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Original Research Article

Synergistic effects of drought and deforestation on the resilience of the south-eastern Amazon rainforest

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ABSTRACT

The south-eastern Amazon rainforest is subject to ongoing deforestation and is expected to become drier due to climate change. Recent analyses of the distribution of tree cover in the tropics show three modes that have been interpreted as representing alternative stable states: forest, savanna and treeless states. This situation implies that a change in environmental conditions, such as in the climate, could cause critical transitions from a forest towards a savanna ecosystem. Shifts to savanna might also occur if perturbations such as deforestation exceed a critical threshold. Recovering the forest would be difficult as the savanna will be stabilized by a feedback between tree cover and fire. Here we explore how environmental changes and perturbations affect the forest by using a simple model with alternative tree-cover states. We focus on the synergistic effects of precipitation reduction and deforestation on the probability of regime shifts in the south-eastern Amazon rainforest. The analysis indicated that in a large part of the south-eastern Amazon basin rainforest and savanna could be two alternative states, although massive forest dieback caused by mean-precipitation reduction alone is unlikely. However, combinations of deforestation and climate change triggered up to 6.6 times as many local regime shifts than the two did separately, causing large permanent forest losses in the studied region. The results emphasize the importance of reducing deforestation rates in order to prevent a climate-induced dieback of the south-eastern Amazon rainforest.

1. Introduction

Every year, large areas of rainforest are being deforested in the Amazon. In addition, increased drought is expected to affect parts of the rainforest over the course of the coming century (Malhi et al., 2008). In recent years there has been much interest in the question whether climate change and deforestation may cause the forest to die back, or even collapse due to positive feedbacks that cause alternative stable states (Cox et al., 2000; Lenton et al., 2008; Nepstad et al., 2008; Malhi et al., 2009; Davidson et al., 2012). Analyses of MODIS satellite data of tree cover by Hirota et al. (2011) and Staver et al. (2011b) have added new evidence for alternative states (Scheffer and Carpenter, 2003) by showing that the frequency distributions of tree cover in the tropics have three modes, which roughly correspond to a treeless ecosystem, savanna (tree-grass mosaics) and forest. The probability of finding these modes depends non-linearly on mean annual precipitation (MAP) (Hirota et al., 2011).

The existence of alternative stable states implies that an ecosystem can be in several alternative states under the same external conditions. When the system is perturbed slightly, it will return to the stable equilibrium. However, when a perturbation exceeds a certain size, the system will move to an alternative equilibrium. Such a regime shift can also occur when the environmental conditions cross a fold bifurcation point, often called 'tipping point' (Scheffer et al., 2009). Restoring the conditions that were present prior to the shift requires a larger change in environmental conditions, a phenomenon called hysteresis. We refer to these regime shifts as critical transitions (Scheffer, 2009). A slow change in environmental conditions can make a system more vulnerable to a regime shift. The maximum

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possible perturbation without causing a regime shift is defined as a system state's (ecological) resilience (Holling, 1973).

There is increasing evidence that fire is the mechanism for creating alternative stable states of tropical rainforest and savanna (Staver et al., 2011b; Hoffmann et al., 2012; Murphy and Bowman, 2012). Savannas are open, grassy landscapes, which can be maintained by frequent fires. As fire-exclusion experiments (e.g. Moreira, 2000) have shown, fires can prevent the establishment of forest when the climate would allow for its presence (Bond, 2008). Indeed, the grasses in savannas may fuel natural or anthropogenic fires, which kill forest tree species (Hoffmann et al., 2012). Fires are sometimes seen as external disturbances maintaining an unstable savanna regime (Sankaran et al., 2005). However, fires can be regarded as a self-stabilizing mechanism of savannas, as the low tree cover in savannas enhances fires. Closed-canopy forests, on the other hand, suppress fires through the creation of a humid understory microclimate (Uhl and Kauffman, 1990) and can thereby stabilize the forest state itself (Hoffmann et al., 2012; Murphy and Bowman, 2012). Fragmentation of the canopy results in a much higher vulnerability to fire. Both grasses invading the forest and trees killed by fire can fuel fires, making burned forest areas even more susceptible to burning (Cochrane et al., 1999; Brando et al., 2014). After a number of fires a savanna ecosystem may establish. Next to the internal feedbacks, also climatic conditions influence the probability of fire; the drier it is, the more intense fires tend to be (Pueyo et al., 2010), so the more likely a regime shift from forest to savanna would become. On centennial to millennial time scales, however, these shifts need not be permanent. For an African savanna, for example, back-and-forth transitions between savanna and forest have been reported (Gil-Romera et al., 2010). Such repeated shifting between alternative stable states is called flickering (Scheffer, 2009).

