



Replacing trees by bamboos: Changes from canopy to soil organic carbon storage



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ABSTRACT

Disturbances such as selective logging in a forest may lead to a degradation process, where new species become dominant and replace the original vegetation. This is the case of the Semi-deciduous Atlantic Forest, where bamboos replace trees and palms, affecting the forest structure and dynamics. As bamboos show plant traits that contrast those of trees and palms, we hypothesize that forest degradation affects ecosystem properties, generating changes in litterfall and litter decay rates, which transfer from plants to soil. We tested this hypothesis in twelve 0.36 ha plots along a forest degradation gradient in the subtropical forest of Northeastern Argentina. Total litterfall did not change along forest degradation, but litter layer necromass decreased more than 60% and litter thickness doubled in highly degraded sites. Litter layer thickness was associated with bamboo necromass present in the litterfall. Forest degradation also caused a deceleration in decomposition of the two most contrasting litter types under study, while the soil organic carbon content in the top 5 cm suffered a 50% decrease, from 21.5 to 10.9 Mg ha⁻¹. Forest degradation has a cascade effect on carbon storage and on its cycling from vegetation to soil by means of changes in different ecosystem processes mediated by plants. In the end, these changes affect soil organic carbon. This study provides a better understanding on the mechanisms behind carbon losses in relation to forest degradation, one of the greatest uncertainties in the carbon budget.

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1. Introduction

Plant species differ in quantity and quality of resources that they store, release to the atmosphere and return to the soil. For this reason, changes in plant abundance and composition lead to important effects on ecosystem functioning (Malhi et al., 1999; Wardle et al., 2004). Particularly, plant litter acts as a major system of input-output of nutrients, mineral elements and energy fluxes in the ecosystems (Olson, 1963). The rates at which litter falls, decays and accumulates on the floor influence nutrient turnover, which regulates plant growth, community composition and soil fertility in terrestrial ecosystems (Berg and McClaugherty, 2008; Vitousek and Sanford, 1986). In forests, plant litter is the largest source of organic matter and typically comprises a substantial proportion of the total amount of aboveground carbon stock (Chambers et al., 2000; Palace et al., 2012). Disturbances such as selective logging alter forest structure resulting in forest degradation

(Campanello et al., 2009), which would lead to changes in litter cycling, including litter decomposition and carbon storage. Nevertheless, in spite of we can easily predict this kind of changes as a degradation's consequence, the studies that have addressed this issue thoroughly are scarce. Even, none of them was carried out for the Atlantic Forest.

Plant litter decomposition, a biogeochemical process mediated by microbial enzymes, is one of the two major C-transforming processes on the planet (Berg and McClaugherty, 2008). The efficiency of this process strongly depends on climatic conditions, like temperature, humidity and UV radiation (Austin and Vivanco, 2006), and on biotic factors, such as the composition of the soil fauna community (Bardgett and Wardle, 2010). This, in turn, is determined by the vegetation on the ground (Ayres et al., 2009). The efficiency of plant litter decomposition also depends on plant litter quality (Hättenschwiler and Jørgensen, 2010). Even though organic C concentration is similar among plant litter (about half of dry mass is C), the relative amount of initial soluble (such as sugars, amino acids and phenols) and non-soluble (or recalcitrant compounds (lignin + cellulose + hemicellulose) change

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(Pérez-Harguindeguy et al., 2015), and may control litter decay rates (Hättenschwiler and Jørgensen, 2010). However, litter decay is not directly controlled by the quality of the litter; what actually controls litter decay are the effects caused by litter on the efficiency of microbial substrate use (Cotrufo et al., 2013), and these decomposers are, in turn, highly influenced by climate conditions (Wall et al., 2008; Bradford et al., 2016).

Forest degradation is one of the most influential changes of terrestrial ecosystems when it comes to carbon fluxes and stocks (Malhi et al., 1999). During this process, different ecosystem components may act either as a carbon source or as a carbon sink (Guo and Gifford, 2002), although until now the net effect has been a loss of carbon in forests (Malhi et al., 1999). The accelerated transformation of forests may affect ecosystem processes (Quesada et al., 2007). For example, litter decomposition could be affected if timing, abundance and quality of the litter inputs (Cornelissen et al., 1999; Aragón et al., 2014) and the associated soil biota composition (Zak et al., 2003) are modified, which would thereby affect the above and belowground feedback (Wardle et al., 2004).

The Atlantic Forest hosts one of the highest degrees of species richness and rates of endemism in the world, but has also undergone an intense fragmentation and degradation, remaining less than 15% of its original cover (Ribeiro et al., 2009; Joly et al., 2014). Virtually its entire surface, even the one within protected areas, has suffered different levels of degradation, affecting environmental conditions and gap dynamics (Campanello et al., 2009). These changes interact with strong biotic understory filters as native bamboo species (Altman et al., 2016). In the southernmost area of this biome, the Semi-deciduous Atlantic Forest (SAF) of Argentina, bamboo abundance is promoted by a decrease in stem basal area (Campanello et al., 2009). Thus, in relatively more open sites, bamboos show an invasive behaviour and gain dominance, forming dense clumps and extending their rhizomes along topsoil (Montti et al., 2014). As a result, bamboos outcompete tree seedlings, arresting sapling regeneration, reducing tree abundance and decreasing plant diversity (Tabarelli and Mantovani, 2000; Larpkern et al., 2010; Rother et al., 2013; Montti et al., 2014). Contrary to most fast-growing tree species that regenerate in gaps, bamboo litter has low quality and a slower decomposition rate (Montti et al., 2011). Consequently, ecosystem changes associated to the increment in bamboo abundance could explain carbon losses in relation to forest degradation.

Subtropical forests can assimilate carbon in excess of respiration throughout the year and they are, probably, among the largest carbon sinks across terrestrial ecosystems worldwide (Zhang et al., 2016). The increase in bamboo dominance through forest degradation would slow down the carbon and nutrient cycling in the ecosystem (Liu et al., 2011; Montti et al., 2011). However, more information about the underlying mechanisms is needed in order to be able to quantify the global effects of subtropical forest degradation. The main objective of this work was to study changes in ecosystem stocks and fluxes related to carbon cycling, along a forest degradation gradient in the SAF of Argentina. We hypothesize that forest degradation affects ecosystem properties, generating changes that are transferred from plants to soil through processes such as litterfall and litter decomposition. First, we expect the decrease in stem basal area to be reflected in changes in composition, quality and quantity of litterfall. Second, we expect forest degradation to influence the litter layer storage; given that low quality bamboo litter should tend to accumulate. Finally, we predict that all these changes will ultimately affect soil organic carbon (SOC) storage. In order to test this hypothesis, we performed field studies on forest structure, litterfall productivity and composition, litter layer storage, litter decomposition and SOC content along a forest degradation gradient.

