaced by annual crops (Tosi et al., 2016).

2.2. Sampling Design

We analyzed the temporal evolution of land use in the region with Landsat TM satellite images (1986, 1992, 1996, 2000) and Google Earth (2012). We select these images for being free-cloudiness images available for the zone, which better allowed to evaluate the vegetal cover. Satellite images were analyzed with Erdas Imagine®. Similarly to the BDFFP studies (Laurance et al., 2017) we selected the fragments according to their size, age, shape and original vegetation (we discarded secondary forest fragments). We defined two patch-size categories: three

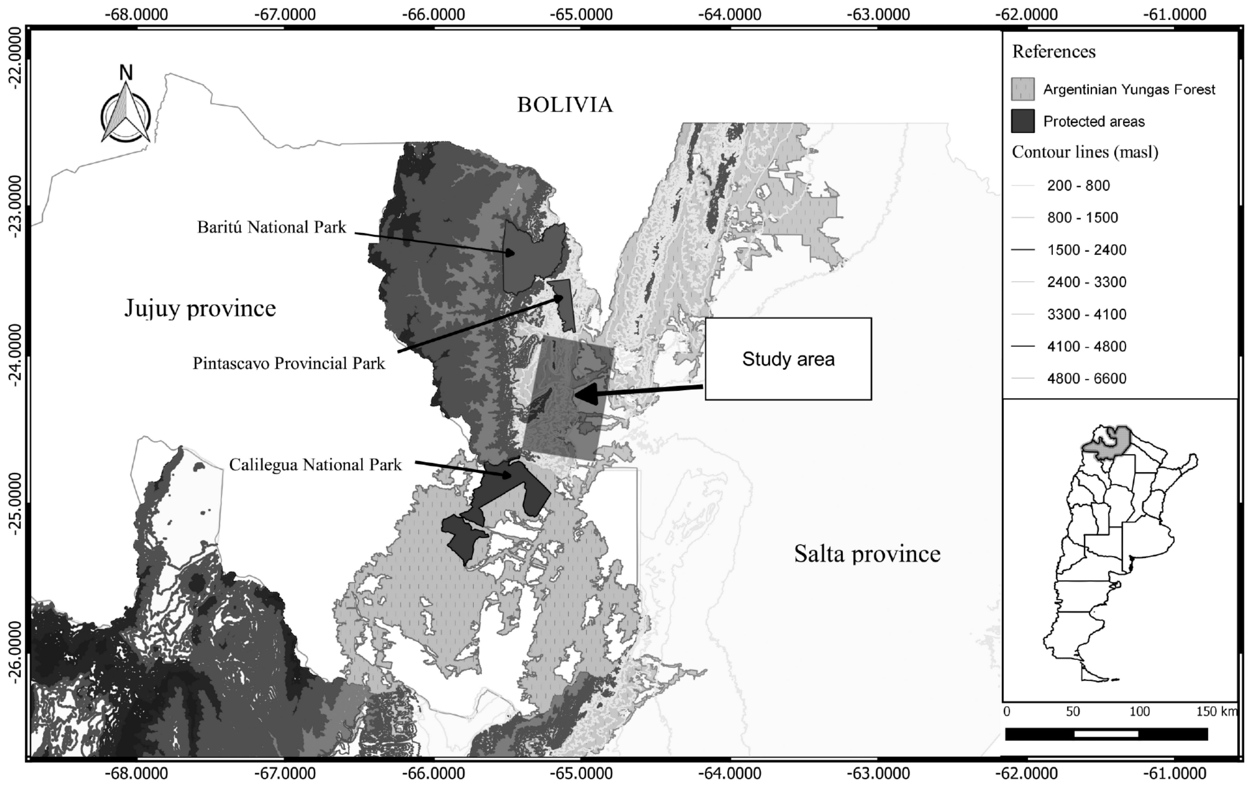

Figure 1. Location of the Yungas ecosystem study area (Salta, Argentina).

5 - 10 hectares (ha) patches and three 100 - 150 ha patches, located in the LYF. All the fragments selected were between 3 - 8 years old. We studied the change in aboveground tree biomass, microclimate and edaphic factors as a function of distance from fragment edge. Knowing that the most striking edge effects could happen within 100 m of forest edges (Kapos, 1989; Laurance et al., 2006a; Newman et al., 2014), we made rectangular plots of 0.01 ha at regular distances inside the fragments: 0, 15, 25, 50, 100, 200 m from edge for aboveground biomass studies. A non-fragmented area over 2000 ha was selected in a nearby continuous forest to serve as experimental control; here we made forest-interior plots (>500 m from edge) for the edge effects (Baker et al., 2016). A key feature was that pre-fragmentation studies had already been conducted in the Yungas ecosystems (Tortorelli, 1956; Mutarelli, 1972; Cabrera, 1976) thereby allowing fragment changes to be assessed far more confidently than in most other fragmentation studies. We did sampling during the dry season (June-July) and wet season (October-November) and we worked in the eastern side of the fragments because under the influence of easterly winds that transport clouds and humidity, precipitation is distributed progressively through the eastern boundary of the Yungas, with the Western hillsides receiving less rainfall. The samples taken and the measured variables are described below.

2.2.1. Microclimate Measures

We took measures at the same time, between 11 and 14 hs (Williams-Linera et al., 1998). We made three repetitions for distance and we registered: 1) SR, solar radiation intensity (W·m^{-2}); 2) RH, relative or air humidity (%); and 3) RT, relative or air temperature (˚C). SR was taken with a pyranometer LI-COR 250 with silicon sensor. This gadget measures a wavelengths range between 0 and 2000 nm, has a resolution of 0.1 W·m^{-2} and a precision of ±5%. RH, was registered at 1.5 m from the ground with a Hydrometer Vaisala HM 34, with capacitive Humicap sensor delivering electrical signals between 0 and 1 volts, in a range of 0 to 100%, and with an accuracy of ±2%. RT was measured with the same Vaisala moisture sensor.

