

Feedbacks between phosphorus deposition and canopy cover: The emergence of multiple stable states in tropical dry forests

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Abstract

Dry forests represent a large percentage of tropical forests and are vulnerable to both anthropogenic and natural disturbances, yet important aspects of their sensitivity to disruption remain poorly understood. It is particularly unclear how changes in land-use or tropical storm patterns may affect the resiliency of phosphorus (P)-limited neotropical forests. In these systems, vegetation is sustained in the long-term by atmospheric P-inputs through rainfall, dust, or fog. Past research supports the idea that dust and fog deposition are dependent on canopy density (e.g. leaf area index). Thus, the canopy may function as a 'trap' for P, enabling a positive feedback between vegetation and P-deposition. We developed a conceptual model to investigate how Neotropical vegetation may respond to reduced P-deposition due to canopy losses. The model suggests that a canopy-deposition feedback may induce bistable vegetation dynamics; under some conditions, forests may be unable to naturally recover from relatively small disturbances.

Keywords: deposition, feedbacks, land-use change, phosphorus, stable states, tropical dry forests

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Introduction

Old tropical forests are commonly found on highly weathered soils that are depleted of mineral phosphorus (P) and low in nonoccluded, inorganic-P (Walker & Syers, 1976; Vitousek & Sanford, 1986). This lack of 'plant-available' P has led to P-limitations in many of these forests, particularly in the Neotropics (Sarmiento, 1984; Vitousek, 1984; Cleveland *et al.*, 2002). In these cases, vegetation is sustained in the long-term by atmospheric inputs (rainfall, dust, or fog) that contribute to the plant-available P supply (Crews *et al.*, 1995; Chadwick *et al.*, 1999). Dependency on small atmospheric sources may make these old forests vulnerable, especially in the case of disturbance. Lower annual rainfall in seasonally dry forests increases the relative significance of atmospheric sources that may be more sensitive to changes in canopy cover (e.g. dust or fog). Thus, tropical dry forests are a particularly interesting case.

Dry forests make up 42% of tropical forests and represent a significant amount of global biomass (Murphy & Lugo, 1986). These forests, known for their strong seasonality, receive 250–2000 mm rain per year dispersed among 2 to 10 months (Murphy & Lugo, 1986).

Although water limits the length of the growing season, it may not be limiting during the growing season.

Land use change in the tropics is particularly widespread in dry forests because these areas tend to attract development (Murphy & Lugo, 1986; Trejo & Dirzo, 2000). Some of these forests are also prone to damaging storms, the frequency and intensity of which may be impacted by climate change. It has been hypothesized that many savannas, woodlands, and grasslands are actually the product of disturbed dry forests (Murphy & Lugo, 1986), suggesting that these systems are prone to permanent state shifts. Despite increasing disturbances to dry forests, studies of the significance for feedbacks between vegetation and limiting resources are lacking.

Plant communities are known for their ability to modify the environment in ways that favor their own growth (Wilson & Agnew, 1992). An example of these feedbacks is the contribution of canopy condensation (or 'fog precipitation') to water-limited forest ecosystems, which facilitates biomass growth and, in turn, increases fog precipitation (Wilson & Agnew, 1992). Plant communities have also been found to promote themselves by influencing infiltration (e.g. Greene, 1992), water table elevation (Ridolfi *et al.*, 2006), and the ground surface elevation (e.g. van de Koppel *et al.*, 2005).

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In cases where nutrients are the most limiting factor to plant growth, plant communities appear to improve the quality of their immediate surroundings by creating 'islands of fertility' (see Schlesinger & Pilmanis, 1998). Enhanced fertility near canopies has been found in the southwestern American deserts (Schlesinger & Pilmanis, 1998), Hawaiian rainforests (Matson, 1990), semi-arid New Zealand conifer forests (McGowan & Ledgard, 2005), Neotropical savannas (Kellman, 1979), and other arid and semiarid areas (see review in Vetaas, 1992).

