Ecological Modelling 291 (2014) 224–232

Contents lists available at ScienceDirect

Ecological Modelling

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

Feedbacks between vegetation and disturbance processes promote long-term persistence of forest–grassland mosaics in south Brazil

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ARTICLE INFO

Article history:
Received 6 December 2013
Received in revised form 17 July 2014
Accepted 28 July 2014

Keywords:
DGVM
Alternative stable states
Spatial heterogeneity
Seed dispersal
Forest expansion
Subtropical grasslands

ABSTRACT

Vegetation changes, such as shrub encroachment and forest expansion over grasslands, prairies and savannas have been related to changes in climatic (mainly rainfall and temperature) and atmospheric conditions (CO_2 concentration). However, a longstanding question in ecology is how mosaics of forests and open-canopy ecosystems could persist over millennia in sites where climatic conditions favor forests. Here we tested the influence of interactions between grass-tree competition, environmental heterogeneity (topography), seed dispersal, initial density and spatial aggregation of vegetation patches and disturbance behavior (fire) on the long-term coexistence of forests and grasslands in South Brazil. For this, we incorporated the adaptive dynamic global vegetation model (aDGVM) into a spatially explicit modeling approach (2D-aDGVM). Our results showed that recurrent disturbance related to grasses such as fires plays a key role in maintaining the long-term coexistence of forests and grasslands, mainly through feedbacks between disturbance frequency and grass biomass. Topographic heterogeneity affected the rate of forest expansion by adding spatio-temporal variability in vegetation-fire feedbacks. However, the spatial pattern and connectivity of fire-prone (grasslands) and fire-sensitive (forest) vegetation patches were more important to maintain the long-term coexistence of both alternative vegetation states than the initial proportion of forest and grasslands patches. The model is the first individual-based DGVM to consider the combined effects of topography, seed dispersal and fire spread behavior in a spatially explicit approach.

1. Introduction

Global changes can have strong impacts on natural and managed ecosystems, by accelerating shrub encroachment and forest expansion, and by affecting primary productivity, disturbance regimes, and the geographical distribution of biomes (Bird and Cali, 1998; Cramer et al., 2001; Silva and Anand, 2013; Ursula et al., 2011). Analysis of pollen core and soil carbon isotopes suggest that forests are expanding over natural grasslands, prairies and savannas in several regions worldwide, since the late Quaternary, due to changes in climatic (mainly rainfall and temperature) and atmospheric conditions (CO_2 concentration) and in the frequency of disturbances (e.g. Behling, 2002; Bowman et al., 2004; Camill et al., 2003). In addition, the changes in climate were never as fast as now, mainly due to increasing human activities (IPCC, 2007; Petit et al., 1999). However, the fact that natural grassy ecosystems have persisted over millennia at sites where annual precipitation is sufficient to support forests has puzzled ecologists.

Although it is well-known that climate controls the variability of return intervals of disturbances such as fire, global scale

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http://dx.doi.org/10.1016/j.ecolmodel.2014.07.024
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predictions of current patterns of woody cover mediated by feedbacks between rainfall and disturbances show high uncertainties in transition zones, and some models overestimated woody cover in more humid sites (Bond et al., 2005; Cramer et al., 2001; Hickler et al., 2006). Undoubtedly, direct human activities in ecosystems may also be determinants of vegetation dynamics and distribution patterns (Heubes et al., 2011; Innes et al., 2013), and local spatio-temporal variability (e.g. topography, soil, seasonality, disturbance regime, tree line form) may promote long-term stability (Danz et al., 2011; Harsch and Bader, 2011; Harsch et al., 2009; Mourik et al., 2007; Naito and Cairns, 2011; Silva et al., 2013). However, the effects of local feedbacks between vegetation and disturbances (both natural and anthropogenic) on controlling biome boundary shifts between forests and grasslands have yet to be fully understood.

In some tropical and subtropical regions where rainfall and soils do not limit forest growth, forest and grassy ecosystems can be alternative vegetation states. Continental-scale analysis searching for patterns in the relation between woody cover and rainfall found bimodality in the occurrence of forests and grassy ecosystems in sites with intermediate rainfall (Hirota et al., 2011; Staver et al., 2011). In these regions, climatic conditions are sufficient to support dense humid forests but these regions can also adopt an open grassland state with a high frequency of disturbances related to grasses such as fire and grazing. The primary productivity of grasses is high, and hence the persistence of natural open-canopy ecosystems becomes dependent on disturbances (Higgins et al., 2010; Sankaran et al., 2005; Staver and Levin, 2012). Therefore, in the landscape, the alternative vegetation states can form mosaics with sharp grassland–forest boundaries, and vegetation dynamics are mediated by positive feedbacks between vegetation and the history of disturbance regimes, such as fire and grazing (Bond and Parr, 2010; Warman and Moles, 2009; Wood and Bowman, 2012).