2.2.2. Soil Samplings

We took three samples of soil per plot at 10 cm depth, using a bladed hole. We had previously removed the superficial material. In the laboratory, organic carbon, OC (%), and soil moisture, SM (%), were studied. Oxidizable carbon was measured by the WB method (1947) and corrected by the 1.3 factor (Richter et al., 1973) for a more accurate estimate of the total organic carbon. The OC was also expressed as organic matter considering a factor of 1.724. SM was estimated by drying the sample in an oven at 105˚C ± 5˚C. We collected three additional samples with the 100-m^3 cylinder method and we studied bulk density in the lab. In addition, soil temperature (˚C), ST, was recorded with a FLUKE 54 II digital thermometer whose accuracy is 0.05%.

2.2.3. Vegetation Sampling

Forest fragments contain a limited subset of any regional biota, in part because small patches have inevitably fewer species and less habitat diversity than larger patches. Many species could be missing from any fragment or reserve simply because they never occurred there in the first place. For avoid this *sample effects* (Wilcox & Murphy, 1985), we focuses our studies on five typical forest species (**Table 1**). The species were selected according to their great representativeness, which was measured in terms of density of individuals per surface (and also because they are the species that define the ecosystem of LYF (Cabrera, 1976)). Knowing the situation of the dominant species can guide on ecosystem management guidelines (Steege et al., 2013).

We registered total height (from ground level up to crown point) and diameter at breast height (dbh) in all trees with dbh ≥ 10 cm. When 1 ≤ dbh < 10 cm and height ≥ 50 cm, trees were measured in 50 m^2 plots. In multiple-stemmed trees, only the longest stem was measured. If neither shoot was dominant, an average of similar shoots was calculated. The basal diameter was registered only when the stem was shorter than the dbh. Standing dead trees with dbh ≥ 1 cm and fallen trees with dbh ≥ 10 cm were measured in the same way as living trees. The sampling intensity was 10% of the surface in small fragments and 1% in large fragments (with identical surfaces in the forest). The most representative concomitant species in the area were identified either on site or by samples collected for further analysis in the lab. A photographic database was also created

Table 1. Forest species studied (scientific name from: http://www.catalogueoflife.org). Where: (δ) Density values reported by Cabrera (1976) for dbh ≥ 10 cm; (V) volume, extracted from Malizia et al. (2009); (MCD) Minimum cutting diameter and estimated time to achieve the MCD from Humano (2013).

	Scientific name	Common name	Family	δ (ind·ha^{-1})	V (m^3·ha^{-1})	MCD (cm) and years needed
1	*Phyllostylon rhamnoides* (J.Poiss.) Taub	Palo amarillo*	Ulmaceae	137	20.2	30 cm (85 years)
2	*Calycophyllum multiflorum* Griseb (Castelo)	Palo blanco	Rubiaceae	55	13.2	30 cm (135 years)
3	*Anadenanthera colubrina* (Vell.) Brenan	Cebil colorado	Fabaceae	23	24.2	30 cm (35 years)
4	*Cedrela odorata* L	Cedro*	Meliaceae	7	3.2	40 cm (50 years)
5	*Astronium urundeuva* Engl	Urundel	Anacardiaceae	6	16.6	30 cm (55 years)

(*)Species declared Vulnerable by IUCN (http://www.iucnredlist.org). The rest of the species have not been assessed for the IUCN Red List nor have deficient data.

during the trips. Because of the degradation and our first-hand observation of the current state of the ecosystem, we decided to record the following: extraction of firewood or wood, livestock grazing, burning and signals of human presence (trash, objects, path and trail).

2.2.4. Data Analysis

We estimated the aboveground tree biomass (AGB) using allometric equations. AGB refers to the total amount of aboveground living organic matter in trees (≥1 cm dbh and height ≥ 50 cm) expressed as ovendried tons per hectare. When no specific equations were found, we use general allometric equations already employed in the area. Equations (1), (2), and (3) were obtained from a global database (http://www.globallometree); while Equation (4) belongs to Chave et al. (2014).

$$\text{For } P.\ rhamnoides\text{:}\quad V = -3.2794 - 0.0734 * \log H^2 + 1.0580 * \log\left(D^2 * H\right) \quad (1)$$

$$\text{For } C.\ multiflorum\text{:}\quad V = -2.2910 + 0.0558 * \log D^2 + 0.83235 * \log\left(D^2 * H\right) \quad (2)$$

$$\text{For } A.\ urundeuva\text{:}\quad V = -2.4385 + 0.9560 * \log\left(D^2 * H\right) - 0.80350 * \log\left(H/D\right) \quad (3)$$

$$\text{For } A.\ colubrina \text{ and } C.\ odorata\text{:}\quad AGB = 0.0673 + \left(pD^2H\right)^{0.976} \quad (4)$$

where:

V= volume (dm^3);

D = diameter at breast height (dbh) measured at 1.3 from the ground (cm);

H = tree total height (m);

AGB = above-ground tree biomass (kg);

ρ = wood basic density (g·cm^{-3}).

The volume values were transformed to biomass by applying the basic density of the species (INTI-CITEMA, 2007). After obtaining the biomass per tree, discount factors were applied based on the quality of the tree (Penman et al., 2003): 0.9 for sick or hollow trees; 0.8 for standing dead trees; 0.7 for fallen or decaying trees. The soil organic carbon weight of each plot (SOC, in $t \cdot ha^{-1}$), was obtained by multiplying the percentage of organic carbon by the bulk density of the soil ($g \cdot cm^{-3}$) and the depth at which samples were taken (m). The data was statistically analyzed with INFOSTAT™ software 3.0. Due to the lack of normality of the data, the Kruskall-Wallis test was applied to compare AGB, microclimate and SOC between sites. Later a multiple comparison test was applied. To study the effect of distance, the Spearman Correlation test was applied. We considered significant for $p < 0.05$ and highly significant for $p < 0.001$. When we found the effect of the distance on some variables, the Kruskall Wallis test was applied to observe if the differences between distances were significant.