Although the ways in which a forest canopy can influence nutrient cycling are multiple and complex (Prescott, 2002), the ability of the canopy to 'trap' nutrients may have a critical role in the fertility of these areas (Kellman, 1979; Vetaas, 1992; McGowan & Ledgard, 2005; Lawrence *et al.*, in press). A few studies have successfully, directly measured the ability of the canopy to 'trap' deposition (e.g. see Rea *et al.*, 2000), but the majority of this research relies on indirect measurements (i.e. comparisons between the concentrations of nutrients or pollutants in throughfall vs. rainfall). In these cases, distinguishing between changes in throughfall concentrations that are due to dry deposition vs. active canopy exchange (leaching) can be difficult. Although this is the nature of the little work that has been done to develop this concept with respect to P, research does support the idea that canopies may collect P via both dry deposition (Nye, 1961; Jordan *et al.*, 1980; Kellman *et al.*, 1982; Lovett & Lindberg, 1984; Potter *et al.*, 1991; Newman, 1995; Tobón *et al.*, 2004) and fog (e.g. Fowler *et al.*, 1989; Weathers & Likens, 1997; Bruijnzeel & Veneklaas, 1998). If this canopy function exists, then plant communities that are dependent on deposition as a source of limiting nutrients may provide yet another example of a vegetation feedback. P-limited tropical forests, particularly in the Neotropics, do appear to rely on dust for small but critical P-inputs (Swap *et al.*, 1992; Chadwick *et al.*, 1999; Okin *et al.*, 2005). In cases where canopy interference has control over the quantity of deposition, these forests could be affected by a deposition-canopy feedback.

Systems affected by positive feedbacks are known for their ability to exhibit multiple stable states (Scheffer *et al.*, 2001). In the absence of major disturbances, these systems can evolve towards a stable state in which the positively reinforced community achieves a maximum density. However, if the feedback cycle is perturbed (e.g. disturbance or climate change), the system may diverge to a different stable state (e.g. bare ground, alternate community). Thus, the identification of a significant positive feedback suggests the possible existence of bi-stable dynamics (e.g. Rietkerk & van de Koppel, 1997; Gunderson, 2000).

In this paper, we develop a conceptual model of vegetation and phosphorus dynamics to explore how feedbacks between P-deposition and canopy cover in dry Neotropical forests may lead to the emergence of multiple stable states. This model will be used to show how the resiliency of these forests could be affected by changes in climate and disturbance regimes.

Conceptual model for vegetation-deposition feedbacks in seasonally dry forests

We investigate the dynamics of tropical dry vegetation using the canopy density, V , as an indicator of the state of the system. We express the canopy density in terms of leaf area index (LAI) ($\text{m}^2 \text{m}^{-2}$), which is a good proxy for plant biomass and basal area in tropical dry ecosystems (e.g. Hoffmann *et al.*, 2005). To model the relationship between tropical dry vegetation and phosphorus in P-limited forests, we first make the assumptions that (1) at relatively high levels of P, some other factor (e.g. nitrogen, light, water) will become limiting and increases in P will no longer influence the canopy density, V , and (2) that tropical dry forests have a maximum canopy density, V_{\max} , which, expressed in terms of LAI, falls between 4 and 6 (Murphy & Lugo, 1986).

With respect to these assumptions, we use a logistic equation (e.g. Murray, 1989) to represent the dynamics of vegetation, V ,

$$\frac{dV}{dt} = rV \left(1 - \frac{V}{V_{cc}} \right), \quad (1)$$

where t is time, r (time^{-1}) is the reproduction rate of the logistic growth, and V_{cc} is the vegetation carrying capacity of the system, (i.e. the maximum value of V sustainable with existing resources). V_{cc} has the same dimensions as V and is a function of the limiting resources, (i.e. of plant-available soil phosphorus, P_s (kg P ha^{-1}), in the case considered here). Based again on the assumptions listed above, we use a nonlinear relationship to express the $V_{cc}(P_s)$ dependence

$$V_{cc} = \begin{cases} 0 & (\text{if } P_s < P_{cr}) \\ V_{\max} \left(1 - \frac{1}{1 + a(P_s - P_{cr})^b} \right) & (\text{if } P_s \geq P_{cr}), \end{cases} \quad (2)$$

where P_{cr} represents the minimum value of P_s required for the existence of forest vegetation. Here, we use a value of 5 for V_{\max} .