In natural forest–grassland mosaics that persist over millennia in Southern Brazil, forests expand gradually from the borders and through facilitation effects promoted by nurse plants. These nurse plants colonize grasslands and rocky outcrops, where disturbances related to grasses (e.g. fire, grazing) are less severe (Carlucci et al., 2011; Duarte et al., 2006; Duemig et al., 2008; Müller et al., 2012a, 2012b; Silva and Anand, 2011). Although geomorphic and pedogenetic factors may be related to the original distribution of grasslands and forest patches, soils apparently do not limit forest expansion (Duemig et al., 2008; Garcia Martinez, 2005; Pinillos et al., 2009). Therefore, environmental heterogeneity may influence the rate of expansion at the expense of the native and high diverse grasslands. On the other hand, irrespective of the disturbance that promotes the long-term persistence of natural grasslands (e.g., fire, grazing), its effectiveness on promoting persistence should rely on the maintenance of feedbacks between primary productivity and disturbance frequency, but not threatening the key ecological processes associated to both ecosystems. Understanding the mechanisms promoting the long-term stability of ecotones could help to monitor and predict abrupt changes in these zones of high regional biodiversity and important ecosystem services (Bond and Parr, 2010; Risser, 1995). Theory suggests that shifts between alternative vegetation states can be rapid, relative to the periods of stability (Scheffer et al., 2001; Scheffer and Carpenter, 2003), and some models predict changes in the geographical location of bistable areas in the near future (Higgins and Scheiter, 2012). However, the timescale of vegetation shifts may be dependent on site-specific characteristics, such as environmental covariates (e.g. topography), the proportion of forest and grassland cover (i.e., the current vegetation abundance and distribution patterns) and disturbance regimes (Higgins and Scheiter, 2012; Mayer and Khalyani, 2011).

Here we simulated spatio-temporal dynamics of natural forest–grassland mosaic in Southern Brazil. We evaluated the effects of environmental heterogeneity, seed dispersal, initial density and spatial aggregation of vegetation patches on mosaic dynamics. In sites with limiting resources, environmental heterogeneity potentially defines vegetation patterns and dynamics (Danz et al., 2011; Stanton et al., 2013). In contrast, it is expected that under conditions of less limiting resources (e.g. rainfall, soil nutrients), biotic feedbacks between vegetation and disturbance have stronger effect on promoting long-term stability of alternative vegetation states than environmental heterogeneity such as topography. To test this hypothesis, we have incorporated an existing dynamic global vegetation model (the aDGVM, Scheiter and Higgins, 2009) into a spatially explicit modeling framework, which considers seed dispersal, fire spread and microclimatic variations associated to topography. We simulated and compared pattern formation and dynamics from different initial vegetation scenarios under the same current climatic conditions. In addition, this multiscale approach also allowed us to evaluate how considering spatially explicit environmental heterogeneity, biotic and abiotic processes in models influence predictions of observed vegetation patterns and processes.

2. Methods

2.1. Model description

We developed a dynamic vegetation model (hereafter 2D-aDGVM) to simulate forest–grassland dynamics at a regional landscape scale. We therefore incorporated the adaptive dynamic global vegetation model (aDGVM, Scheiter and Higgins, 2009) into a spatially explicit modeling framework (i.e., considering a grid of cells) that simulates seed dispersal and the effects of topographic variation (slope inclination and aspect) on micro-climate and fire spread patterns among cells. A detailed description of the 2D-aDGVM, as well as model parametrization and benchmarking are presented in the Supplemental material. Here we provide a brief overview.

2.1.1. Vegetation

In the 2D-aDGVM, a regular grid of cells with specified size represents the landscape. Inside each cell, the aDGVM simulates vegetation dynamics as a function of biotic (competitive interactions) and abiotic (climate, soil and fire) factors. The aDGVM simulates biophysical, physiological and demographic processes at the leaf, canopy, plant, population and ecosystem level in an individual based framework. The aDGVM simulates these processes in daily time steps to account for interannual seasonality. Trees (C_3-photosynthesis) are simulated individually (but their locations are ignored inside each cell) and are represented by a “typical” tree type. Grasses (C_4-photosynthesis) are not considered individually. They are represented by the grass cover below and between tree canopies, i.e. population structure and demography of grasses are ignored. The aDGVM does not simulate different species. Competition within and between grass and tree populations is mediated by light and water. Fire is simulated by a semi-empirical model, in which fire intensity is a function of fuel biomass, fuel moisture and wind speed (Higgins et al., 2008). Fire consumes aboveground grass biomass whereas biomass consumption of trees is a function of fire intensity and tree size. Hence, fire acts as a demographic bottleneck and potentially delays transitions of small trees to tall tree size classes (Higgins et al., 2000). For a detailed description of the aDGVM, see Supplementary material S1 from Scheiter and Higgins (2009).