3. Results

3.1. Habitat Structure and Composition

The comparison of the structural parameters expressed as AGB (**Figure 2**), clearly show a different figure between the forest and the fragments. Not all the species studied are present in all the sites, and with a smaller area of forest, there is a reduction in the biomass contribution of the species. In general, the best-represented species is *P. rhamnoides* with an average of 30.2 $t \cdot ha^{-1}$ distributed between small fragments (4%), large fragments (42%) and forest (53%). It is followed by *A. colubrina* (average of 25.5 $t \cdot ha^{-1}$, distributed in 6%, 48% and 45%, respectively by category) and thirdly *C. multiflorum* (20.4 $t \cdot ha^{-1}$, with a participation of 2%, 37% and 61% in the sites). The two species with less contribution are *C. angustifolia* (10.4 $t \cdot ha^{-1}$) and *A. urundeuva* (11.3 $t \cdot ha^{-1}$). The total AGB of fragments implies only 6% and 60% of the AGB of the forest (161.92 ± 26.02 $t \cdot ha^{-1}$), considering the small and large fragments respectively, with significant differences between sites ($H = 53.66$, $p < 0.05$). The fraction dbh ≤ 10 cm of dbh ("regeneration") reaches up to 6% of AGB per site, but it is higher in small fragments (15%). The AGB consists of trees with average diameters of 23.9 ± 5.97 (95% confidence interval) and an average height of 17 ± 2.51 (95% confidence) in the large fragments. In the small ones, the dbh average is 18.57 ± 6.96 (95% confidence) and the height 12 ± 4.1. In the forest, the dbh is 30.3 cm ± 6.24 and 18 m height ± 2.33. The density of trees varies from 322 $ind \cdot ha^{-1}$ in forest, 272 $ind \cdot ha^{-1}$ in major fragments and 141 $ind \cdot ha^{-1}$ in small fragments. Total basal area values of the five species are also shown in **Figure 2**.

The continuous forest presents the upper and middle strata (over 5 meters) dominated by the five species studied and accompanied by *Tabebuia lapacho, Erythrina dominguezii, Cordia trichotoma, Patagonula americana, Myroxilum peruiferum, Terminalia triflora, Phoebe porphyria, Chlorophora tinctoria, Piper sp, Myrcianthes mato, Myrcianthes pungens*. There are very few shrub and herbaceous species in general. The field trips allowed the observation of evidence of

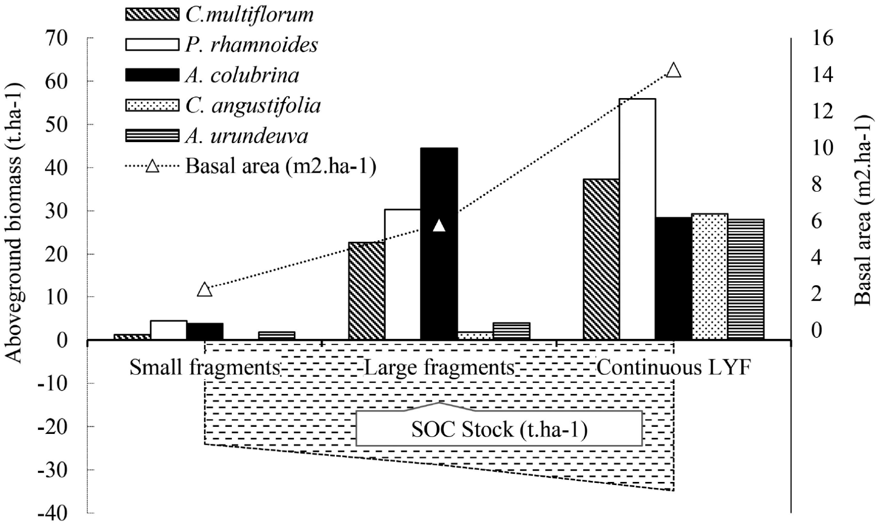

Figure 2. Aboveground biomass stock (t·ha^{-1}) of the five species studied. The SOC stocks (t C·ha^{-1}) are shown below the AGB as a continuous reservoir just for a graphic idea, but the lower line is linking the average carbon pool in the soil for the three sites. Mean basal area (m^2·ha^{-1}) for each site is shown.

extraction of firewood or wood in 15% of the plots. Livestock grazing activity was not easily detectable inside the forest.

In the fragments there are species of disturbed environments (Digilio & Legname, 1966) such as *Tecoma stans, Ricinus comunis, Solanum riparium,* and some grasses, present even in the interior of the fragments and not only in their periphery. A dense understory was observed, mainly dominated by lianas, vines, supportive shrubs such as *Celtis* spp and some genus of Amaranthacea family, and thick webs of *Macfadyena unguis-cati* with *Serjania sp* and several species of Celtis. 60% of the plots in small fragments recorded signs of extraction of firewood or wood, while livestock grazing was recorded in almost 100% of them. In the large fragments, only 16% of the plots denoted signs of grazing pressure, but fire wood or wood extraction was also observed in a similar percentage.

At the edges of the fragments a dense formation of shrubs and herbaceous plants was observed, with a predominance of heliophyte, pioneer species and low crown cover (little growth in height). There are abundant *Senecio sp, Ricinus comunis, Eragrostis sp, Panicum maximum, Serjania sp,* as well as some of the trees previously mentioned as *Solanum riparium* and *Tecoma stans*. Dead trees were more abundant at the edges of the large fragments and the effect of distance was significant in them (r = −0.62; $p < 0.001$), with a total 15.5% of dead trees (standing or fallen) on the sampling surface of 15.5%. There was not an effect of distance on the number of dead trees found (r = 0.02; $p > 0.05$), although the percentage of dead trees standing and falling was 22% in small fragments and 6% in the forest.

The small fragments have a soil carbon reserve (SOC) of 21.29 ± 4.92 tC·ha^{-1}, which is smaller than that of larger fragments (28.91 ± 12.19 tC·ha^{-1}), and that of the forest (34.82 ± 8.84 tC·ha^{-1}). These differences were highly significant between sites (H = 16.78, $p < 0.001$) and they are in coincidence with the AGB observed in surface: the higher the AGB, the higher the SOC, although the variations are less accentuated than on the surface. However, the Spearman correlation between AGB and SOC is only significant in the larger fragments (r = 0.46, $p = 0.0229$), where there is a direct and relatively strong correspondence between the AGB (considering the five species) and the carbon stored below the ground. In other cases, the linear relationship is weak (r < 0.21) and not significant.

