Savanna–forest hysteresis in the tropics

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ABSTRACT
A simple dynamic model relating forest area in a region, its contribution to dry season precipitation and the effect on its own establishment was developed. The model equation shows hysteresis between forest and savannas as a function of imported dry season precipitation. Regions are either dominated by forests or savannas, with each ecosystem showing stability despite changes in imported dry season precipitation. Deforestation beyond a certain threshold value, however, could cause a collapse of forest ecosystems and replacement by savannas in marginal areas. The predictions of this model corroborate pollen core analysis in the Amazon basin, where historical stability of tropical forest cover has been shown despite global climate change.

Key words Conservation, hysteresis, palaeoclimate, palynology, refuge hypothesis, saddle node bifurcation, savanna, tropical forest.

INTRODUCTION
In the beautiful story L’Homme qui plantait des arbres [The man who planted trees] by Jean Giono (1983), a single man was able to change the climate of a desolate region of Provence in Southern France by planting and establishing oak forests. Although this story may be fictional, there are elements of truth to it. Vegetation has the potential to change regional and global climate. At the regional level the clearest examples occur in tropical forests. Documentation of this phenomenon is particularly convincing for forests in the Amazon basin. Several studies show that 40–60% of precipitation in the Amazon is recycled (Villa Nova et al., 1976; Molion, 1979; Salati et al., 1979). According to these studies part of the precipitation over the Amazon basin is returned to the atmosphere by evapotranspiration to be re-precipitated. It is estimated that precipitation over the basin is 14.1*10^{12} \text{ m}^3 \text{ years}^{-1}, and yet the discharge from the Amazon River is only 6*10^{13} \text{ m}^3 \text{ years}^{-1} (Victoria et al., 1991). Further work has shown that the main conduit for this recycling process is the transpiration stream of forest trees (Moreira et al., 1997; Moreira, 1998).

Therefore, tropical forests modify regional climate by increasing precipitation. Interestingly, tropical forests modify climate so that it becomes more favourable for their own establishment and maintenance. In addition to modifying climate on a regional scale, vegetation cover can have important global climatic consequences. Tropical and boreal forests, for example, can serve as enormous carbon sinks of atmospheric CO\textsubscript{2} (Tans; Dixon et al., 1994). Release of this CO\textsubscript{2} by humans is contributing to the increase in the atmospheric CO\textsubscript{2} concentration, with the likely consequence of an increase in average global temperatures. An additional example of how tropical forests can alter climate is the observation that convective precipitation within the Amazon basin releases sufficient energy to impact global climate (Peagle, 1987).

Another element of truth in Giono’s story, which I will attempt to demonstrate here, is that some regions can have two alternate stable ecosystems. In the case of Giono’s story, the arid region of Provence could either be covered by a xeric scrubby vegetation or by oak forests. In this paper a mathematical model will be presented showing that tropical savannas and forests are two alternate stable ecosystems in certain seasonal
environments, as postulated previously (Sarmiento, 1984). Tropical savannas (Sarmiento, 1984) are found in New and Old World tropical regions and are warm (lowland) tropical ecosystems dominated by bunch grasses and sedges that are more than 30 cm high during the wet season. Savanna may also have woody species as a minor component of its biomass. The herbaceous cover shows seasonality in its development with a decrease in productivity induced by drought during the dry season. Most relevant to the model developed here is that there is a substantial decrease in the evapotranspiration flux during the dry season in savannas. Since savannas throughout the world surround tropical forests with high species diversity, it has been conjectured that savannas act as ‘species pumps’, wherein specification occurs in savannas and is preserved in tropical forests (Stebbins, 1952).

Tropical evergreen forest is defined here as a forest growing in a warm tropical climate with an average yearly temperature above 25 °C and with at least 1500 mm of annual rainfall distributed well throughout the year. Although there may be some loss of leaf area during the dry season, this is not sufficient to decrease the overall evapotranspiration flux, which may increase or remain the same during the dry season. This evaporative flux will certainly be greater than that of savannas during the dry season. These forests are usually found in climate regions having average annual precipitation between that observed in tropical rain forests and savanna regions.