Both deforestation and climate change in the Amazon are relatively severe in the drier, south-eastern part of the basin, an area characterized as the "arc of deforestation" (Aragão et al., 2007; Davidson et al., 2012; Coe et al., 2013). Therefore, in particular tree cover in the south-eastern Amazon can be expected to be out of equilibrium and vulnerable to future regime shifts, but the resilience of the forest is only poorly understood. Our objective was to assess how deforestation (defined as a reduction in tree cover; Sternberg, 2001) and climate change (a reduction in mean annual precipitation) may interact to induce fire-mediated regime shifts from forest to savanna in the south-eastern Amazon. Current forest models are generally not suited for analyzing tipping point behavior, while there is a need for models that are (Reyer et al., 2015). Previous studies concerned with alternative stable states in the Amazon have mainly focused on a regional forest-precipitation feedback instead of the tree cover-fire feedback (Nobre and Borma, 2009). We present a simple model for tree cover in South America that includes the tree cover-fire feedback and was fitted to near-continent-wide satellite data. We use it to simulate deforestation- and climate change-induced regime shifts to savanna in the south-eastern Amazon rainforest.

2. Methods

2.1. The model

We adapted a simple tree-cover model by Van Nes et al. (2014). It can have three stable tree-cover states, corresponding to treeless, savanna and forest states, and has been fitted to satellite data of tree cover across the Earth's tropics. The model consists of a logistic growth function for the expansion of tree cover T (fraction) to carrying capacity K (fraction) and two loss terms. The expansion rate depends on precipitation P (mm yr^{-1}) and saturates at r_m (yr^{-1}) with a half saturation of h_P (mm yr^{-1}). The first loss term includes increased mortality at low tree-cover densities, called an Allee effect. This represents the facilitative effect of adult trees on tree-seedling establishment in the seedling's competition with grasses (Holmgren et al., 1997; Baudena et al., 2010). The Allee-effect-induced loss rate decreases from m_A (yr^{-1}) with T according to a Monod function with half saturation h_A (fraction). The growth function and Allee effect are given as:

$$\frac{dT}{dt} = \frac{P}{h_P + P} r_m T \left(1 - \frac{T}{K}\right) - m_A T \frac{h_A}{T + h_A} \quad (1)$$

The Van Nes et al. (2014) model also includes a second mortality term that mimics the effect of fire at intermediate tree cover. A Hill function describes the sigmoidal shape of the negative relation between tree cover and fire-induced mortality. Thus, fire depends solely on tree cover in Van Nes et al. (2014) and not on environmental conditions. However, in reality fire occurrence and intensity also depend on rainfall (Staver et al., 2011b). Therefore, we adjusted the fire term accordingly for this paper, although we do not depart from the simple approach of Van Nes et al. (2014). In this new model, fire-induced tree-cover mortality depends on fire intensity I, whereby trees are resistant to low-intensity fires through a Hill function. Fire intensity depends negatively and non-linearly on tree cover. This can be thought of as representing the availability of fuel (grass), which is determined by the openness of the landscape. Although a fragmented canopy may affect tree cover in several ways (Cumming et al., 2012), this landscape openness mainly promotes the continuity of the grassy (i.e. non-forested) portion of the landscape such that above a certain threshold of this continuity fires can percolate through the landscape (Archibald et al., 2009; Pueyo et al., 2010; Hoffmann et al., 2012; Staver and Levin, 2012). Therefore, I depends on a variable landscape continuity $C(T)$, which is a function of tree cover T through a saturating sigmoidal function (Hill function). When T equals the half saturation h_C the largest change in C occurs.

Following the rationale that the moisture content of the fuel, and therefore its flammability, depends on soil moisture (Hirota et al., 2010; Murphy and Bowman, 2012), fire intensity I also depends on a soil moisture index SMI. This index depends on P via a sigmoidal Hill function (Hirota et al., 2010; Staver and Levin, 2012). The choice for a sigmoid is empirically supported by Bucini and Hanan (2007), who found that it could best describe the relation between mean annual precipitation (MAP) and tree cover in the African savannas. Because our model represents processes on an annual basis, the fire-induced mortality is divided by a constant fire return interval FRI. The resulting differential equation for tree cover T (fraction) is as follows:

$$\frac{dT}{dt} = \frac{P}{h_P + P} r_m T \left(1 - \frac{T}{K}\right) - m_A T \frac{h_A}{T + h_A} - T \frac{1}{FRI} \frac{I(P,T)^\gamma}{h_I{}^\gamma + I(P,T)^\gamma} \quad (2)$$

with the fire intensity $I(P,T)$ (–) defined as:

$$I(P,T) = C(T) \cdot \mathrm{SMI}(P), \quad (3)$$

landscape continuity $C(T)$ (–) as:

$$C(T) = \frac{h_c^\beta}{h_c^\beta + T^\beta} \quad (4)$$

and the soil moisture index SMI(P) (–) as:

$$\mathrm{SMI}(P) = \frac{h_{SMI}^\alpha}{h_{SMI}^\alpha + P^\alpha} \quad (5)$$

For an explanation of the parameters, see Table 1.