3.2. Micro Environmental Factors: Seasonal Variation and Changes in the Edge

The wet and dry seasons in the northern region of the country coincide with summer and winter, respectively, which are characterized by means of the microclimatic and edaphic variables shown in **Table 2**. The absolute values recorded in the dry season have decreased in general terms between 50% - 100% with respect to those recorded in the wet season (depending on the variable considered) with the exception of the organic matter of the soil which shows the inverse behavior. Although the absolute values have changed between seasons, the trends are similar: the forest has lower solar radiation (average of 25% - 30%), lower relative temperature (~23% less in summer) and higher relative humidity (between 15% and 50%, according to season), with respect to the fragments. The forest soil has more moisture (~15%), less temperature (5% - 15%) and higher content of organic matter (~25%). Moreover, the fragments differ from each other, and in some cases, the larger ones do not register significant differences

Table 2. Microclimate and edaphic variables (means and SD in parentheses) for the three types of sites studied. Where: SR = solar radiation intensity (W·m^{-2}), RH = relative humidity (%), RT= relative temperature (˚C), ST = soil temperature (˚C), SM = soil moisture (%), OM = organic matter (%).

Variable	Wet season			Dry season		
	Small fragments	Large fragments	Continuous Forest	Small fragments	Large fragments	Continuous Forest
SR (W·m^{-2})	789.5b (146)	603.7b (238)	313.3a (47)	419.7c (344)	234.9b (271)	42.4a (26)
RH (%)	37.7a (8.33)	49.4ab (18.01)	73.19b (15.07)	21.58a (8.55)	38.17b (18.13)	45.11c (2.51)
RT (˚C)	30.09b (6.64)	30.93b (3.64)	24.73a (2.29)	17.39a (2.08)	18.60a (5.23)	18.79a (1.19)
ST (˚C)	24.27a (0.50)	23.52a (1.60)	22.23a (0.60)	16.18b (2.36)	13.84a (1.36)	13.42a (0.28)
SM (%)	8.11a (1.38)	12.70ab (2.23)	17.2b (0.89)	6.25a (1.20)	9.03ab (1.92)	12.4b (2.17)
OM (%)	2.70a (0.22)	4.03b (0.47)	5.49c (0.30)	2.90a (0.28)	4.34b (0.64)	5.56b (0.31)

Values with a common letter within the same season (wet or dry) and for the same row are not significantly different ($p > 0.05$).

with the forest in some variables (e.g. ST in wet season, and ST, RT in dry season).

In the fragments, solar radiation and relative temperature both visibly decline as the distance from the edge increases (**Figure 3**). Soil moisture and organic matter in the soil increase from the edge to the interior of the forest (**Figure 4**). The temperature of the soil oscillates less perceptibly and with a lower dispersion range. In general, the microclimatic factors oscillate more sharply when the distance to the edge increases (e.g. intensity of radiation and relative temperature) (**Figure 3**), than the edaphic factors (greater amplitude among means) (**Figure 4**). In the forest, the records remain relatively constant for any of the distances, and in no case do the correlations made reach statistical significance ($p > 0.05$), nor they allow the recognition of linear correlations ($r < 0.2$).

For large-size fragments, the edge distance had a significant effect ($p < 0.05$) on all the micro-environmental variables recorded in the dry season, and on 4/6 of them in the wet season (exceptions were ST and OM) (**Table 3**). Solar radiation and relative humidity were two of the factors with the greatest response ($\rho = -0.89$ and $\rho = 0.59$, in wet season, respectively and $\rho = -0.6$ and $\rho = 0.48$ in dry season). The small fragments were measured up to 52 m to avoid the influence of narrower sides or exposed edge of the opposite side. In these fragments, effects of distance on soil moisture (wet season) and solar radiation, relative humidity and soil temperature (dry season) were found.

For each significant correlation, we evaluated the differences between distances by means of the Kruskall Wallis test. (These results are not showed.) The test detected differences only for solar radiation ($p < 0.001$) and relative humidity ($p < 0.05$) for the large fragments in both seasons. Solar radiation influences the plots in a different way and constitutes three homogeneous groups: 1) the first plot (0 meters); 2) 15 and 25-meter plots (dry season) and 50 meters plots (wet season); 3) the last two interior plots (100 - 200 meters for wet season) or three plots: 50-100-200 (for dry season). Only two groups have been separated according to their relative humidity: 0 - 15 meters on the one hand, and the other plots on the other hand.

4. Discussion

4.1. The Microclimate and the Aboveground Biomass Are Different in the Fragments

Microclimatic changes seem to be the most evident effects of fragmentation (Williams-Linera et al., 1998; Baker et al., 2016). All the fragments show, on average, different values to the forest, defining for the latter a more shaded and fresher environment, with higher humidity and lower relative temperature, and richer in organic matter soil. The differences are significant when comparing edaphic and microclimatic factors between the forest and the small fragments (with the exception of ST in wet season and RH in dry season), and they are only significant in some cases with respect to large fragments.