There are a few reports based on palynological records from the Neotropics, showing that during the Pleistocene and Holocene, the vegetation cover of various localities in the vicinity of tropical forests changed from savanna to evergreen forest and vice versa (e.g. Kendall, 1969; Van der Hammen, 1974; Absy et al., 1991; Van der Hammen & Absy, 1994). Recently the validity of the core collected at Serra dos Carajas, Para, Brazil (Absy et al., 1991) as being representative of large-scale vegetation shifts has been questioned (Colinvaux et al., 2000). In their review, Colinvaux et al. (2000) concluded that if these changes did occur, they represent only localized changes at the forest/savanna boundaries. The extent of these boundary changes is an open question that can only be answered by more intensive palynological and sedimentary studies.

Climate, fire, edaphic and anthropogenic manipulation are possible factors causing vegetation shifts in savanna–forest boundaries (Sarmiento, 1984). Of the above factors, climate distinguishes tropical forests from savannas most distinctly, specifically by seasonality of rainfall. Tropical savannas may have wet season rainfall as high as tropical forests but the seasonal dry spell found in savannas is too extreme to support tropical forests. In a study of over 4000 weather station records, Nix (1983) summarized the climatic characteristics of tropical savanna ecosystems as follows:

- solar radiation of 6–8 GJ m⁻² years⁻¹;
- annual precipitation between 1000 and 1500 mm;
- high rainfall seasonality;
- rainfall during the wettest 6 months greater than 600 mm;
- rainfall during the driest 3 months less than 50 mm;
- annual mean air temperature above 24 °C; and
- mean minimum temperature of the coldest month between 13 and 18 °C.

It is reasonable to suppose that if an area occupied by savanna, having precipitation during the driest 3 months close to Nix’s (1983) threshold value for dry season (d.s.) precipitation (5th characteristic), were to be occupied by a forest with its additional contribution to precipitation, then (d.s.) precipitation could be augmented enough to sustain growth and maintenance of a forest ecosystem. Similarly, if an area occupied by forest with dry season rainfall close to the threshold value were to be partially deforested, it could experience a decrease in d.s. precipitation so as to only support savanna. The eventual fate of this area would be a savanna ecosystem. Such areas at the edge of the Amazon basin where d.s. precipitation is less than 100 mm would be prime candidates for savannization given sufficient deforestation (Fig. 1). The dark grey area shown in Fig. 1 was delineated by highlighting areas where precipitation during the driest 3 months is ≤100 mm (Nix, 1983) and tropical forests are present. Since tropical forests can contribute up to 60% of the precipitation, especially during the dry season, these areas could have less than 50 mm rainfall during the dry season without the presence of forests and could be turned into savannas. Forest associated with rivers (varzea)
would probably turn into gallery forests after savannization.

In the following section equations will be established relating the proportional area of savannas and forest ecosystems to their respective contribution to d.s. precipitation, imported precipitation, and the subsequent effect on the establishment of forests or savannas. This model will demonstrate that the above scenario is probable.

**MODEL**

All results of this model are given in terms of relative forest and savanna coverage. Therefore, the size of the region considered here is not critical. Several previously published vegetation–climate interaction models in the Amazon basin, however, have a resolution ranging from 1.8° to 4.5° latitude and 2.8° to 7.5° longitude (Lean et al., 1996). When the establishment of forest seedlings is considered, this region can be subdivided into individual cells having different d.s. precipitation requirements for forest establishment. The size of these cells was chosen to be $5 \times 5$ m (metres), as in a previous cellular automata model predicting the relative abundance of trees and grasses in savannas (Jeltsch et al., 1996). The ability of these cells to support forest establishment will vary depending on the slope, orientation, edaphic and several other microhabitat factors. Therefore, some cells found in ‘favourable’ conditions will support forest establishment with as little as 50 mm d.s. precipitation (Nix’s threshold value). Other cells, having less ‘favourable’ conditions, will support forest vegetation only with a greater amount of d.s. precipitation. The frequency of cells having their respective minimal d.s. precipitation requirement for forest establishment will probably follow a bell-shaped curve (Fig. 2) and be described by the normal probability density function (Sokal & Rohlf, 1995):

