Forest Ecology and Management 400 (2017) 208–217

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

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

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A R T I C L E I N F O

*Article history:*
Received 3 March 2017
Received in revised form 25 May 2017
Accepted 25 May 2017
Available online 12 June 2017

*Keywords:*
Atlantic Forest
Degradation
Decomposition
Litterfall
Ecosystem processes
Necromass

A B S T R A C T

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.



## 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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http://dx.doi.org/10.1016/j.foreco.2017.05.047
0378-1127/

(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 (Quested 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 $m^2$ 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,