2. Material and methods

2.1. Study site

We carried out field studies in the Semi-deciduous Atlantic Forest (SAF) of Argentina over a thirteen-month period (Oct-2012–Nov-2013), in a protected forest area adjacent to the Iguazú National Park (25°48'56"S–54°32'17"W). This zone was subjected to selective logging until 1987 (Chediack, 2008). The timber harvesting methods were similar those used elsewhere in tropical and subtropical forest, where only a few species of commercial interest are selected (Campanello et al., 2009). This results in forest areas of heterogeneous structure that ranges from highly impacted sites to untouched patches (Rivero et al., 2008).

The study area has a subtropical humid climate with no dry season. The mean annual rainfall is 2000 mm while the mean annual temperature is 20 °C, with monthly average from 15 °C in July to 25 °C in January (Campanello et al., 2009). The relief is rolling and soils are mostly Ultisols (Soil Survey Staff, 2014). The Semi-deciduous Atlantic Forest is greatly heterogeneous in structure. It is characterized by the presence of three well-defined canopy strata including more than 70 tree species, usually covered with numerous lianas and epiphytes, and mixed with shrubs, bamboos and grasses (Chediack, 2008; Campanello et al., 2009). The dominant tree species are *Nectandra megapotamica* (Spreng.) Mez (Lauraceae), *Cedrela fissilis* Vell. (Meliaceae), *Balfourodendron riedelianum* (Engl.) Engl. (Rutaceae), *Chrysophyllum gonocarpum* Mart. & Eichler (Sapotaceae), *Cordia trichotoma* (Vell.) Arráb. Ex Steud. (Boraginaceae) and *Lonchocarpus campestris* Mart. ex Benth. (Fabaceae). The most common sub-canopy tree species are *Sorocea bonplandii* (Baill.) W.C.Burger, Lanj. and Wess.Boer (Moraceae), *Trichilia catigua* A.Juss. and *Trichilia elegans* A.Juss. (Meliaceae). There are two palm species (Arecaceae), *Euterpe edulis* Mart. and *Syagrus romanzoffiana* (Cham.) Glassman, that are also frequent in this forest (Gatti et al., 2008). In open canopy areas, the understory is dominated by woody bamboo species (Poaceae), mainly of the genus *Chusquea* and *Merostachys* (Montti et al., 2011), forming gaps of impenetrable thickets (Tabarelli and Mantovani, 2000).

2.2. Experimental design

We located twelve plots of 0.36 ha (60 × 60 m), separated each other by more than 80 m, covering a degradation gradient in the same type of forest, soil and topography (ESM Fig. S1). The sites were selected considering bamboo dominance and the prevalence of either continuous or open forest canopy. This forest gradient is reflected in structural variables, as stem basal area and density (Table 1). One end of this gradient is characterized by *highly degraded sites* where the forest canopy is mostly open (large gaps), and by the presence of isolated stems immersed in a matrix dominated by bamboos with a density of 4 culms m⁻² (Campanello et al., 2009). The other end of this gradient is characterized by *closed sites*, where the forest canopy is continuous with nearly 35 m in height. Bamboos are scarce and restricted to small areas in the understory, with a density of <1 culm m⁻² (Campanello et al., 2009). The diverse intermediate states between both ends of this forest gradient were characterized by more or less canopy gaps immersed in a forest matrix.

2.3. Litterfall production

We estimated aboveground litterfall production by the systematic placing of five squares 1 m² litter traps 1 m aboveground per plot (with a total amount of 60 traps). These traps capture all litter lesser than 2 cm in diameter. We did not consider palm leaves,

Table 1
Forest structure along plots representing a degradation gradient in the Semi-deciduous Atlantic Forest, Argentina. The table shows basal area (BA) and the stem density per hectare and plot for stems >5 and >10 cm DBH, distinguishing between trees, palms and total stems (trees + palms).

Structure variables	Sites											
	← Highly degraded						→ Closed					
	1	2	3	4	5	6	7	8	9	10	11	12
>5 cm DBH												
Tree BA (m ² ha ⁻¹)	18.8	18.0	23.1	23.3	26.9	25.8	28.7	30.0	30.7	32.9	32.7	33.6
Palm BA (m ² ha ⁻¹)	0.3	1.7	0.0	0.7	0.9	3.1	3.0	1.9	1.5	2.5	4.5	5.3
Stem BA (m ² ha ⁻¹)	19.2	19.7	23.2	24.0	27.8	28.9	31.7	31.9	32.2	35.4	37.3	38.9
Tree density (ind ha ⁻¹)	561	614	814	706	825	858	722	744	661	881	981	864
Palm density (ind ha ⁻¹)	11	128	3	56	31	294	292	136	44	211	464	522
Stem density (ind ha ⁻¹)	572	742	817	761	856	1153	1014	881	706	1092	1444	1386
>10 cm DBH												
Tree BA (m ² ha ⁻¹)	17.7	16.7	21.1	21.8	25.3	23.9	27.1	28.6	29.5	31.1	30.5	31.8
Palm BA (m ² ha ⁻¹)	0.3	1.5	0	0.6	0.9	2.66	2.45	1.8	1.5	2.1	3.7	4.5
Stem BA (m ² ha ⁻¹)	18	18.2	21.2	22.4	26.2	26.6	29.5	30.4	31	33.3	34.2	36.3
Tree density (ind ha ⁻¹)	300	281	339	336	433	347	294	372	344	428	353	392
Palm density (ind ha ⁻¹)	8	86	3	36	28	178	167	111	44	136	292	344
Stem density (ind ha ⁻¹)	308	367	342	372	461	525	461	483	389	564	644	736

which tend to be too large to be trapped, or the litterfall produced at a height lesser than 1 m. We laid out litter traps in Nov-2012 and collected litter each 15 days until Nov-2013 (Proctor et al., 1983). We dried the collected material at 65 °C to constant weight, so as to estimate necromass (Sierra et al., 2007). The dried material was separated into four categories: (1) bamboo debris (*Chusquea ramosissima* Lindm.), (2) leaves debris (subdivided into *Balfourodendron riedelianum*, *Chrysophyllum gonocarpum*, *Cordia trichotoma*, and other leaves), (3) twigs and sticks debris, and (4) miscellanea debris (reproductive parts –fruits and flowers– and remains).

2.4. Litter layer aboveground

Aboveground necromass stock of litter layer included all organic matter from leaves, flowers, fruits and fine woody fractions less than 2 cm in diameter. It was quantified between Nov-2013 and May-2014, by placing nine 0.25 m² wire squares per plot, each separated from the other by at least 10 m. At the same places, we measured the thickness of litter layer from the top of the litter to the mineral soil. All material within this area was collected and dried at 65 °C to constant mass and weight.