To find realistic values for parameters a and b , we fit Eqn (2) to data reported by Goodland & Pollard (1973), who investigated changes in plant biomass along a gradient in available soil phosphorus (PO_4^{-3}) content in the Brazilian savannas (Fig. 1a). We use this specific data set only as a means to consider the possible dynamics of Neotropical vegetation with changing soil

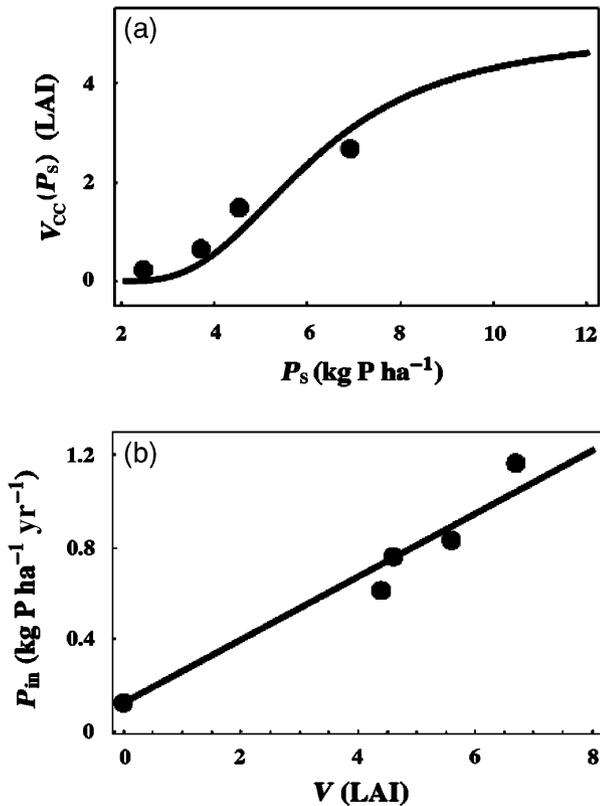


Fig. 1 This figure shows the relationships between P and V that were used as a basis to investigate the possible dynamics of a P -limited, dry Neotropical forest. (a) Vegetation carrying capacity (V_{cc}) (LAI) vs. available soil P (PO_4^{-3} , P_s , kg P ha^{-1}), fit to data from Goodland & Pollard (1973) along a biomass gradient in a Brazilian savanna. V_{cc} was converted from total basal area of trunks (BA) ($\text{cm}^2 \text{ h}^{-1}$) to leaf area index (LAI) using a relationship from Hoffmann *et al.* (2005), also in Brazilian savannas: $V_{cc} = 0.0902 \times BA - 0.0378$ ($r^2 = 0.95$). P was converted from mEq. PO_4^{-3} per 100 mL soil to kg P ha^{-1} by scaling to the top 10 cm of soil ($a = 0.021$, $b = 2.75$, $P_{cr} = 2.1$, $V_{max} = 5$). (b) P -inputs (P_{in}) ($\text{kg P ha}^{-1} \text{ yr}^{-1}$) vs. V (LAI). A linear curve is fit to results from Tobón *et al.* (2004) that express PO_4^{-3} inputs (converted here to P) as total annual solute fluxes for four Columbian forest sites: $P_{in} = \alpha V + \beta$, ($\alpha = 0.1364$, $\beta = 0.1239$, $r^2 = 0.9435$).

P fertility. Similar fertility trends have been found in other forests (Kellman, 1979; Vetaas, 1992).

To account for the effect of a canopy-deposition feedback, we couple Eqn (1) with a soil P balance equation expressing the temporal variability of P_s as the difference between deposition-driven P -inputs, P_{in} ($\text{kg P ha}^{-1} \text{ yr}^{-1}$), and P -outputs, P_{out} ($\text{kg P ha}^{-1} \text{ yr}^{-1}$),

$$\frac{dP_s}{dt} = P_{in} - P_{out}. \quad (3)$$

For this relationship, we assume that organic P in the vegetation is locally cycled with no net removal of biomass due to burning or major logging operations.

The major P inputs in old weathered systems are from atmospheric deposition, which supplies an average of $0.07\text{--}1.7 \text{ kg P ha}^{-1} \text{ yr}^{-1}$ (Newman, 1995) and varies globally and seasonally. Wet deposition occurs primarily in the rainy season, whereas forested regions where slash-and-burn agriculture occurs may have enhanced dry deposition in the burning season (e.g. Kellman *et al.*, 1982; Vitousek & Sanford, 1986; Campo *et al.*, 2001). Large-scale dust transport is another important P -source in old, weathered regions such as the Amazon Basin (e.g. Swap *et al.*, 1992; Chadwick *et al.*, 1999; Okin *et al.*, 2005). Finally, fog deposition may be a source of nutrients in humid regions with limited precipitation (e.g. Weathers & Likens, 1997; Bruijnzeel & Veneklaas, 1998), though the contributions of this type of deposition (especially with respect to P) are often overlooked. Here, we investigate how the dependence of P deposition rates on V affects forest vegetation and phosphorus dynamics in dry Neotropical forests. To this end, we use a simple linear relation to express P_{in} as a function of V ,

$$P_{in} = \alpha V + \beta, \quad (4)$$

where α expresses the strength of vegetation-deposition feedbacks, [i.e. the fraction of P_{in} enhanced by the presence of a canopy (i.e. dry and fog deposition)]. The coefficient β represents the fraction of deposition that is not strongly dependent on canopy cover (e.g. wet deposition).

