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Why are forests so scarce in subtropical South America? The shaping roles of climate, fire and livestock

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ABSTRACT

Forest cover is notoriously sparse across neotropical southeastern South America. In particular, the practically treeless landscapes of the Campos, as they are locally known, have puzzled ecologists since Darwin's time. We used remote-sensing information and spatial regression models to relate tree cover to resource availability (i.e. climate, soil fertility, soil water holding capacity), disturbances (i.e. fire occurrence, cattle grazing) and landscape features that can mediate the effects of both (i.e. topography, distance to rivers). To better understand these relationships, we conducted the analysis at different spatial scales across non-cultivated areas of southeastern South America. Overall, tree cover in southeastern South America increases with precipitation but is limited by livestock densities and fire occurrence. Forests are concentrated close to rivers, especially in the Campos region, where cattle grazing seems to prevent tree expansion into the grasslands.

1. Introduction

The extensive grasslands of the Uruguayan Savanna Ecoregion, also known as Campos, represent a regional ecotone between the subtropical and tropical forests and the temperate grasslands of South America (Soriano, 1992; Olson et al., 2001). These practically treeless landscapes have fascinated ecologists as far back as the 19th century. Darwin, during the voyage of the Beagle, noted the "general, almost entire", "remarkable" absence of trees in Uruguay despite the relatively high rainfall level (Darwin, 1890). This strong correlation between increasing rainfall levels and higher tree cover has long been recognized (Whittaker, 1975; Woodward et al., 2004; Sankaran et al., 2005). More recently, analyses at global scales have found an increasing probability in the occurrence of savannas and forests as mean annual precipitation increases (Hirota et al., 2011; Staver et al., 2011).

The treeless landscapes of southeastern South America are likely the combined result of past and current processes. It has been suggested that large areas of grasslands, in today's moister climate, may be relicts of drier periods (Pillar and Quadros, 1997) that were common in the past 13,000 years (Piovano et al., 2009). Indeed, trees and shrubs have expanded locally across the region during the moister climate condition of the last century suggesting the potential for larger tree cover (Gautreau and Lezama, 2009; Gautreau, 2010; Müller et al., 2012; Anadón et al., 2014). Anthropogenic effects may also play an important role in explaining this process (Lauenroth, 1979; Sala, 2001; Lemaire et al., 2005), as suggested by the expansion of shrubs and trees in sites where fire or grazing have been excluded (Pillar and Quadros, 1997; Oliveira and Pillar, 2004; Overbeck et al., 2007; Chaneton et al., 2012; Müller et al., 2012; Cingolani et al., 2014; Lezama et al., 2014).

To understand the large scale patterns of tree cover across the Campos region, we analyzed the distribution of tree cover in relation to resources (i.e. climate, soil fertility, soil water holding capacity), disturbances (i.e. fire occurrence, cattle grazing) and landscape features (i.e. topography, distance to rivers). We compared the patterns of the Campos with those of subtropical and tropical regions in southeastern South American (SSA) within the same precipitation range than the Campos. These large scale analyses aim to unravel the common processes that contribute to shape the structure of distinct plant communities regardless of their differences in species composition. The climate of this region has become moister and warmer during the last century (Haylock et al., 2006), a trend that is expected to continue with climate warming (Marengo et al., 2010; IPCC, 2013) and that can favor tree

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growth. Understanding how climate and disturbance regimes interact today may contribute to anticipate potential changes in one of the world's most important rangelands.

2. Materials and methods

2.1. Study regions

We studied tree cover distribution in the Uruguayan Savanna ecoregion (NT0710) (Olson et al., 2001), formed by the entire Uruguay and southern Brazil (hereafter the Campos as it is locally known, Fig. 1). Mean annual precipitation in the Campos ranges between 1000 and 1900 mm (period 1961–2002; Climatic Research Unit database, Jones and Harris, 2013). We also analyzed the wider region within the same precipitation range than the Campos (1000–1900 mm), covering (1) the subtropical range delimited using the subtropical regions (Cf and Cw) in the original Köppen-Geiger classification, currently described as warm temperate, humid or winter-dry regions in updated classifications (Kottek et al., 2006; Peel et al., 2007); and (2) expanding the analysis following the 1000 and 1900 contours beyond the subtropics to include the tropical regions of southeastern South America (hereafter SSA) (14–38°S and 62°W-Atlantic Ocean, Fig. 1). Areas with precipitation outside the 1000–1900 mm range within both the subtropical and tropical ranges of southeastern South America were excluded from the analysis. These regions have the same precipitation range than the Campos but a wider variation in environmental conditions, enabling us to assess the potential interacting role of other drivers with precipitation. We did not include cultivated or urban areas where the original vegetation cover has been lost, therefore we did not assess forest conversion to cropland or urbanization, which are well-known primary causes of forest change.

2.2. Tree cover and environmental variables

We related tree cover to environmental variables describing resource availability (climate, soil fertility), landscape features, and disturbance regimes (grazing and fire occurrence) (Table A1, Supplementary data). Tree cover was obtained from the Landsat vegetation continuous fields (VCF) with a 30-m resolution (Sexton et al., 2013). This dataset is particularly suitable for areas with sparse vegetation (Hansen et al., 2003, 2005; Sexton et al., 2013; Staver and Hansen, 2015). We also used the tree cover dataset from the Modis Mod44b VCF Collection 5 with a resolution of 250 m (DiMiceli et al., 2011), using the quality assurance layer to exclude those pixels with low quality on two or more input surface reflectance files (Townshend et al., 2011), and obtained the same results (data not shown).

Climatic variables included mean annual precipitation (MAP), mean annual temperature (MAT), precipitation seasonality measured by the Markham seasonality index (MSI) and interannual variability based on the Standardized Precipitation Index (SPI). We used the SPI to estimate the percentage of severely wet (SPIW)

Uruguayan Savanna Ecoregion (Campos) MAP: 1000-1900 mm)

Final model: Tree cover ~ DR

R^2 = 0.20

Variable	Coefficient	P-values
Distance to rivers (DR)	0.137	< 0.0001

Subtropical South America (MAP: 1000-1900 mm)
Final model: Tree cover ~ MAP - CD –FO

R^2=0.41

Variable	Coefficient	P-value
Mean annual precip itation (MAP, mm)	0.0050	0.0009
Cattle density (CD, units km^{-2})	- 0.0028	0.0001
Fire occurrence (FO, #)	- 0.075	0.008

Southeastern South America (MAP: 1000-1900 mm)
Final model: Tree cover ~ MAP - CD - FO

R^2 = 0.42

Variable	Coefficient	P-value
Mean annual precipitation (MAP, mm)	0.00025	0.079
Cattle density (CD, units km^{-2})	- 0.0028	< 0.0001
Fire occurrence (FO, #)	- 0.085	< 0.0001

Fig. 1. Tree cover distribution and explanatory drivers. Left panel: Generalized least squares spatial models for tree cover percent (arcsine square-root transformed; Landsat data). Region of analysis expands from top to bottom. Top: Uruguayan Savanna Ecoregion (Campos); Middle: subtropical South America (delimited by Köppen-Geiger subtropical regions); Bottom: southeastern South America (delimited by 14°S, 62°W and the Atlantic Ocean). Mean Annual Precipitation (MAP) ranges within 1000–1900 mm in all three regions. Gray areas have precipitation levels outside the 1000–1900 mm range and were excluded from the analysis.