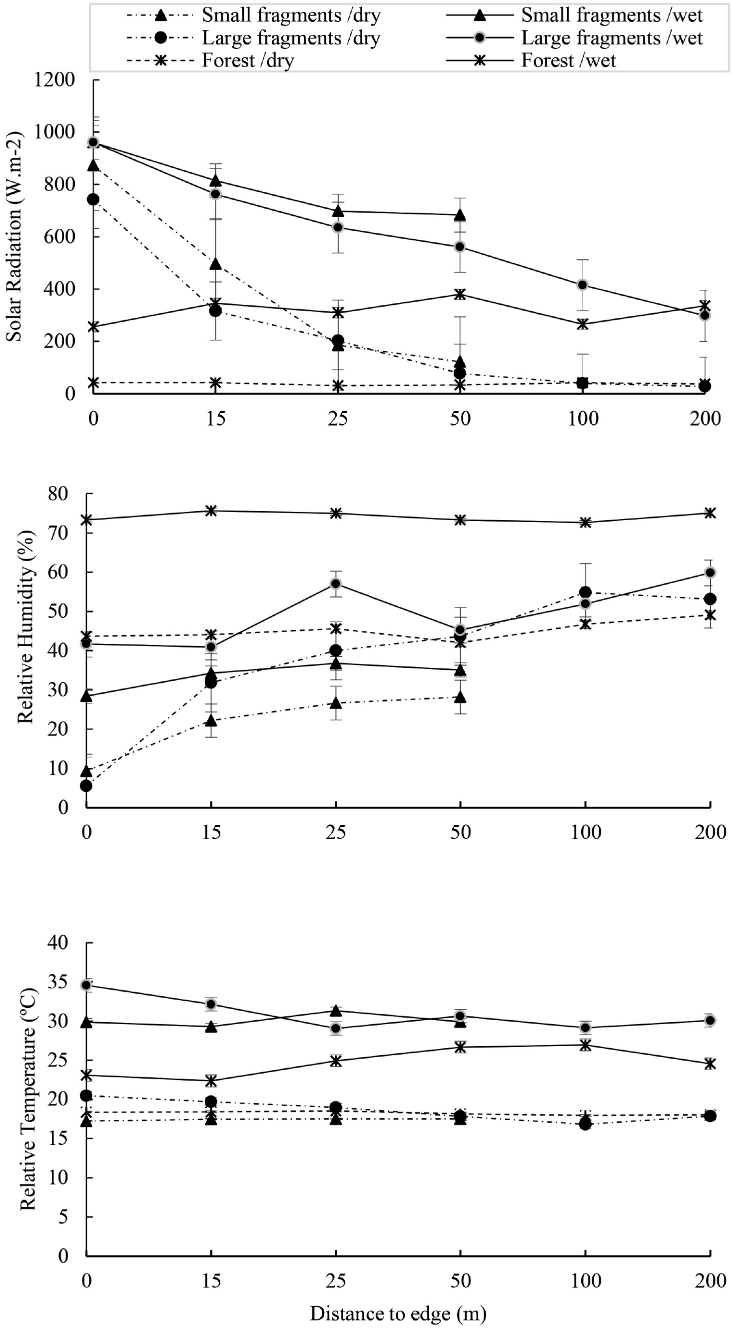

Figure 3. Microclimatic factors for different distances to forest edge (meters). Values shown are means ± S.E. (standard error). The results of the dry season (dry) are drawn in a dotted line and the results of the wet season (wet) in a continuous line.

The distance to the edge has effects on the micro-environmental variables studied only in the case of large fragments. In small fragments, human influence seems to have greater relevance than microclimatic changes, possibly because the high level of alteration directly makes them a great edge (Kapos, 1989) and there is not notorious gradients of humidity, temperature or light. Near edges, reduced humidity, increased light, and greater temperature variability penetrate up

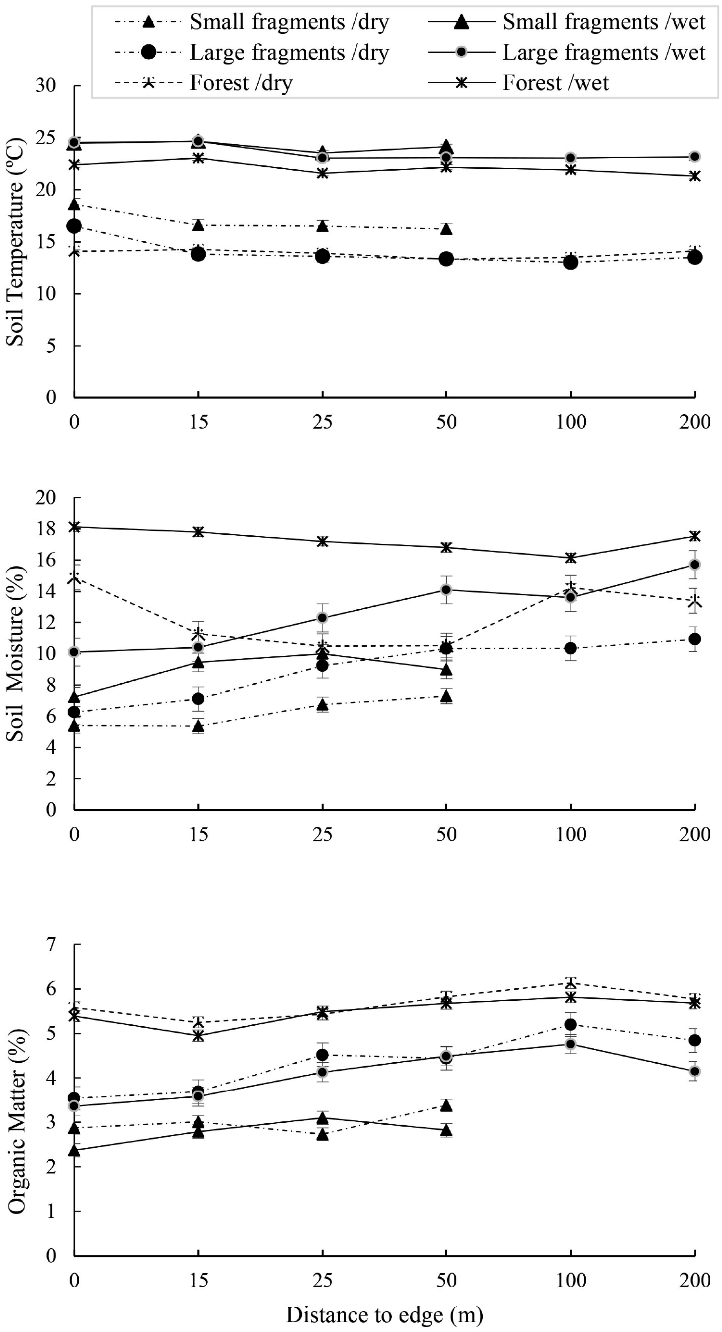

Figure 4. Edaphic factors for different distances to forest edge (meters). Values shown are means ± S.E. (standard error). The results of the dry season (dry) are drawn in a dotted line and the results of the wet season (wet) in a continuous line.

to at least 100 m into large-size fragment interiors (considering the values of the forest), while edaphic factors undergo less noticeable changes: moisture and organic matter of the soil increase towards the interior of the fragment while soil temperature decreases (Ripley et al., 2010). Microclimatic edge effects are usually stronger during summer (similar to Silbernagel et al., 2001) and both the SR and RH are the most influential on the plots. Edge effects can be detected up to 50

Table 3. Spearman correlation between the microenvironmental variables and the recording distance by site and for each season. Where: SR = solar radiation intensity ($W \cdot m^{-2}$), RH = relative humidity (%), RT = relative temperature (˚C), ST = soil temperature (˚C), SM = soil moisture (%), OM = organic matter (%).