2.5. Leaf litter quality

We collected fallen senescent leaves from four selected species once and air-dried them in the laboratory. We selected the bamboo *C. ramosissima* and three common tree species: *B. riedelianum*, *C. gonocarpum*, and *C. trichotoma*. The quality of the leaf litter from these species was determined by the percentage content (%) of soluble (e.g. sugars, amino acids and phenols) and non-soluble or recalcitrant compounds (lignin + cellulose + hemicelluloses). We carried out the analytical procedures with ANKOM equipment (Van Soest, 1982; AOAC International, 1990) at the Laboratorio ECFyA (INTA EEA Bordenave, Argentina). This sequential analysis first determines neutral detergent fibre content, which removes soluble C compounds from the litter (expressed in percentage as %SLCC), causing the neutral detergent fibre content to be the percentage of non-soluble fraction remaining (Delaney et al., 1996). Afterwards, the acid detergent fibre content procedure removes Hemicelluloses (also expressed in percentage as %HEMI). Finally, the acid detergent lignin procedure removes cellulose (%CELL), leaving the residue referred to as LIGN, formed by lignin and

“lignin-like” compounds such as cutin, acid detergent insoluble nitrogen and acid insoluble ash (%LIGN).

2.6. Leaf litter mass loss rates

We studied the leaf litter decomposition by determining the mass loss of the leaf litter in the field through the litterbag technique (Cuevas and Medina, 1988; Montti et al., 2011), during 360 days (1 yr). We prepared a total of 288 fibreglass litterbags (20 cm × 20 cm) containing 2.1 g of air-dried leaf litter, which were placed in groups on the floor in each permanent plot. We used a 2.85 mm mesh size with the purpose of excluding minor possible quantity of macro-fauna (Bradford et al., 2002) because of the critical role that soil-faunal community composition plays in decomposition in subtropical ecosystems (Wall et al., 2008). The bags were kept side by side and were fixed to the soil surface. The different types of studied substrates were (1) tree-mixed litter (ML1): mix of equal parts of leaf litter from the three tree species mentioned above (*B. riedelianum*, *C. gonocarpum* and *C. trichotoma*); (2) bamboo litter: pure litter of *C. ramosissima*; (3) bamboo with tree-mixed litter (ML2): mix of equal parts of leaf litter from bamboo and from the different tree species; (4) pure litter from each of the different tree species. For types of substrates 1 to 3 we placed a series of five litterbags. For substrates type 4 we placed a series of three litterbags. The litterbags were collected from the field by random selection every 1; 3; 6; 9 and 12 months. In the case of type 4, litterbags were collected every 1; 9 and 12 months. After recovering the bags, they were cleaned and oven-dried at 65 °C to constant weight.

We applied the composite-exponential decay function (or asymptotic model), where the decomposition rate decreases from an initial value ($a + b$, at $t = 0$) to a final value (a , at $t = \infty$) (Manzoni et al., 2012). This decomposition follows an exponential decay dynamics:

$$f(t) = a + b \cdot e^{-Kt} \quad (1.1)$$

where $f(t)$ is the amount of mass remaining at time t ; a is the amount of initial soluble necromass; b is the amount of initial recalcitrant necromass; K is the decomposition rate of soluble necromass (per year⁻¹).

Instead of K tending to zero, it tends towards a positive constant (the asymptote), indicating that the recalcitrant fraction is completely resistant to degradation. Although the goodness of fit of this

model is questionable, under certain experimental conditions where a part of soil biota is excluded, it can adequately describe data (Marqués López, 2013).

Additionally, we used Chi-square test to know if the decomposition rates of mixtures were similar to those expected without interaction between the different substrates.

2.7. Soil organic carbon storage

Soil samples were collected at two depths, 0–5 cm (five combined samples) and 10–20 cm (three combined samples) (Eclesia et al., 2012) in each plot, so as to determine the amount of organic carbon. The analysis of percentage of total soil organic carbon fraction (%SOC) and soluble or particulate organic carbon fraction (%POC), were carried out at the Laboratorio de Servicios Analíticos de Suelos, Plantas y Ambiente, Universidad Nacional del Sur, Bahía Blanca, Argentina. At the same time, soil bulk density (BD; Mg m^{-3}) was measured by the cylinder method (Blake and Hartge, 1986). Through %SOC, %POC and BD data, we obtained the SOC and POC mass (Mg ha^{-1}):

$$\text{organic carbon in soil (Mg ha}^{-1}\text{)} = P \cdot T \cdot \text{BD} \quad (1.2)$$

where **P** is the percentage (%) of SOC or POC and **T** (m) is the thickness of the soil.

2.8. Micro-environmental variables

During the study, we recorded air temperature (AT), air relative humidity (RH), and soil water content (SWC). Data loggers HOBO U23-002 (Onset Corporation, USA) were placed 5 cm aboveground in each plot to record the AT and RH. We alternated the systems among the plots for a year. The SWC was estimated gravimetrically. A part of every soil sample described above was oven-dried at 105 °C to constant weight, and SWC was calculated as follows:

$$[\text{SWC}] = (\text{WSW} - \text{DSW}) / \text{DSW} \quad (1.3)$$

where **WSW** is the wet soil weight and **DSW** is the dry soil weight.

2.9. Statistical analysis

To evaluate the effects of forest degradation on the ecosystem process of litterfall production and decomposition, and the stocks in litter layer and soil organic carbon, we analysed litterfall ($\text{Mg ha}^{-1} \text{ yr}^{-1}$), necromass and percentages of types of debris, litter layer necromass (Mg ha^{-1}), litter layer thickness (cm), proportion of remaining leaf litter mass per time, decomposition rate *K* (yr^{-1}), SOC and POC percentage (%) and mass (Mg ha^{-1}) at 0–5 cm and 10–20 cm of soil depth in the 12 plots along the forest degradation gradient. We also analysed the micro-environmental variables, AT (°C), air RH (%) and SWC (%). The main factor we analysed to determinate the relation between forest degradation and all these variables was BA, through Pearson's correlation coefficients (2-tailed) and linear regressions. Moreover, we performed one-way ANOVA (when the variances were equally distributed) or nonparametric one-way Kruskal-Wallis tests (when the variances were not equally distributed) to test for differences between (1) seasons (autumn-winter and spring-summer) to litterfall, (2) decomposition rates (*K*) of types of substrates, (3) depths (0–5 cm and 10–20 cm) to SOC, POC and SWC. We also performed Tukey tests for multiple mean comparisons (to ANOVA) and Post-hoc comparisons between the mean ranks (to K-W), to detect any significant difference ($\alpha = 0.05$).