$$f(p) = \frac{1}{\sigma \sqrt{2\pi}} e^{-\frac{1}{2} \left[ \frac{p-\mu}{\sigma} \right]^2}$$

where $p$ is the minimum d.s. precipitation required for establishment of forest seedlings in a cell (mm/d.s.), $\sigma$ is the standard deviation (mm/d.s.) and $\mu$ is the mean minimal d.s. precipitation for forest establishment in a cell in this region (mm/d.s.). The bell-shaped curve in Fig. 2 indicates that there are few cells able to support forest establishment when d.s. precipitation is $< 50$ mm. Cells needing a minimum of 60 mm precipitation for forest establishment are observed most frequently in this region, and few cells need

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**Fig. 1** Regions of the Amazon basin that can potentially be converted to savanna after some deforestation. Black regions represent regions in the Amazon basin with tropical forest and having d.s. precipitation $> 100$ mm. Dark grey regions represent regions having tropical forest with d.s. precipitation $\leq 100$ mm. This region could potentially be converted to savanna, given enough deforestation. Light grey regions represent other types of vegetation but mainly savannas having precipitation during the dry season $\leq 100$ mm. The dry season precipitation isoline was derived from Nix (1983).
more than 70 mm d.s. precipitation to have forest establishment.

Relative forest coverage in a region \((A)\) as a function of its average d.s. precipitation \((P)\) is therefore described by the integral of the function given in equation 1:

\[
A = F(P) = \int_0^P f(p) \, dp \quad (2)
\]

This function, known as the normal distribution function (Sokal & Rohlf, 1995), does not have an explicit solution and must be approximated by a polynomial (Hastings, 1955) or by computer iteration. In the present analysis, a Matlab© integration function was used to calculate the cumulative area under the curve described by equation 1 (Fig. 3). This is a sigmoidal-shaped curve showing forest coverage as a function of d.s. precipitation in the region. Dry season precipitation just above 50 mm leads at first to forest colonization only in 'favourable' patches. Seedlings will establish in less 'favourable' patches as d.s. precipitation in the region increases and the cumulative forest cover increases further. Eventually, further increases in d.s. precipitation produce no further increases in relative forest cover, indicating that the region is saturated.

When we consider the effect of locally produced d.s. precipitation in the subsequent establishment of forest in the region, the situation becomes much more dynamic. Specifically, this occurs when precipitation is between threshold and saturation values. The total d.s. precipitation in a region, including the contribution of vegetation, is represented by:

\[
g(A) = P = P_{imp} + A^*\Phi_f + [(1 - A)^*\Phi_r] \quad (3)
\]

where \(P\) and \(P_{imp}\) are total and imported d.s. precipitation, respectively (mm/d.s.), and \(\Phi_f\) and \(\Phi_r\) represent the d.s. precipitation contributed by forest and savanna evapotranspiration, respectively (mm/d.s.). This equation can be rearranged to:

\[
g(A) = P = P_{imp} + \Phi_r + [A^*(\Phi_f - \Phi_r)] \quad (4)
\]
where the bracketed term on the right represents the increase in precipitation by the contribution of forest evapotranspiration.

The amount of d.s. precipitation produced by forests and savannas ($\Phi_f$ and $\Phi_s$, respectively) is determined by the amount of d.s. evapotranspiration, amount of d.s. evaporated vapour exported from the region and the holding capacity of the atmosphere, and is given by the following equation:

$$\Phi = Ed\alpha$$

where $E$ is the daily d.s. evapotranspiration by forests and savannas, respectively (mm/day). This has been measured by using the soil water budget to be on the average of 4.5 mm/day for forests (Jipp et al., 1998) and by using eddy correlation measurements to be 1.5 mm/day for savannas (Miranda et al., 1996). The number of days ($d$) during the dry season is chosen to be 90 days, according to Nix’s criteria. Vapour from evapotranspiration can either be transported outside the region, stored in the atmosphere or precipitated. $\alpha$ is unit-less and is the proportion of evaporated vapour that is precipitated. A value of 0.1 was used based on the following reasoning. Consider a forested area in a region where precipitation during the driest 3 months is between 50 and 100 mm of rain (Fig. 1). If 60% of this precipitation is recycled, then 35–60 mm of rain in this region is produced by evapotranspiration of the forest. If these forests are evapotranspiring at a rate of 4.5 mm per day during the driest 3 months, their total vapour output is about 405 mm for the dry season. Out of the 405 mm contributed from forest evapotranspiration only 35 mm (or 7%) to 60 mm (or 15%) is actually converted to precipitation. Therefore, $\alpha$ has a value between 0.07 and 0.15, and a value of 0.1 was selected. It is important to note that the proportion of vapour from the evaporated flux that is actually converted to precipitation will vary from region to region. For example, atmospheric storage will decrease as temperature declines, therefore in cooler areas evapotranspiration could be converted more readily to precipitation, i.e. $\alpha$ is larger for cooler areas. The parameters $E$ and $\alpha$ will change with the amount of precipitation during the dry season. This change will, however, be such that $\Phi$ will remain constant. For example, lower rainfall during the dry season increases the vapour pressure deficit, increasing evapotranspiration ($E$), but at the same time the capacity of the atmosphere to hold vapour will increase, decreasing the value $\alpha$. For this reason it was assumed that $\Phi$ remains constant, with a value of 40.5 mm for forests and 14.0 mm for savannas, regardless of precipitation during the dry season. This assumption is possible because soil storage in Amazonian seasonal forests has been shown to be adequate to support evapotranspiration by forests during the dry season (Nepstad et al., 1994).

The focus of this study is to determine the d.s. precipitation conditions leading to a positive feedback loop in which a forested area in the region will generate sufficient precipitation to support further expansion of forested areas. Consider a region with some forested area $A_i$ being subject to global climatic change (i.e. $P_{mp}$ has changed), such that the dry season imported precipitation has changed, bringing the total precipitation in the region to $P_e$:

$$P_e = P_{mp} + \Phi_f + [A_i^\Phi_f (\Phi_f - \Phi_s)]$$

Will the region’s vegetation remain as it is or will there be changes? The qualitative answer to this question can be derived from the step-stair diagram shown in Fig. 4. This shows the relationship between the forest area generated from

![Fig. 4 Curves generated by equation 2 (forest area as a function of precipitation) and equation 6 (total d.s. precipitation as a function of vegetation). The figure also shows a step-stair sequence for two scenarios having different initial relative forested areas. See text for explanation.](image-url)
precipitation (solid line, equation 2) and the total precipitation including that generated from the forest area (dashed line, equation 6). The vertical arrows indicate the forested area that can be supported by the d.s. precipitation, whereas the horizontal arrows indicate the total d.s. precipitation in the region, including that generated by the vegetation. Consider the first scenario. The region has a relative forest area of A1 for a given imported precipitation. The total precipitation in this region, however, cannot support the relative forest cover (A1). Therefore, the relative forest area in the region will decrease (vertical arrow). This in turn will decrease the total precipitation (horizontal arrow), which will subsequently support even less forested area. As a result, the positive feedback generated here will lead to the eventual disappearance of the forested area in the region. Consider the second scenario. The region has the same amount of imported precipitation but more relative forest coverage (A2). The total precipitation in the region can now support a relative forest area even greater than A2 and therefore relative forest area will increase (vertical arrow). This new area will in turn generate even more precipitation (horizontal arrows). The region will undergo a positive feedback loop leading to full forest establishment. To formalize mathematically the above demonstration, one can state that this process is a repeated mapping of d.s. precipitation domain (P) into the range of forest area (A):

\[ F: P \rightarrow A \]  (7)

and forest area into range of d.s. precipitation:

\[ g: A \rightarrow P \]  (8)

This can be summarized by the following equation:

\[ A_{n+1} = F(g(A_n)) \]  (9)

The intersection(s) between \( F(P) \) and \( g(A) \) function represents the equilibrium point(s) where:

\[ A_s = F(g(A_s)). \]  (10)

In other words, the relative forest area supported by the dry season precipitation in the region will not generate additional precipitation to support further expansion of forested areas.