Variable	Wet season			Dry season		
	Small fragments	Large fragments	Continuous Forest	Small fragments	Large fragments	Continuous Forest
SR ($W \cdot m^{-2}$)	−0.30	−0.89**	−0.12	−0.41**	-0.6**	0.21
RH (%)	−0.13	0.58**	0.18	0.31*	0.48**	-0.22
RT (˚C)	−0.01	−0.47*	0.07	0.03	−0.36**	-0.18
ST (˚C)	−0.25	−0.44	0.14	−0.30	−0.31**	0.05
SM (%)	0.34*	0.55**	0.10	0.24	0.43**	0.14
OM (%)	−0.29	−0.34	0.09	0.17	0.31*	0.13

*Significant for $p < 0.05$ and **highly significant for $p < 0.001$.

meters, because the differences between the parcels of the edge (0, 15, 25 and up to 50 meters) and those of the interior (100 and 200) are significant. Otherwise, the edge effect can be detected by considering that at a distance of 100 meters almost all variables show records similar to the forest.

Gradients in microclimate can significantly affect the ability of species to recolonize after a disturbance because the hydrological and biogeochemical dynamics of the fragments are altered (Baker et al., 2016) and could negatively affect the species that have adapted to humid, dark forest interiors (Ferraz et al., 2003). For the five species studied, it is not possible to gauge to what extent these changes are influencing their current structural manifestation within the fragments. Although the structure and vegetal composition is different from that of the forest, it was not possible to estimate the previous forest structure before the definitive separation from the continuous zone happened. The numerous signs of human and animal presence in the area are indicative of an intervened reality.

It could be thought that, given the higher accessibility to which fragments are exposed, they also experience greater degradation due to human and animal influence as time passes. Factors such as grazing and burning could modify and strongly condition the future vegetation of the forest (Pacheco et al., 2005). Likewise, beyond human intervention, the existence of an edge with a spatial and temporal microclimatic dynamics must be considered for a better understanding of the biological responses and the distribution and abundance of organisms in forest fragments (Didham & Lawton, 1999; Newman et al., 2014). Radiation, temperature and humidity, which drive many biological processes, could be influencing the germination and survival of the dominant tree species (Ferraz et al., 2003; Gibson et al., 2011). Furthermore, there could be a temporary mismatch between landscape changes and the regression of a species, since a species response to such changes does not necessarily manifest itself immediately (Tilman et al., 1994).

It would be possible that there are also simultaneous inverse processes of "recovery" of forest biomass, since constant intervention could keep fragments in a state of permanent growth. A number of studies have reported similar trends in forest growth: the AGB accumulation is faster in the early stages of a forest (greater growth than death). Then it slows down as the forest ages until it reaches the biomass carrying capacity of a forest ecosystem or climax (balance between growth and death) (Clark & Clark, 1996; Edwards et al., 2014). If these forests are properly managed, their ability to accumulate biomass could be maintained over time (Thornley & Cannell, 2000). Although these forests have not been managed, the permanent intervention on them could be keeping them in a stage of growth, since the state of degradation found suggests that the biomass accumulation capacity of these forests is likely to be greater than estimated.

The size of the fragments may be an impediment in this regard. Edwards et al. (2014) suggest that forest remnants, although they contain old growth, might contribute less to the ecosystem functioning and might have reduced resilience compared to large contiguous forests because key ecosystem processes are disrupted by the loss of connectivity with other wildlife habitats in the same landscape and by their greater exposure. The reduction of forest area and its confinement to fragments necessarily implies a direct reduction for individuals and their AGB. The surface ratio between the small and large fragments studied is around 1:10, which is reflected in a decreased AGB value of the five species studied in that proportion. However, the particular analysis of each one (density, basal area, dbh and heights) is what allows us to estimate that the loss of biomass in the fragments does not have a linear relationship with the reduction of surface area. It should be considered that the value of AGB is an integrated index that can be obtained with a similar value from more small trees or few large trees. Clark & Clark (1996) recognize that in a tropical humid forest, the biomass of a tree of 150 cm in diameter is equal to approximately 607 trees of 10 cm in diameter. In the case of the continuous LYF, there are larger trees (although no individuals greater than 50 cm of dbh were found), with lower density, while in the fragments there are smaller trees. This is of fundamental importance because the big trees are seed parent trees and when the dbh is higher, the production of the fruits and seeds will be higher (Grau, 2005; Cramer et al., 2007). Since the specimens of lower sizes, and therefore those of younger ages, are left, the possibility that these will be cut without having been reproduced is much higher. The time needed to allow these forest value species to reach the prescribed minimum cutting diameters (CMD) for the area is shown in **Table 1**. In studies conducted in the Bolivian Yungas, with 20-year shifts and similar CMD, 70 years are needed to recover the volume extracted (Brienen et al., 2003). Therefore, the replacement of lost adult specimens in the LYF implies a waiting time of between 35 and 135 years, which has not been and is not being respected in the area.