3. Results

3.1. Litterfall production

Total litterfall did not change along the forest gradient ($R = 0.158$; $p = 0.623$, Fig. 1a). The litterfall average was $7.46 \pm 0.54 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ (mean \pm SE), without variations between seasons (ANOVA; $F_{12;1} = 0.50$; p greater than 0.05; autumn-winter: $3.87 \pm 0.31 \text{ Mg ha}^{-1} \text{ yr}^{-1}$; spring-summer: $3.58 \pm 0.27 \text{ Mg ha}^{-1} \text{ yr}^{-1}$). Leaves debris were the main contribution to aboveground $\approx 55\%$ ($4.05 \pm 0.22 \text{ Mg ha}^{-1} \text{ yr}^{-1}$), and were higher in autumn-winter season than in spring-summer (62%, 53%, respectively; K-W; $H_{12;1} = 8.67$; $p = 0.0032$). However, miscellanea

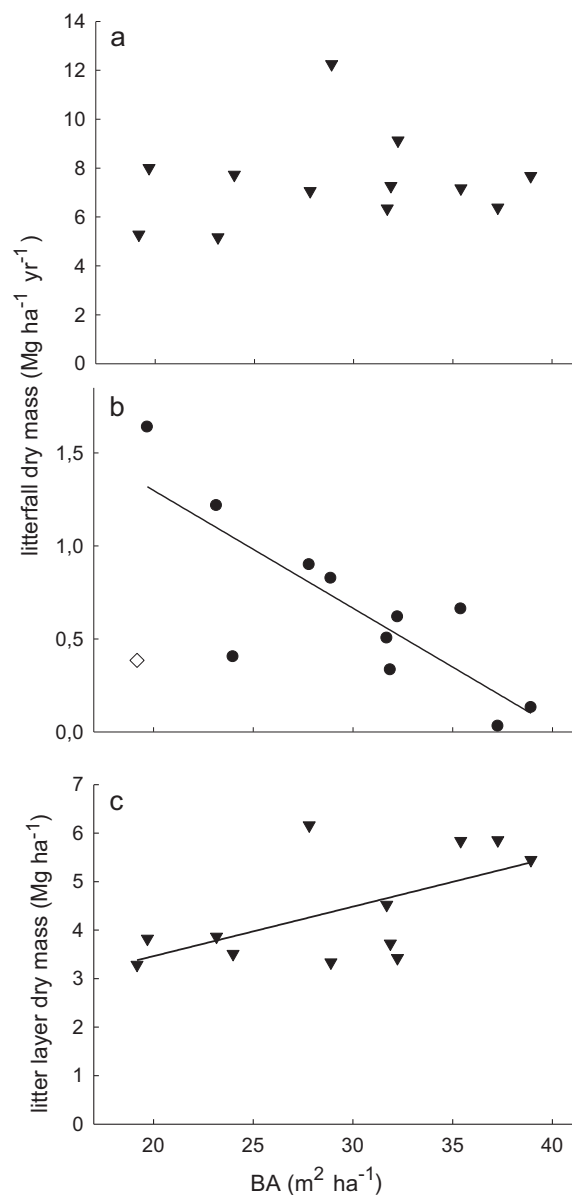


Fig. 1. Changes in litterfall and litter layer dry mass along the stem basal area (BA) gradient in the Semi-deciduous Atlantic Forest, Argentina. (a) Total litterfall and, (b) bamboo litterfall related to BA gradient (bamboo: linear function, $f(x) = 2.5650 - 0.0633 x$; $R^2 = 0.6635$; $p = 0.0023$); (c) litter layer dry mass related to BA gradient (linear function: $f(x) = 1.4221 + 0.1021 x$; $R^2 = 0.3663$; $p = 0.0370$). Averages of total litterfall and total litter layer dry mass are represented by triangles and bamboo litterfall dry mass by circles. The open diamond was not considered for the adjustment of the linear function (see explanation in text). Note that scales differ between graphs.

also represented a great contribution with $\approx 30\%$ ($2.29 \pm 0.31 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) that was higher in spring-summer season than in autumn-winter (31.95% and 23.92%, respectively; K-W; $H_{12;1} = 12$; $p = 0.0005$) (ESM Fig. S2). Twigs represented only $\approx 15\%$ ($1.11 \pm 0.14 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) without variation between seasons ($\approx 14\%$ in autumn-winter and 15% in spring-summer; K-W; $H_{12;1} = 2.25$; $p = 0.1333$). In contrast to total litterfall, bamboo debris decreased with the increment of stem BA, comprising 25% in low BA sites and only 0.38% in high BA sites (Fig. 1b). Bamboo litterfall in the most degraded sites did not show changes along the year (ANOVA, $F_{4;3} = 0.18$; $p = 0.9065$) in contrast to other plants litterfall in the most closed sites, which decreased more in spring (ANOVA, $F_{4;3} = 11.09$ $p = 0.0032$; ESM Fig. S3).

3.2. Fine litter layer aboveground

Litter layer necromass increased when forest BA increased (Fig. 1c), to more than 60%. However, litter layer thickness decreased with the increase in BA (Fig. 2a), to less than 50%. Interestingly, as bamboo litterfall during the spring-summer season increased, litter layer thickness increased too (Fig. 2b).

3.3. Leaf litter quality

Leaf litter quality, measured from the initial percentage of organic carbon compounds (%), changed among the different types of leaf litter under study (Table 2). The clearest difference was observed for soluble C organic compounds (SLCC) content; being the *B. riedelianum* substrate the leaf litter with the highest percentage of these compounds and the bamboo leaf litter with the lowest. The cellulose (CELL) and hemicelluloses (HEMI) contents showed a similar pattern, but less clearly. Instead, the lignin (LIGN) content was similar for *B. riedelianum* and bamboo, and for *C. trichotoma* and *C. gonocarpum*.

3.4. Leaf litter mass loss rates

The response of the proportion of remaining mass along the BA gradient was species-specific (ESM Fig. S4). Bamboo and *B. riedelianum* leaf litter showed an increase in the loss of mass when stem BA increased (bamboo: linear function at 1-yr incubation: $f(x) = 0.5921 - 0.0115 x$; $R^2 = 0.3851$; $p = 0.0313$; ESM Fig. S4a. *B. riedelianum*: linear function at 0.75 yr: $f(x) = 0.4076 - 0.0098 x$; $R^2 = 0.6287$; $p = 0.0021$; linear function at 1 yr: $f(x)$

$= 0.2280 - 0.0056 x$; $R^2 = 0.6325$; $p = 0.0034$; ESM Fig. S4f). This trend occurred since the beginning of the incubation period, even though it became significant only at the final dates. The *C. gonocarpum* leaf litter showed a similar trend, but it was not significant (ESM Fig. S4e). On the other hand, *C. trichotoma* litter (ESM Fig. S4b) and the mixed-litter (ML2 and ML1; ESM Fig. S4c and d) did not show relationships with the changes in forest basal area.