Figure 1b shows the dependence of P_{in} on V obtained by fitting Eqn (4) to data from Tobón *et al.* (2004), who studied solute fluxes (throughfall and stemflow) in four forested sites in northwest Amazonia. In this study, the authors suggest that dry deposition may be the critical source of P_{in} , but acknowledge the difficulty of distinguishing between P enrichment by dry deposition vs. canopy leaching (see also i.e. Lovett & Lindberg, 1984; Potter *et al.*, 1991). As live leaves do not tend to lose much P through leaching (Tukey, 1966; see also: montane forests, Zamierowski, 1975; temperate forests, Haines *et al.*, 1985; taiga, Chapin & Kedrowski, 1983), we assume for the sake of this theoretical model that the throughfall P in Tobón *et al.* (2004) is attributable to dry deposition. Although the P -deposition concentrations reported here were within the ranges published from other research in the Neotropics (see Newman, 1995), we realize that this assumption may represent a slight overestimation of P_{in} . However, we believe that this estimate of the dependence of P_{in} on canopy density is sufficient to explore the potential dynamics of our proposed feedback.

Losses of P in tropical forests are normally dominated by leaching from the soil (Vitousek & Sanford, 1986), though the relative insolubility of P keeps even these outputs very small (Bruijnzeel, 1991; Campo *et al.*, 2001).

Here, we assume P-output to be a small proportion of available soil phosphorus, P_s

$$P_{\text{out}} = cP_s, \quad (5)$$

where c is the proportionality coefficient with the dimensions of 1/time.

Although P-output is likely to be dependent on V as well, we have omitted this detail in favor of simplicity. Because P losses would most likely decrease with increasing V (Prescott, 2002), we expect that adding this detail to our model would only enhance the strength of the nutrient-vegetation feedback.

Using the general relationships between P and V established above, we explore the possible dynamics of tropical dry forests with varying vegetative states, P-deposition rates (both canopy dependent and independent), and soil fertility.

Model results and discussion

To find the stable states of Neotropical dry forests, we first determined the equilibrium conditions, where (1) P-inputs balance outputs [i.e. $dP/dt = 0$ in Eqn (3)], and (2) V has reached an equilibrium condition [$dV/dt = 0$, in Eqn (1)]. Using Eqns (4) and (5) in (3) and taking $dP/dt = 0$ we have

$$\alpha V + \beta = cP_s, \quad (6)$$

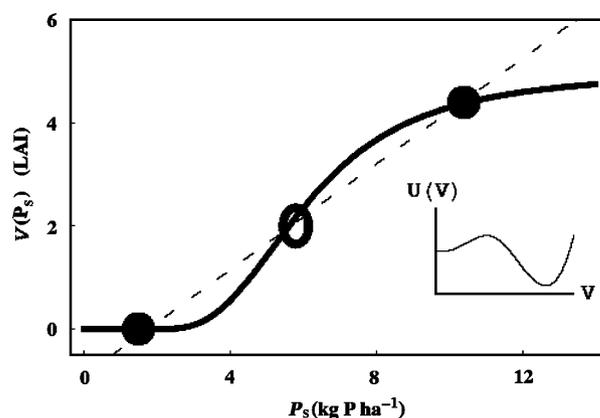


Fig. 2 Solutions for equilibrium ecosystem conditions (where vegetation, V , and soil $\text{PO}_4^{3-}\text{-P}$, P_s , remain constant, i.e. $dP/dt = 0$ and $dV/dt = 0$), using the relationship between P_s and vegetation carrying capacity (V_{cc}) in Fig. 1a (solid curve) and the canopy-deposition feedback in Fig. 1b combined with the equilibrium soil P balance as in Eqn (6) (dashed curve). Solutions are shown as intersections of the curves; filled circles denote stable states, the open circle represents an unstable state. If a system is not already at an equilibrium state then either a) the system has not yet reached the maximum V supported by the amount of P_s or b) the existing amount of vegetation will 'trap' P at a rate such that P-inputs are not balanced with outputs. In either case, the system will continue to adjust itself until a stable state is reached. Minima of the potential, $U(V)$, correspond to stable states whereas maxima represent unstable states.

