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Unravelling ecosystem functions at the Amazonia-Cerrado transition: II. Carbon stocks and CO_2 soil efflux in *cerradão* forest undergoing ecological succession☆

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ABSTRACT

The transition region between two major South American biomes, the Amazon forest and the Cerrado (Brazilian savanna), has been substantially converted into human-modified ecosystems. Nevertheless, the recovery dynamics of ecosystem functions in this important zone of (ecological) tension (ZOT) remain poorly understood. In this study, we compared two areas of *cerradão* (a forest-woodland of the Brazilian savanna; Portuguese augmentative of *cerrado*), one in secondary succession (SC) and one adjacent and well preserved (PC), to test whether the ecosystem functions lost after conversion to pasture were restored after 22 years of regeneration. We tested the hypothesis that the increase in annual aboveground biomass in the SC would be greater than that in the PC because of anticipated successional gains. We also investigated soil CO_2 efflux, litter layer content, and fine root biomass in both the SC and PC. In terms of biomass recovery our hypothesis was not supported: the biomass did not increase in the successional area over the study period, which suggested limited capacity for recovery in this key ecosystem compartment. By contrast, the structure and function of the litter layer and root mat were largely reconstituted in the secondary vegetation. Overall, we provide evidence that 22 years of secondary succession were not sufficient for these short and open forests (e.g., *cerradão*) in the ZOT to recover ecosystem functions to the levels observed in preserved vegetation of identical physiognomy.

1. Introduction

The transition region between the Amazon and the Cerrado in Brazil is a zone of (ecological) tension (ZOT) that extends for more than 4500 km (Marimon et al., 2006). This region encompasses complex mosaics of savanna and forest vegetation with highly variable structure (Ratter et al., 1973) along the so-called "Arc of Deforestation" (Nogueira et al., 2008). Land use patterns in the ZOT have changed rapidly in recent decades, with the area of transitional forests now largely reduced by deforestation (Alencar et al., 2004). In addition to increased land conversion to agriculture, forests of the ZOT are also subject to more intense seasonal variations and climate change than those in the central Amazon (Malhi et al., 2008). These conditions, allied to the contact tension between the two biomes, result in a hyperdynamic vegetation (i.e. fast mortality and recruitment), given their rapid turnover rates of individuals of trees (mortality vs recruitment) with many sites exceeding 3% annual turnover rates for stems >10 cm diameter (Marimon et al., 2014).

One of the most important forest types in the ZOT is the so-called *cerradão* (Portuguese augmentative of *cerrado*), as

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described by Ratter et al. (1973). Like other tree-dominated physiognomies of the transition zone the *cerradão* is "hyperdynamic" (Marimon et al., 2014). The *cerradões* contain a mixture of species from both the Cerrado and the Amazon (Ratter et al., 1973) and are an important vegetation type in the region that connects the two biomes (Ratter, 1992; Marimon et al., 2006). This vegetation type has been drastically reduced in the southern and southeastern Amazon since the 1970s (Marimon et al., 2014), particularly because legislation is less strict for removing *cerradão* vegetation, as this vegetation type is often considered a component of the Cerrado biome. As a result, most areas of *cerradão* are lost and only disconnected fragments remain.

Based on empirical evidence and computing modelling, approximately 2.1 million km^2 of vegetation is at risk of being lost in the Amazon by 2050, with only 53% of the original coverage remaining (Soares-Filho et al., 2006). Converting the native vegetation for agriculture and/or cattle causes losses of ecosystem functions on regional and local levels, resulting in changes in the CO_2 emissions (Malhi et al., 2008) and consequently in the carbon stock (Santos et al., 2004; Aragão et al., 2014). Such activities are responsible for disrupting the carbon balance, resulting in estimated emissions of 1.1 $\pm$ 0,7 Pg C to the atmosphere every year from tropical deforestation (Friedlingstein et al. (2010), often concentrated in marginal areas such as the Amazon-Cerrado where the climate is more seasonal than in core forest areas. Important ecosystem functions are endangered by this, including forest evapotranspiration, resulting in rainfall reduction (Aragão, 2012) and the consequent increase in carbon emissions (Malhi et al., 2008). As a "domino effect", other components have also been modified through time due to land use change, such as decreasing of organic matter of the soil, which, consequently, alters the nutrient cycling (Diez et al., 1991; Varella et al., 2004) and soil respiration (Atarashi-Andoh et al., 2012).