There was a clear difference in the decomposition rate among studied species (ANOVA; $F_{12;5} = 67.25$; $p < 0.0001$; Fig. 3a). The *B. riedelianum* leaf litter showed higher decomposition rate, which was nearly ten times greater than the *C. ramosissima* leaf litter decomposition rate. *Cordia trichotoma* leaf litter showed a decomposition rate higher than bamboo but lower than *C. gonocarpum*, which was similar to the mixtures (ML1 and ML2) rates. Moreover, all the substrates were adjusted to a similar decomposition curve (Fig. 3b).

Litter decomposition decelerated over time, although the bamboo kept a constant decomposition rate throughout the year. After one year of incubation, there was virtually no mass remaining of *B. riedelianum* (10%) and *C. gonocarpum* (16%), but *C. ramosissima* and *C. trichotoma* still had enough mass remaining in litterbags ($\approx 31\%$). The proportion of remaining mass in both mixtures were similar to that expected without interaction between types of substrates (in all the cases, χ^2 ; $p < 0.999$). Interestingly, as the SLCC in litter increased, the decomposition rate also increased ($R^2 = 0.9917$; $p = 0.0041$; ESM Fig. S5a), although it decreased in relation to the proportion of remaining mass in the first month of the incubation period ($R^2 = 0.9623$; $p = 0.0190$; ESM Fig. S5b).

3.5. Soil organic carbon storage

The percentage of SOC content did not show a relation with BA at 0–5 cm depth ($R = 0.4797$; $p = 0.1146$; Fig. 4a), but at 10–20 cm depth it increased when BA increased (Fig. 4b). In contrast, the percentage of POC showed an increase when BA increased at 0–5 cm depth (Fig. 4a), a phenomenon that did not occur at 10–20 cm depth ($R = 0.4511$; $p = 0.1638$; Fig. 4b). On the other hand, the mass of SOC and POC at 0–5 cm depth increased when BA increased by 100% and 900%, respectively (Fig. 4c). However, at 10–20 cm depth no changes were observed neither in SOC nor in POC mass along the BA gradient (SOC: $R = 0.3116$; $p = 0.3509$; POC: $R = 0.3837$; $p = 0.2440$; Fig. 4d). At 10–20 cm depth, SOC was $20.33 \pm 0.9 \text{ Mg ha}^{-1}$ and POC was $1.97 \pm 0.20 \text{ Mg ha}^{-1}$.

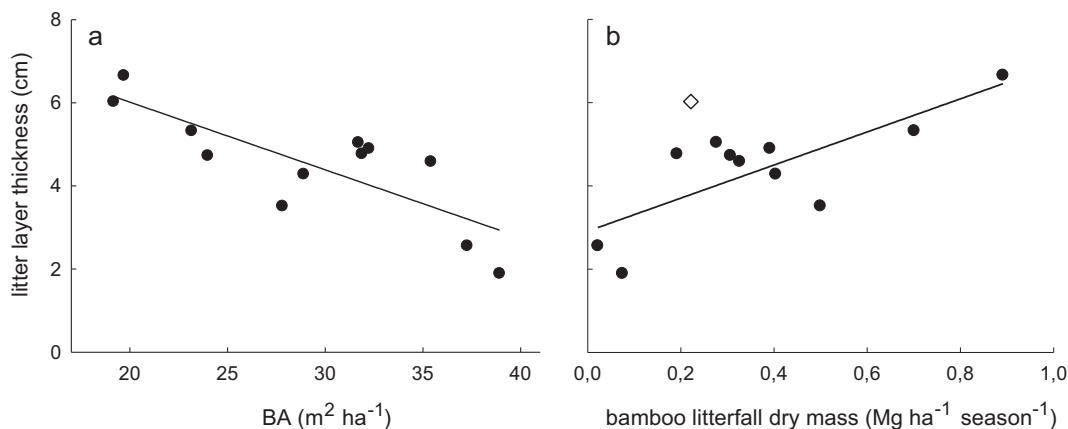


Fig. 2. Changes in litter layer thickness (a) along the stem basal area (BA) gradient (linear function: $f(x) = 9.2707 - 0.1628 x$; $R^2 = 0.6389$; $p = 0.0018$), and (b) related to bamboo litterfall during spring-summer season (linear function: $f(x) = 2.9094 + 3.9737 x$; $R^2 = 0.5957$; $p = 0.0054$) in the Semi-deciduous Atlantic Forest, Argentina. Symbols are averages. The open diamond was not considered for the adjustment of the linear function (see explanation in text).

Table 2

Initial percentage of organic carbon compounds (mean \pm SE) of different types of leaf litter (bam: *C. ramosissima*, C.tri: *C. trichotoma*, C.gon: *C. gonocarpum*, B.rie: *B. riedelianum*). Organic compounds abbreviations: SLCC, soluble carbon compounds; CELL, cellulose; HEMI, hemicelluloses; LIGN, lignin. Different letters indicate significant differences ($p < 0.05$) between the types of leaf litter.

Leaf litter	SLCC		CELL		HEMI		LIGN	
<i>bam</i> (bamboo)	31.77	$\pm 0.66^a$	29.89	$\pm 0.95^c$	28.45	$\pm 0.64^c$	9.90	$\pm 0.91^a$
<i>C.tri</i> (tree)	40.83	$\pm 0.48^b$	17.99	$\pm 0.42^{bc}$	19.09	$\pm 0.50^b$	22.10	$\pm 0.21^b$
<i>C.gon</i> (tree)	45.31	$\pm 0.86^c$	17.22	$\pm 0.35^{ab}$	15.62	$\pm 0.31^a$	21.85	$\pm 1.01^b$
<i>B.rie</i> (tree)	63.97	$\pm 0.95^d$	9.69	$\pm 0.56^a$	14.99	$\pm 0.44^a$	11.35	$\pm 0.24^a$
Test	ANOVA: $F_{4,3} = 319.44$; $p < 0.0001$		K-W: $H_{4,3} = 13.26$; $p = 0.0041$		ANOVA: $F_{4,3} = 161.53$; $p < 0.0001$		K-W: $H_{4,3} = 11.67$; $p = 0.0086$	