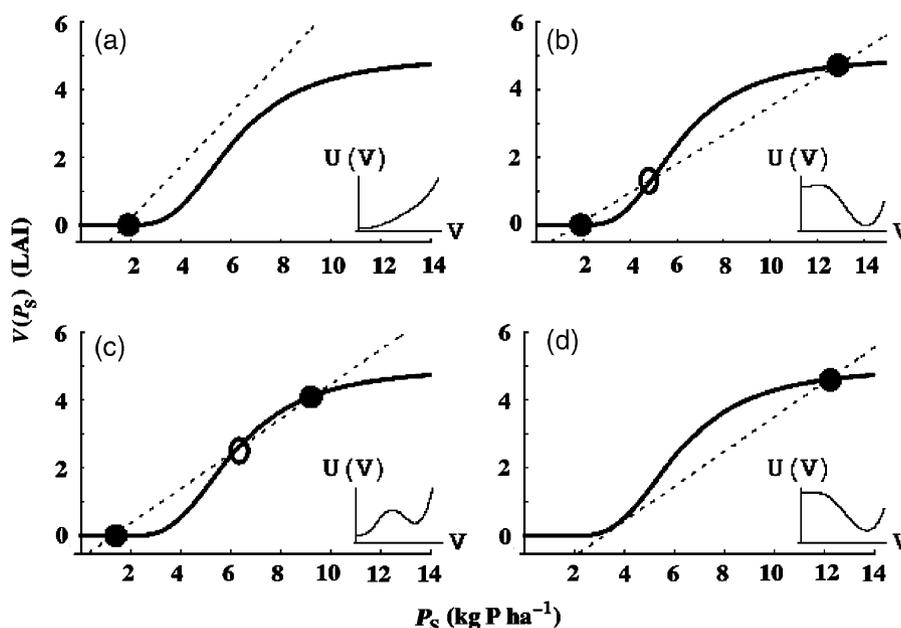


Fig. 3 Both α and β are expected to vary spatially and temporarily. Here, we show solutions that are obtained using values of α and β that differ with respect to those used in Fig. 2. The number and type of the solutions (filled circles represent stable states, open circles represent unstable states) change as α and β are adjusted. (a) ($\alpha = 0.0900$, $\beta = 0.1239$), (b) ($\alpha = 0.1650$, $\beta = 0.1239$), (c) ($\alpha = 0.1364$, $\beta = 0.0900$), (d) ($\alpha = 0.1364$, $\beta = 0.2200$).

while Eqn (1) with $dV/dt = 0$ leads to the conditions

$$V = 0 \text{ and } V = V_{cc}. \quad (7)$$

Equation (6) and the second of Eqn (7) with V_{cc} expressed as a function of P_s [Eqn (2)] provide a set two algebraic equations in the two unknowns, V and P_s . Plots of these equations in the (V, P_s) coordinates are known as *isoclines*, [i.e. lines of constant V [Eqn (6)] or P_s [Eqn (7)]]. Solutions of this set of equations are steady (or equilibrium) states of the system (i.e. $dP/dt = dV/dt = 0$) and correspond to intersections of the isoclines in the (V, P_s) plane, as shown in Figs 2 and 3. Depending on the isoclines, there will be one to three intersection points, (i.e. equilibrium states).

Figure 2 shows the results of this analysis obtained when V_{cc} is expressed as in Fig. 1a and P_{in} is modeled as in Fig. 1b. Under these conditions there are three equilibrium states, two stable and one unstable. If the system is at a stable point, it will remain there until it is perturbed. If it is between stable states, however, then either (a) the system has not yet reached the maximum V supported by P_s or (b) the existing vegetation will 'trap' P at a rate such that P_{in} does not balance P_{out} . In either case, the system will continue to adjust itself until a stable state is reached. Specific properties of the system are calculated by Eqns (1)–(5). The function, $U(V) = -\int (\frac{dV}{dt}(V)) dV$, is the potential of the system and can be calculated for a range of vegetative states (Fig. 2 inset). The system tends to minimize $U(V)$, moving away from unstable states [i.e. maxima of $U(V)$] towards stable states where the system may settle [minima of $U(V)$].