The deleterious effects of establishing pasture include diminishing the nutrient cycling and organic matter of the soil, which, in general, makes the deforested lands subsequently unproductive and typically abandoned, leading to development of secondary vegetation (Günter et al., 2007; Houghton et al., 2012). Typically, tropical secondary landscapes may have forests at different stages of succession (Feldpausch et al., 2004), where during the first years of abandonment the successional process is slower compared to later stages (Vieira et al., 2003), and maybe affected by fragmentation (Günter et al., 2007). There is no clear evidence that such successional vegetation is fully capable of returning to its complete, original state in Amazonia, since diversity and the carbon stock, even in late stages of succession, is typically lower than in pristine vegetation (Houghton et al., 2012). Nevertheless, considering the vegetation growth of occupied areas by secondary succession, their atmospheric carbon absorption is potentially a major contributor to restoring the carbon balance in tropical regions (Aragão et al., 2014; Poorter et al., 2016). Unfortunately, due to the landscape fragmentation, the regeneration of abandoned pastures is a very slow process.

It is important to consider that the natural regeneration of abandoned pastures depends on the management systems and the consequent impact on the soil and on the capability of receiving new species in terms of seed sources, germination, and establishment (e.g., Cheung et al., 2009). Vegetation with a history of intense and prolonged uses, usually undergo slower regeneration (Uhl et al., 1988). Indeed, the total removal of the vegetation and processes associated with introduction of grasses (e.g. soil ploughing) can damage tree seeds and hinder the capacity of restoring the vegetation (Cheung et al., 2009). In such areas, other factors may act to limit the successional process, such as the distance between the pasture to the remaining forests (Günter et al., 2007) and the micro-climates under tropical conditions (e.g., high temperature and low soil moisture) (Nepstad et al., 1996). Cattle grazing can also affect the soils, both physically and chemically, increasing the apparent density and decreasing porosity and fertility (Reiners et al., 1994).

Throughout the different stages of succession a few key species are typically essential for providing vegetation structure and for restoring ecosystem functionality. For example, key-species of *cerradão*, such as *Tachigali vulgaris* L. G. Silva & H. C. Lima (Fabaceae), strongly influence both the vertical structure (Franczak et al., 2011) and the hyperdynamic condition of the vegetation (Marimon et al., 2014), and its nutrient cycling rates (Oliveira et al., 2017). According to Morandi et al. (2015), this species promotes a strong rate of change in the primary successional seres. The same authors identified that the fragments of *cerradões*, when protected, have the potential to expand naturally into damaged areas via ecological succession, including into land previously occupied by 'typical cerrado' vegetation (cerrado tipico, i.e. cerrado *sensu stricto*), so demonstrating that these forests can occupy open environments. Similar results were observed in another Brazilian c*erradão* landscape where the reduction of human activity reduced the area occupied by 'cerrado tipico', while the area occupied by *cerradão* increased (Durigan and Ratter, 2006). These observations suggest that conservation action involving *cerradões* in the ZOT may have the effect of increasing forest cover and, consequently, Net Primary Productivity (NPP), and hence resulting in a positive carbon balance. Such measures could at least partially reverse the effects of increased CO_2 emissions and recover ecosystem functions lost by clear-cutting and burning of native vegetation in the region.

Although the deforested area in the ZOT continues to increase, in this region in particular little is known about the consequences of this disturbance on primary ecosystem functions, including changes in biomass, soil CO_2 efflux and organic matter. For example, little is known about how the replacement of native vegetation by pasture in the ZOT affects soil carbon fluxes (Varella et al., 2004), which emphasizes the urgent requirement to understand the magnitude of such fluxes in natural and modified ecosystems (Santos et al., 2004). Measuring each or most components of the carbon cycle should help increase understanding of the interactions among components and of the effects that the climatic characteristics of each environment have on the components (Huasco et al., 2013). Additionally, these types of studies can reveal the effects of man-made disturbances on ecosystem functions and their consequences for NPP and carbon balance in hyperdynamic vegetation systems.

In this study, we compared the carbon stocks and soil CO_2 efflux of a preserved area (PC) and a successional area of *cerradão* (SC) that has been used as pasture for 22 years. We tested whether the ecosystem functions linked to carbon balance had recovered after two decades, and specifically, we asked whether the natural 'hyperdynamic' properties of the vegetation (i.e., the tendency to have much more rapid rates of stem recruitment and mortality than typical for tropical forests (Marimon et al., 2014), cf. e.g. Phillips et al. (1994) contributed to the natural recovery of vegetation and of ecosystem functions via ecological succession. Thus, we compared the carbon cycles of the PC and the SC to test the following hypotheses: 1) the SC has higher annual increments of biomass but lower aboveground biomass, soil CO_2 efflux, litter layer content, and biomass of the superficial layer of fine roots; 2) seasonal variation is observed in CO_2 efflux, litter layer content, and biomass of the superficial layer of fine roots in both areas; 3) soil moisture is the main abiotic factor of subcanopy controlling CO_2 efflux; 4) CO_2 efflux increase with the increases in litter layer, fine root biomass, and/or aboveground biomass in both areas.