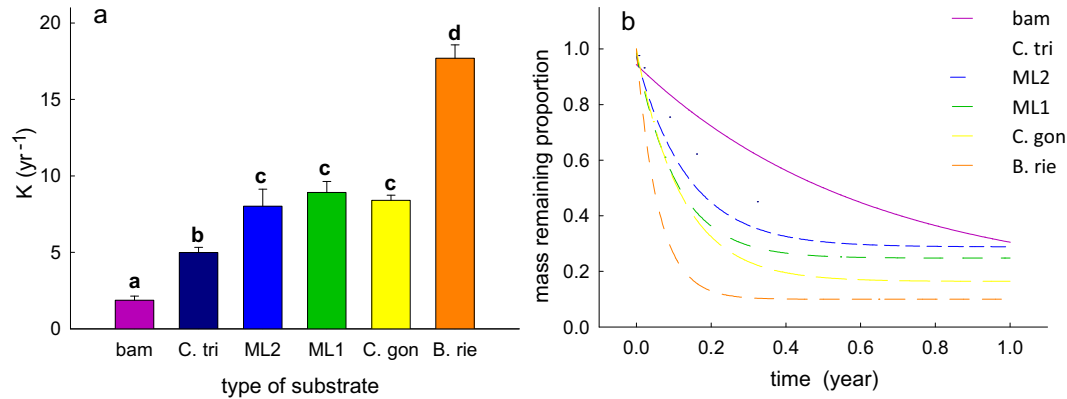


Fig. 3. Decomposition rates and mass loss in field for six substrate types: bam, *C. ramosissima*; C.tri, *C. trichotoma*; C.gon, *C. gonocarpum*; B.rie, *B. riedelianum*; ML1, mix of three tree native species; ML2, mix of the tree native species + bamboo. (a) Decomposition rates of substrates (K). Different letters indicate significant differences between K. (b) Initial proportion of remaining mass along one-year incubation period. The field experimental data were adjusted to the composite-exponential decay model (Eq. (1.1), see above for more details). Bam: $f(x) = 0.1490 + 0.7947 e^{(-1.6300 x)}$; $R^2 = 0.8300$; $p < 0.0001$; C.tri: $f(x) = 0.3082 + 0.6907 e^{(-4.8886 x)}$; $R^2 = 0.9644$; $p < 0.0001$; ML2: $f(x) = 0.2877 + 0.6848 e^{(-7.2672 x)}$; $R^2 = 0.9068$; $p < 0.0001$; ML1: $f(x) = 0.2472 + 0.7381 e^{(-9.2947 x)}$; $R^2 = 0.9420$; $p < 0.0001$; C.gon: $f(x) = 0.1634 + 0.8362 e^{(-8.2396 x)}$; $R^2 = 0.9786$; $p < 0.0001$; B.rie: $f(x) = 0.0991 + 0.9009 e^{(-17.0817 x)}$; $R^2 = 0.9821$; $p < 0.0001$.

3.6. Micro-environmental variables

The annual air temperature (AT) was similar along the forest BA ($R^2 = 0.0538$; $p = 0.868$), with a mean of 20 ± 0.67 °C. The annual air relative humidity (RH) increased with the forest degradation (quadratic function: $f(x) = 85.9421 + 1.0435x - 0.0228 x^2$; $R^2 = 0.6819$; $p = 0.006$), with a maximum of 98.5% in the most degraded sites and a minimum of 91.4% in closed sites. However, the soil water content (SWC), both at 0–5 cm and 10–20 cm depth, did not change significantly along the forest gradient ($p = 0.07$).

4. Discussion

Our study clearly shows that forest degradation has a cascade effect on carbon cycling and storage that moves from forest structure to soil through changes in different ecosystem processes mediated by plants, such as litterfall, litter accumulation and decomposition. This degradation also affects soil organic carbon (Fig. 5). The reduction in stem basal area and the increase in bamboo abundance, associated to forest degradation, affect the litterfall composition and its quality, through the increase in the amount of bamboo litter. This increase can slow down the average decomposition rate of the whole litter layer, given the lower decomposition rates of this detritus. Forest degradation also causes the litter layer to undergo a decrease in necromass and an increase in thickness. A more unexpected finding is that litter decomposition rates of the two most contrasting species (*C. ramosissima* and *B. riedelianum*) are also decreased by forest degradation, even when microclimate conditions at soil level remain mostly unaltered by forest structure changes. All these changes seem to affect processes related to carbon input to the soil, given that soil organic carbon also changes

accordingly along the forest degradation gradient, storing less soil organic carbon per hectare in highly degraded sites. At present, the carbon flux from forest degradation may be one of the greatest uncertainties in the carbon budget (Grace et al., 2014). However, nowadays there is growing agreement on forest degradation being almost as important as deforestation in terms of gross carbon emissions to the atmosphere (Harris et al., 2012). In this sense, our study provides a better understanding on the mechanisms behind carbon cycling and storage along forest degradation that go beyond the loss of biomass due to tree harvest. Information provided here could improve our understanding on the matter, as well as the predictive power of carbon balance models.

4.1. Litterfall production

Changes in forest structure are not reflected in changes in total litterfall amounts. This is an unexpected result and could be explained considering the replacement of litterfall from trees by litterfall from bamboos and other fast growing herbaceous species developing in degraded sites. Fast growing species have high turnover rates and short leaf life span compared to the shade tolerant and slow growing species typical of the closed forest sites (Valladares and Niinemets, 2008). Consequently, they generate more detritus than slow growing species, which tend to conserve resources (Campanello et al., 2011). It is also possible that the number of traps used here is insufficient to detect those changes in litterfall that are related to canopy, which could occur at smaller spatial scales (Hirabuki, 1991). This observation is supported by a preliminary analysis, which indicates that litterfall actually increases with basal area when considering a smaller area around the trap (0.01 ha; $R^2 = 0.33$; $p < 0.0001$).