Solutions shown in Fig. 2 are clearly dependent on the specific relationships defined in this paper, and other solutions would be found if the relationships between P and V were altered. These relationships are likely to differ spatially, but may also fluctuate temporally within a set area. For instance, variations in α represent changes to the strength of canopy 'trapping' and could be due to depositional pattern changes related to either dust (from local fires or large-scale events) or fog (local weather). Different values of β may be due to changes in precipitation, which is not tightly related to V . Figure 3 shows how the solutions are affected by changes to α or β in Eqn (4).

While there are certain ranges of α and β that support both a stable plant community as well as a bare-ground scenario, there are also values at which only one stable state is supported. Although this behavior can be observed in Fig. 3, it is more clearly visualized by plotting stable states of V vs. α and β , individually. These relationships exhibit a clear hysteresis (Fig. 4) and small changes in either α or β , (i.e. small changes in the nature of the deposition-canopy feedback, may lead to abrupt

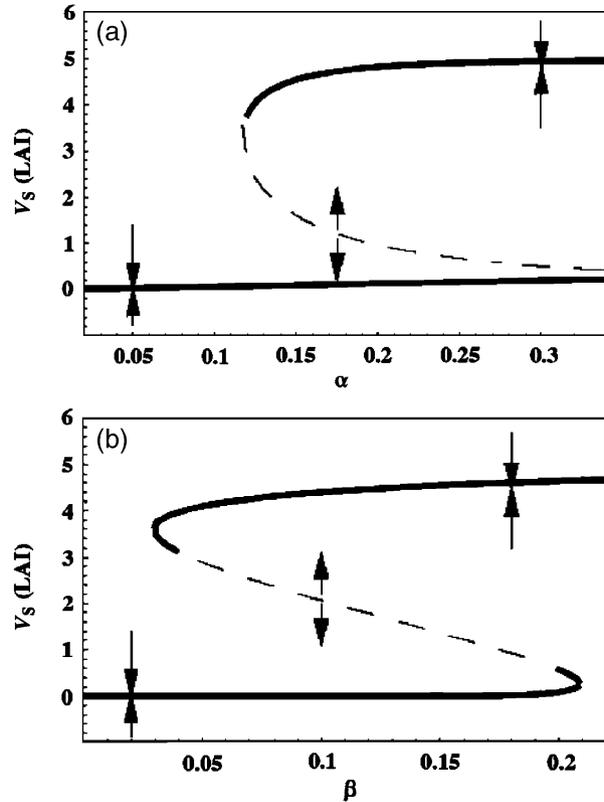


Fig. 4 Hysteresis in vegetation dynamics due to P-deposition. (a) Stable vegetation state, V_s (LAI) vs. α : changes in α , which represent the strength of the deposition–canopy relationship, affect the number and type of steady-state solutions. The solid and dashed lines show stable and unstable solutions, respectively. Arrows show the direction of change of V_s for a system in a specific region of the figure (i.e. movement towards stable and away from unstable states). Within a limited range of α , two stable vegetative states are supported. (b) V_s vs. β , changes in β represent the quantity of P-inputs that are not strongly tied to the canopy density (i.e., precipitation). As in (a), stable states, unstable states, and directions of change are shown.

and highly irreversible state changes). For example, if changes in environmental conditions affect the feedback such that α decreases below a critical value ($\alpha = 0.12$ in Fig. 4) the vegetated state will not be in equilibrium and the only stable state is at $V = 0$. Changes in the canopy independent fraction of deposition, β , may also induce a switch from a condition with two stable states to only one stable state (either $V = V_{cc}$ or $V = 0$). Thus, the adjustment of α or β (Fig. 4) (e.g. change in land-use change or climate) away from the range for multiple stable states may represent a loss of resilience to disturbances.

Conclusions

A modeling framework has been developed to investigate the effect of feedbacks between plant canopies and

phosphorus deposition on the dynamics of tropical dry forests. These feedbacks are able to induce strong nonlinearities and hysteresis in the ecosystem dynamics. In particular, the ability of the canopy to enhance P-input may induce bistability in the dynamics of dry, P-limited Neotropical forests. In this case, natural and anthropogenic disturbances may be capable of shifting the system from its current state to an alternative stable state in which the dynamics would remain locked even after the disturbances cease. Moreover, small changes in environmental conditions may lead to abrupt and irreversible changes in the state of the system. These mechanisms may help to explain past and future shifts from tropical dry forests to alternate states, such as savannas, woodlands, and grasslands.

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