There are three equilibrium points for the previous example: the two outer points are stable equilibria whereas the middle one is unstable. Any small shifts from this middle equilibrium point will cause a positive feedback loop leading either to full or no forest coverage in the region.

A question relevant to palaeoecologists is what are the perturbations to this dynamic system as the amount of imported d.s. precipitation changes? The qualitative answer to this question is illustrated in Fig. 5, showing five hypothetical scenarios of \( g(A) \) on the basis of different conditions.
Fig. 6 Hysteresis loop for a forest–savanna system perturbed by different amounts of imported d.s. precipitation. The solid line indicates a stable equilibrium and the dashed line indicates an unstable equilibrium. Consequences of deforestation for this system are also illustrated.

amounts of imported d.s. precipitation. The first case shows a region with a low amount of imported precipitation. In this case, there is only one stable equilibrium point: that leading to little forest coverage in the region. As the imported d.s. precipitation increases (case 2), this system approaches a saddle-node bifurcation leading to two additional equilibrium points: one stable and the other unstable. Further increase in imported d.s. precipitation (case 3) shows the system with the three equilibrium points. Two are stable (nearly complete or no forest coverage) and one is unstable (partial forest coverage). As imported d.s. precipitation increases even further the system approaches another saddle-node bifurcation (case 4), which will lead to only one stable equilibrium point (case 5): complete forest coverage. The saddle node bifurcations of this dynamic system lead to hysteresis, a phenomenon typical of many biological systems (Fig. 6). This bifurcation will occur at two distinct values of imported d.s. precipitation and these can be calculated easily since they will occur when the line generated by \( g(A) \) is tangential to \( F(p) \) (cases 2 and 4 in Fig. 5):

\[
F'(p) = f(p) = \frac{1}{g'(A)} \quad (11)
\]

For the values of forest- and savanna-generated precipitation and the parameter values of the normal probability density function \((\sigma, \mu)\), the bifurcation of this dynamic system will occur at 28.3 mm and 37.0 mm per dry season, respectively. Therefore, if imported d.s. precipitation is less than 28.3 mm the region will always evolve towards a savanna ecosystem regardless of the initial forest area. Similarly, if imported d.s. precipitation is greater than 37.0 mm the region will always evolve towards complete forest coverage regardless of the initial forest area. For values of imported d.s. precipitation between and including 28.3 and 37.0 mm, the fate of forest coverage in the region will depend on the initial forest coverage, as demonstrated in Fig. 4.

A more general, but important question is: when can one expect a region to show hysteresis for two alternate ecosystems? First, the region must have an external input of a substance (e.g. dry season precipitation), that will affect the establishment of the two ecosystems. Secondly, the ecosystem most dependent on this external input can generate its own substance, and therefore aid its own establishment. Thirdly, an area of the ecosystem most dependent on the external agent must generate enough of this agent to support a greater than equivalent area of this ecosystem. For the case presented here this third prerequisite simply means that the slope of the line generated by \( g(A) \) must be greater than the steepest part of the line generated by \( F(P) \), which for Figs 4 and 5 simply means that:

\[
\frac{1}{g'(A)} < F'(\mu) = f(\mu) = \frac{1}{\sigma \sqrt{2\pi}} \quad (12)
\]

Therefore, if the standard deviation of cell quality \((\sigma)\) is large, or if savannas and forests contribute equally to dry season precipitation, then it is unlikely that hysteresis will occur, and the region will have stable equilibria ranging from zero to complete forest coverage.