In general, in all the studied sites including the forest, the vegetal structures (diameters and heights) are diminished with respect to the information previously reported for this ecosystem (Tortorelli, 1956; Mutarelli, 1972; Cabrera, 1976). Although no estimates of AGB were found for these five species, there are reports for basal areas (Malizia et al., 2009). More recently, the maximum values of basal area are mentioned by Humano (2013) in Ledesma (19.42 $m^2 \cdot ha^{-1}$) and San Martín (16.72 $m^2 \cdot ha^{-1}$) in the province of Jujuy; while the smallest reports are the ones estimated in the present work for the fragments: 2.27 $m^2 \cdot ha^{-1}$ for the small ones and 5.8 $m^2 \cdot ha^{-1}$ for the large ones. In all cases, the history of forest use could be one of the main factors that define the vegetal structure. Although the creation of logging and tree removal gaps in many respects resembles natural forest dynamics, generally the high impact forest exploitation (poor techniques, without forestland planning, amount and speed of extraction) create greater disturbances than the natural ones. This causes a quantitative change towards species which have adapted to the disturbances (Ferraz et al., 2003; Laurance 2006a). *C. odorata* has historically been considered a quality wood in the market and its exploitation has been carried out since 1920. The pressure of forest extraction for almost a century could have decimated its populations in the area; thus, since it is a species with a lesser appearance frequency it is less likely to be represented in the fragments. The *A. urundeuva* is the second most commercially valuable species, and then the other three have been marketed more intensively for the last 30 years (Brouver & Manghi, 2006).

The size of the fragment could also be affecting the species differently according to their own ecology and survival strategies (**Table 1**). The fragmentation may have severe consequences for shade-tolerant plant species, due to the modification of the humid and fresh microclimate in the fragments (Williams-Linera et al., 1998; Didham & Lawton, 1999) as well as for those whose seeds are dispersed by animals, since their populations may be affected (Cramer et al., 2007; Van Houtan et al., 2007). *A. colubrina* is a shade-intolerant species of faster growth with less ecological requirements than the others, so it is more flexible in the face of changes (Digilio & Legname, 1966). Its seeds are dispersed by the wind; it carries on one sole stem both male and female flowers (monoecious); and it has not been fundamentally searched for timber purposes. Therefore, its higher AGB in the studied sites could be due to this conjunction of factors. On the other hand, the *A. urundeuva* (a shade-tolerant species), requires special conditions of shade and humidity for its growth, which is relatively slow (more than 50 years to reach 30 cm of dbh). Given its requirements, its low density, its high commercial value, and its seed dispersal strategy with animals, its populations could be under threat. In addition, *A. urundeuva* is the only species of the five that has male flowers on one stem and female flowers on another ("dioic"), so the reduction of tree population because of forest degradation can affect pollination and gene fluxes of remnant trees fitness (Cramer et al., 2007).

C. multiflorum and *P. rhamnoides* still show predominance among the five selected species, possibly due to their high original density in this ecosystem, lower ecological requirements, lower commercial value and better dispersion strategy (wind). However, because the distance between fragments is growing as the forest retreats, both dispersion strategies could fail for the species studied.

On the other hand, the number of plant strata has decreased in the fragments, and there is a greater frequency of shade-intolerant species. The shrub layer and low canopy appears more developed than in the forest and herbaceous species of heliophyte and pioneer habits, vines, lianas and supporting shrubs proliferate. The edges of the fragments have a dense formation of shrubs and herbaceous, with a predominance of heliophytic (intolerant) pioneer species or species which have adapted to environments with some type of disturbance.

4.2. Fragmentation Alters Carbon Storage

In the light of the evidence found, it can be thought that in the fragments the biochemical cycling is being altered. Carbon storage in fragmented forests could be affected by a set of interrelated changes. First, when there is no data available, it can be assumed that mature-phase trees that predominate in continuous forests can live for centuries sequestering carbon (Thornley & Cannell, 2000) and that the 50% of aboveground biomass is carbon that has been fixed in plant tissues (Penman et al., 2003). In fragmented forests, less biomass is stored in large, wooded old-growth trees and more biomass is stored among more fast-growing pioneer trees, herbs, disturbance-loving lianas, and woody debris. The fast-growing pioneer plants, which proliferate in fragments, have a shorter life and are smaller than the mature-phase trees they replace. They have lower wood density, and thereby sequester much less carbon (Laurance et al., 2006b) around 38% and less than 50%, depending on the species (Razo Zárate et al., 2015). Near forest edges, there are trees sensitive to microclimate changes (Laurance et al., 2006a) and maybe because of this there are many dead trees. Clearing operations could also have logged or weakened the trees at the edges (Newman et al., 2014). As the biomass from the dead trees decomposes, it is converted to greenhouse gases such as carbon dioxide. Although these processes of degradation of the biomass existing in the fragments would seem imperceptible, they are altering the carbon cycling of the ecosystem. A recent study has managed to quantify carbon emissions not only from deforestation, but also from the degradation of forest biomass in the tropics; this last process resulted in a greater contribution to global total emissions (68.9% of the total) (Baccini et al., 2017).

Although the edges of the large fragments (or the total area for small fragments) had a dense coverage of sun-loving plants, they also have species with lower growth in height. Therefore, fragments do not constitute a high and compact canopy that promotes moisture retention and soil protection as in the continuous forest. The higher soil exposure found (due to lower coverage in addition to microclimatic changes) could affect the nutrient cycle because, even when they remain in the soil, many nutrients are lost through erosion and washing (Ripley et al., 2010). In addition, the change in composition towards mainly pioneer species can alter nutrient cycles due to the lower use of lower levels of the soil (unlike woody vegetation), and depletion of the upper level (also exposed to losses due to washing) (Laurance et al., 2006b). We found that the SOC has decreased significantly from the forest values (34.82 ± 8.84 $\mathrm{tC \cdot ha^{-1}}$), 17% in the large fragments and 39% in the small fragments.

The loss of the dynamic equilibrium of nutrient cycling could influence the many ecosystem functions that depend on it (Laurance et al., 2017). Other biochemical cycles, such as those affecting key nutrients like phosphorus and calcium, may also be altered in fragmented forests, given the striking changes in biomass dynamics, hydrology, and thermal regimes they experience (Volante et al., 2012). The effects of fragmentation are likely to interact synergistically with other anthropogenic threats such as logging, hunting, and especially fire, creating an even greater peril for the LYF biota (Laurance et al., 2017). In addition, since forests are the largest global carbon reservoirs, the alteration of carbon cycling could constitute an enemy of the country's mitigation policies under the Climate Change Convention to which it has adhered.