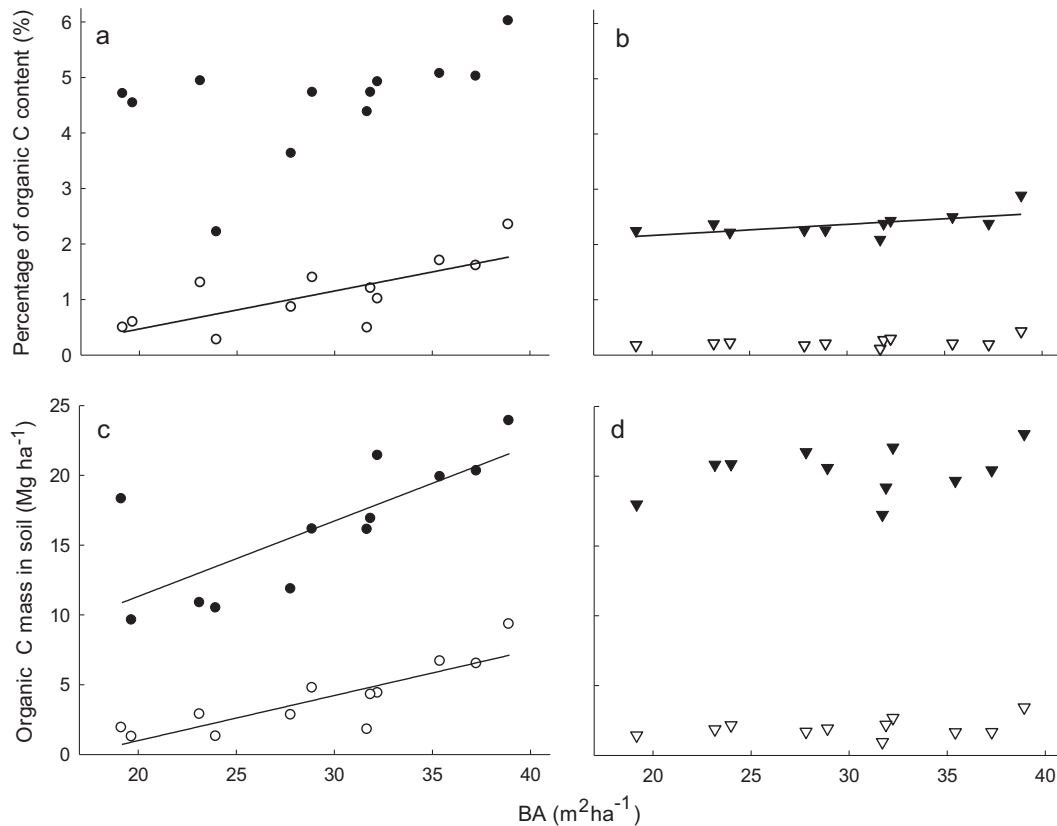


Fig. 4. Changes in percentage and dry mass of total soil organic carbon (SOC; filled symbols) and particulate soil organic carbon (POC; open symbols) at two depths, 0–5 cm (circles) and 10–20 cm (triangles), along the stem basal area (BA) gradient in the Semi-deciduous Atlantic Forest, Argentina. Changes in the percentage of SOC and POC along the BA gradient at a depth of (a) 0–5 cm (POC: linear function: $f(x) = -0.8995 + 0.0685 x$; $R^2 = 0.5504$; $p = 0.0057$) and (b) 10–20 cm (SOC: linear function: $f(x) = 1.7598 + 0.0202 x$; $R^2 = 0.3594$; $p = 0.0513$). Changes in dry mass of SOC and POC related to BA at a depth of (c) 0–5 cm (linear function: SOC: $f(x) = 0.5150 + 0.5405 x$; $R^2 = 0.5692$; $p = 0.0046$; POC: $f(x) = -5.4701 + 0.3233 x$; $R^2 = 0.7193$; $p = 0.0005$) and (d) 10–20 cm.

Forest degradation and increases in bamboo abundance change litterfall composition. These changes can affect the average litter quality, because high quality litter (i.e. tree litter) is replaced by low quality litter (i.e. litter largely composed by bamboo). Additionally, as tree litterfall shows a peak in the spring season, and bamboo litterfall is evenly distributed throughout the year, the replacement of trees by bamboos also affects the timing of litter inputs to the forest floor, which could affect litter nutrient cycling and forest productivity (Prause et al., 2002; Wood et al., 2009).

4.2. Litter layer

Contrary to our expectations, litter layer necromass and thickness change in opposite directions in relation to forest degradation (Fig. 5). This decrease pattern could be explained by the changes in forest structure and its dynamics (Chao et al., 2009), resulting from tree logging and forest degradation, that has caused a low necromass accumulation across the years. At the same time, the increase in litter layer thickness in more degraded sites is directly related to a greater input of bamboo leaf litter reaching the forest floor (Fig. 2). Specific leaf mass of bamboo leaves is lower than that of most tree species leaves, so the weight of bamboo leaf litter is comparatively lower than that of tree litter (Montti et al., 2014) and its decomposition rate is very slow, which generate the formation of a wide and light litter layer. A larger, bamboo-dominated litter layer in degraded sites may influence seedling recruitment by intercepting seedling emergence and preventing newly dispersed seeds from reaching suitable soil substrate (Larperkern et al., 2010).

4.3. Litter decomposition

Two main hypotheses have been proposed over the last years to explain changes in decomposition for the same species under different conditions. These are the Home Field Advantage hypothesis (HFA, Vivanco and Austin, 2008) and the Substrate Quality–Matrix Quality Interaction hypothesis (SMI, Freschet et al., 2012). Both ideas suggest that litter decomposition depends on the interaction between substrate type (fresh decomposing litter) and the matrix (litter layer). Our study shows that forest degradation affects leaf litter decomposition negatively, however our data do not follow the general patterns expected under these two main hypotheses. In the present work, leaf litter decomposition of the most contrasting substrates, *B. riedelianum* and bamboo, is slower in more degraded sites than in closed sites. However, the other four substrates do not change along forest gradient, and we have registered larger differences in decomposition rate (k) among species rather than among more or less degraded forest sites (see explanation in the next section: *Litter Quality*). Unlike the HFA hypothesis, where it is proposed that litter decomposes faster under the species from which they come, here we observe that in more degraded sites, where bamboos are overabundant, bamboo litter decomposes most slowly. Our results do not fit the predictions under SMI hypothesis either, because, even when bamboo litter quality is similar to average matrix quality in bamboo-dominated sites, it decomposes more slowly there than in tree dominated sites, where litter layer quality is higher. A similar response was found by Aragón et al. (2014) in a subtropical mountain forest, where in sites invaded by the exotic species *Ligustrum lucidum* WT Aiton