**DISCUSSION**

The dynamics of forest–savanna ecosystems revealed by this model may have implications for palaeoecology and conservation biology. The observation of hysteresis between forests and savannas suggests that there may be some inertia in the effects of global climate (precipitation) patterns in changing from one ecosystem to
another. This observation is especially relevant to the refuge hypothesis proposed to explain species richness in the Amazon basin (Haffer, 1969, 1974; Prance, 1982). According to this hypothesis, repeated glacial periods during the Pleistocene and Holocene decreased precipitation in the Amazon basin during each glacial period. This decrease in precipitation caused the Amazon basin to become a vast savanna region punctuated with vestigial islands of tropical forests. Reproductive isolation between these islands caused speciation and is responsible for spatial patterns in species diversity and endemism after the region became covered with forests during warmer and more humid periods. There are objections to this hypothesis (Farrell & Mitter, 1993; Colinvaux et al., 1996, 2000). To date the strongest counter evidence takes the form of a pollen analysis of a 17 m pollen core taken at Lake Pata in western Amazon (Colinvaux et al., 1996) and the pollen record from the Amazon fan (Haberle & Maslin, 1999), both of these showing a continuum of forest pollen throughout the last glacial maximum. The model proposed here also suggests that it is unlikely that the Amazon region could have turned into a savanna. The hysteresis loop (Fig. 6) indicates that there is no smooth relationship between dry season imported precipitation and equilibrium forest or savanna coverage in this system. Changes in d.s. imported precipitation, unless drastic, will not cause a change of ecosystem. Furthermore, the cooling of about 5 °C thought to have occurred 10 000 years ago over the Amazon basin (Stute et al., 1995) could, in fact, have increased the efficiency of converting the forest evaportranspirative flux to precipitation, possibly increasing the overall precipitation in the region.

Changes from one ecosystem to another could, however, have occurred in marginal areas of the Amazon basin showing dry season precipitation close to the threshold value (Fig. 1). Evidence from one of the pollen cores from these marginal areas (Absy et al., 1991), purportedly showing evidence of forest–savanna transition throughout the basin, has been re-examined by Colinvaux et al. (2000) and shown to reflect only local conditions. These authors have shown that the pollen spectrum observed in this core is unlike those found in savannas and tropical forests, and conclude that it merely reflects the over-representation of herb pollen in a shrinking marsh. There is other preliminary evidence indicating a reduction in precipitation and localized movement of forest–savanna ecotones (Van der Hammen, 1974; Servant et al., 1981; Van der Hammen & Absy, 1994) during the last glacial period. The model proposed here predicts that if these changes at the ecotone did occur, they can only result in the domination of one ecosystem over another and that situations where an area is partially occupied by savanna and forest is unlikely. This prediction was tested by measuring the frequency of pollen abundance from random locations in two of the above pollen core profiles showing forest–savanna transitions (Van der Hammen, 1974). According to the proposed model one would expect a bimodal distribution of forest pollen abundance from random samples along pollen cores. In other words, either a region is dominated by forests showing a high abundance of forest pollen, or it is dominated by savanna showing a low abundance of forest pollen. The predictions of the model were confirmed (Fig. 7) with the two cores showing a bimodal distribution and negative kurtosis. Interestingly, a review of the current palynological and sedimentary data

![Fig. 7 Frequency of forest pollen abundance for two cores taken at (a) Laguna de Agua Sucia, Llanos Orientales, Colombia and (b) Lake Moreiru, Rupununi, Guyana (Van der Hammen, 1974). Figures of cores were scanned and digitized. A random sample of this digitized figure was used to draw these frequency diagrams.](image-url)
(Colinvaux et al., 2000) indicates that although there might have been some minor shifts in the forest/savanna boundary during the last glacial, forest and savanna ecosystems are remarkably stable despite global climatic change, and this is consistent with the findings of this model.

The second implication of this model relates to conservation issues. It has been proposed that conservation of biodiversity may be accomplished by selecting conservation areas and connecting them with corridors using island biogeographical principles. See Simberloff & Cox (1987) for a critical review on this issue. Conservation models using metapopulation equations to determine ideal size and density of these conservation areas have also been published (Hanski, 1998). These models, however, suffer by considering only the population dynamics of certain species and no consideration is given to the possibility that some ecosystems may not be viable in a biogeophysical sense if reduced in area. According to the model proposed here, for a certain amount of imported precipitation in a region, the forested area must be greater than the unstable equilibrium area shown in Fig. 6. Deforestation causing a decrease in forested area below this threshold value will cause a collapse of the forest ecosystem in the region with its eventual replacement by savanna.

ACKNOWLEDGMENTS

I would like to thank Dr Don DeAngeles (Department of Biology, University of Miami) and Dr Hüseyin Koçak (Department of Mathematics and Computer Science, University of Miami) for their helpful comments.

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