4.3. The Challenge of Safeguarding the Future of LYF

Since a few species dominate the ecosystem, the observation of their behavior enables us to estimate the state of the ecosystem in each site. Steege et al. (2003) found "hyperdominant" species (1.4% of the total) to be so common that together they account for half of all trees in Amazonia, whereas the rarest 11,000 species account for just 0.12% of trees. This implies that a tiny sliver of species diversity performs most of the biogeochemical cycling in the world's largest tropical forest. We study the AGB of five of the most representative forest species and their characterization in the fragments and the forest clearly allow us to infer that the fragments do not keep identical samples of the original ecosystem.

Fragmentation processes are affecting the viability of the LYF remnants, but also of several National Parks and reserves by generating growing conditions of isolation. We made our studies in the Northern portion of the country, where forest fragmentation is most intense, and it constitutes the zone of connection between two protected areas (**Figure 1**). The potential connections and flows (e.g., fauna movements, seed transporting) among reserves were barely considered in the development of regional plans. Therefore, management programs of natural reserves were formulated based on each individual reserve's condition, with little attention to the regional context (Somma, 2006). However, the management of the territory necessarily implies looking at the bigger picture, and even more so from a conservationist perspective of ecological networks. In ecological networks, significance is placed on preserving natural patterns at the regional scale and the interaction between reserves and habitats, more than on establishing isolated conservation islands. The objective is to achieve connectivity of various sorts and to address habitat linkage at multiple scales (Bennett, 1999). This territorial planning process includes the development of a system of habitat reserves with special attention to the conditions in the landscape matrix. However, this has not been totally incorporated or even accepted in the Argentinean system of protected areas, and it would be interesting to explore the possibilities of the approach based on ecological networks (Jongman & Pungetti, 2004). In this sense, not only a larger number of correctly designed reserves and protected areas are necessary in the region (because there are few existing ones and they just keep very small samples of LYF); but their adequate management and control is also essential. In general, protected areas have medium or low levels of implementation, they lack specific management plans, and not all ecologic districts are represented; thus, the creation and maintenance of PA is a regional and national priority (Somma, 2006).

The implementation of management plans and the protection of degraded fragments from human or animal disturbances could begin to recover in around three or four decades (as to diversity, richness of tree species, density of stems, and height of the canopy, Grau, 1997). Forest edges tend to "seal" themselves over time, reducing the intensity of deleterious edge effects, (Didham & Lawton, 1999) and therefore, they could acquire characteristics similar to mature forest in at least 50 years (e.g. basal area or structural complexity, Grau, 2005).

Biomass and ecosystem processes such as carbon cycling represent part of what is lost when the forest is destroyed or degraded. Understanding these processes is essential to the design of management guidelines that allow the survival of forest ecosystems (Laurance et al., 2017). The most probable future scenario is that landscapes that are totally fragmented by incursion, degradation and economic exploitation carried out by man must be managed. In order to accommodate all the human activities of the area (conservation, agriculture, recreation, tourism, industrial forestation, water storage and regulation of the hydrological regime, oil, gas and mining) and to ensure the economic and environmental sustainability of the region, land use schemes that consider the continuity of the natural processes at a regional scale are essential. The preservation of the existing ecosystem samples in the fragments is necessary, as well as our acknowledging that all of them provide complementary benefits (Williams-Linera et al., 1998). Nevertheless, small sites will require more expensive and intensive management than large ones, so it is necessary avoid this situation.

5. Conclusion

In this study, we found that the AGB, microclimate and carbon storage are different in the continuous forest and the fragments detached from it. The smaller fragments have completely changed their appearance. They have a sunnier, drier and hotter microclimate and the soil retains less moisture and organic matter. The AGB of the five species studied makes up 6% of the AGB of the forest (where the average is 161.92 $t \cdot ha^{-1} \pm 26.02$) and is composed mainly of *P. rhamnoides* and *A. colubrina*. *C. odorata* is absent. The trees that remain are of small size (smaller dbh and height than in other places) and there is a high percentage of dead trees standing and falling (around 22%). Other heliophyte and fast-growing species have proliferated, forming a dense understory, but with fewer LYT typical trees. No effect of distance was found on the micro-environmental variables.

The larger fragments show microclimate, forest structure and edaphic conditions more similar to those of the forest. However, the distance exerts a significant effect on microenvironmental variables, gradually modifying the microclimate from the edge to the interior (up to at least 100 meters) where the conditions are more similar to the forest. At the edge, higher values of SR and temperature (ST and RT) and lower values of humidity (RH and SM) and OM content are recorded. Microclimatic edge effects are usually stronger during summer and both SR and RH are influential on the plots. Edge effects can be detected up to 50 meters, where the differences between the edge plots (0, 15, 25 and up to 50 meters) and those of the interior (100 and 200 meters) are significant. Otherwise, the edge effect can be detected by considering that at a distance of 100 meters almost all variables show records similar to the forest. These changes are accompanied by the proliferation of fast-growing pioneer plants and disturbance-loving lianas. The AGB of the studied species has also decreased. The structure of the pre-fragmentation forest remnants cannot be known, but it can be assumed that the predominance of new plant forms (of lower growth and soil cover), in conjunction with the registered microclimatic and edaphic changes, could affect future regeneration of shade-tolerant mature-phase trees. The human and animal intervention detected in the area could be interacting synergistically with the microclimate and biological changes observed, and potentiate the effects of degradation in the fragments, creating conditions of greater threat to LYF's biodiversity.

Biomass and ecosystem processes such as carbon cycling, which have been modified into fragments, both are directly associated with the structure and functioning in LYF remnants. However, the management of the LYF ecosystem within an adequate land use scheme could conserve and even encourage the recovery of the fragments ensuring a natural legacy of great importance for the country. Financing opportunities and globally assumed responsibilities in the context of climate change could constitute a favorable framework for the implementation of strategies to safeguard these forests.

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