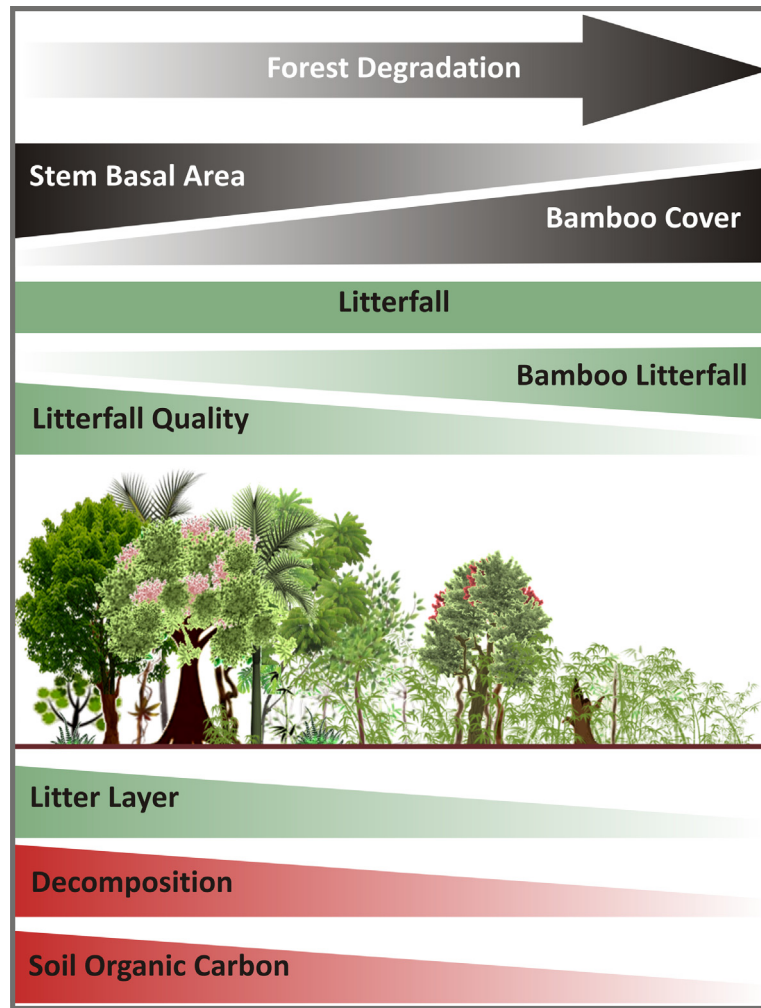


Fig. 5. Semi-deciduous Atlantic Forest degradation, caused by the increase in bamboo cover and the stem basal area reduction, affects the litterfall composition and its quality, through the increase of bamboo litterfall. Total litterfall did not change, but litter layer decreased. At the same time, as the leaf litter quality decreased and decomposition rate was delayed, the average decomposition rate of the whole litter layer could decrease with forest degradation, finally affecting the soil organic carbon, where the more degraded sites storage less soil carbon per surface unit.

(Oleaceae), the litter decomposition of this species is slower than in non-invaded sites, where a more diverse native forest develops. *Balfourodendron riedelianum* litter, in turn, decomposes faster under tree dominated sites where the litter layer is more similar to this type of litter, following the predictions of the SMI hypothesis. In agreement with Perez et al., 2013, SMI assumptions tend to prove higher effects with soluble (*B. riedelianum*) rather than recalcitrant litter (bamboo). Most hypotheses have been proposed and experimented in cold or temperate ecosystems (Vivanco and Austin, 2008; Ayres et al., 2009; John et al., 2011; Freschet et al., 2012; Perez et al., 2013). Hence, since there is a surprising amount of diverse factors that regulate decomposition (Bradford et al., 2016), alternative explanations should be proposed for tropical and subtropical highly diverse forests. However, even though their work has focused on temperate forest, John et al. (2011) have proposed that low-quality litter decomposition can be hastened when surrounded by large amounts of high quality litter, as an indirect consequence of decomposers activity that act by inertia upon new substrates. This last hypothesis is the one that could more accurately explain our findings.

Supporting our hypothesis, changes in litter composition and litter thickness associated with forest degradation can reduce the whole litter quality and the contact of litter with the soil, affecting litter decomposition. Changes in forest structure and composition alter the composition as well as the diversity of the soil biota

(Zak et al., 2003). For example, macro and mesofauna are more affected than microbiota in response to changes in vegetation (Spehn et al., 2000; John et al., 2011), which have an important effect in plant decomposition (Wall et al., 2008). Litter accumulation due to low quality litter can provide more habitats for a large abundance and diversity of decomposers (Perez et al., 2013). However, in forests with high bamboo cover, a homogeneous matrix is formed due to the fact that bamboo leaves are linear and flat and accumulate in a thick layer on the floor (Larperkern et al., 2010). Consequently, this homogeneous litter layer offers less potential microenvironments and habitat diversity for soil biota (Hansen, 2000). In contrast, under closed forest sites, tree-mixed litter comprises tree leaves and other plants detritus of different sizes, shapes and surface structures, forming a more open and complex matrix (Larperkern et al., 2010) with higher habitat heterogeneity. For these reasons, we expect changes in abundance and/or diversity of soil organisms to be involved in the slow decomposition of the bamboo-dominated litter, and to be able to explain it.

4.4. Litter quality

The largest differences were observed in decomposition rates (k) among species rather than along forest gradient. This seems to be the result of different leaf litter quality. As suggested by Pérez-Harguindeguy et al. (2015), we have found that the initial

amount of SLCC and the initial amount of non-soluble compounds (LIGN + CELL + HEMI) in litter are strongly linked to decomposition rates. Decomposition rates are highest when the initial amount of SLCC compounds is highest, too. In addition, this phenomenon can also be related to higher leaf areas (generally deciduous leaves), which is associated with lower hardness and higher palatability, and, hence, higher decomposition rates (Cornelissen et al., 1999).

4.5. Soil organic carbon

Along the forest degradation gradient, we observed changes in SOC and mainly in POC, which shows a quick response to the changes in the use and the management of the land (Videla et al., 2008). In perennial subtropical ecosystems, the main controllers of SOC changes are the quantity and the quality of C inputs incorporated and stabilized by decomposition, rather than the C outputs caused by mineralization (Eclesia et al., 2016). For this reason, high quality litter (composed by more soluble compounds, as *B. riedelianum* and other tree species litter) decomposition results in a more efficient soil organic matter formation than the one produced by low quality litter (as bamboo litter). This is due to a more efficient microbial substrate use (Cotrufo et al., 2013). With high quality litter, the microbes do not have an additional cost, compared to low quality litter, which has high energy costs associated to breakdown (Cotrufo et al., 2013). As a result of forest degradation, soil carbon stock at 0–5 cm depth decreases by a 50%. This is particularly relevant because 50% of the SOC (in the top meter) in forest ecosystems is stored in the top 20 cm (Jobbágy and Jackson, 2000; Eclesia et al., 2012). Given that the soil contains more carbon than the atmosphere and the vegetation combined (Schlesinger, 1997), we must emphasize that, even if the disturbed forest does not recover equilibrium between carbon inputs and outputs during this degradation process, it acts as a carbon source instead of a carbon sink. Thus, low disturbance forests contribute more to global carbon sink than highly disturbed forests.

5. Conclusions

Our study shows that bamboo dominance in degraded forest affects ecosystem carbon cycling and decreases carbon storage in forest soils. This can worsen the forest degradation process since it can have a negative effect on primary productivity.

In summary, in the current context of global change, the information presented in this work can (1) allow to estimate carbon losses associated to forest degradation, quantifying their contribution to the global carbon balance; (2) help to predict the consequences of forest degradation over ecosystem fluxes and stocks, and also (3) help to define forest management strategies to reduce carbon emissions caused by forest degradation and to increase the forest productivity in order to improve carbon sequestration and nutrient cycling.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2017.05.047>.

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