# Viewing tropical forest succession as a three-dimensional dynamical system

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**Abstract** As tropical forests are complex systems, they tend to be modelled either roughly via scaling relationships or in a detailed manner as high-dimensional systems with many variables. We propose an approach which lies between the two whereby succession in a tropical forest is viewed as a trajectory in the configuration space of a dynamical system with just three dependent variables, namely, the mean leaf-area index (LAI) and its standard deviation (SD) or coefficient of variation along a transect, and the mean diameter at breast height (DBH) of trees above the 90th percentile of the distribution of tree DBHs near the transect. Four stages in this forest succession are identified: (I) naturally afforest-ing grassland: the initial stage with scattered trees in grassland; (II) very young forest: mostly covered by trees with a few remaining gaps; (III) young smooth forest: almost complete cover by trees of mostly similar age resulting in a low SD; and (IV) old growth or mature forest: the attracting region in configuration space characterized by fluctuating SD from tree deaths and regrowth. High-resolution LAI measurements and other field data from Khao Yai National Park, Thailand show how the system passes through these stages in configuration space, as do simple considerations and a crude cellular automaton model.

**Keywords** Dynamical systems · Forest dynamics · Attractor · Leaf-area index · Tropical ecosystems

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## 1 Introduction

A tropical forest is a complex dissipative dynamical system with a huge number of state variables resulting from a myriad of actors and underlying mechanisms ranging from earthworms and mycorrhiza to climatic processes. Less than 40% of present tropical forests can be classed as mature or old-growth (OGF, or stage IV in the present paper) (FAO 2010) while the remainder are in some stage of regeneration (Chazdon 2008). Thus secondary forests contribute signifi-cantly to biodiversity conservation and atmospheric carbon regulation which means that an understanding of their dy-namics is of great importance.

Studies on secondary succession have essentially focused on temporal changes in species richness, density, species composition, and simple forest structure (Saldarriaga et al 1988; Peña-Claros 2003; Martin et al 2004; Chazdon et al 2007; Piotto et al 2009; Lebrija-Trejos et al 2010; Dupuy et al 2012). Some of the studies emphasize the path of suc-cession and demonstrate trends such as increases in basal area, height, and species diversity with time (Guariguata and

Ostertag 2001; Chazdon et al 2007; Lebrija-Trejos et al 2010). During the succession, there are also distinct changes in tropical forest structure which Chazdon (2008) categorized into stages, following the framework of temperate forest succession proposed by Oliver and Larson (1996), among others. There are theories or mechanistic models to explain these changes either in continuous time or discrete stages (Pacala et al 1993; Dislich et al 2010), but they are based on detailed simulations involving many variables.

As an alternative to the detailed simulations, allometric (see, e.g., Enquist et al 1999, 2009; West et al 2009) or demographic (see, e.g., Muller-Landau et al 2006) theoretical investigations have been undertaken to explain how generic mechanistic processes lead to power laws describing the structure and dynamics of forests. In these approaches the forest is represented by a simplified, low-dimensional, generic model. These models, though deliberately ignoring trait diversity, provide possible explanations for the scaling in size-frequency distributions. The drawback of these approaches is that it is difficult to include the spatial heterogeneity caused by non-competitive sources, particularly those from external disturbances such as storms and herbivory outbreaks, that cause 'episodic recruitment limitation' (Enquist et al 2009). Moreover, they do not predict or describe gaps due to tree falls. This is thought to be why the measured distributions deviate from the power laws obtained using such models.

The leaf-area index (or leaf area per unit ground area), LAI, along a transect provides information about variations in cover, such as those resulting from gaps, and so a modelling framework which incorporates the LAI is more adapted to include the effects of episodic recruitment resource limitation than the allometric approach. The LAI along a transect sampled at high resolution (every 1–5 m) is straightforward to measure thanks to the inexpensive device developed by Cournac et al which has an accuracy comparable with much costlier and more time-consuming techniques such as using the LICOR LAI 2000 or other devices (Ferment et al 2001).

In this article, to track and describe how tropical forest structure builds up through secondary succession, we propose viewing tropical forest succession as a trajectory in the configuration space of a three-dimensional dynamical system which has the final stage (old-growth forest) as its attractor. We introduce 'diagnostic' or 'proxy' variables which are observable quantities and directly relate not only to the mechanistic variables (e.g., carbon sequestration, water flow, soil nutrients) but also to the output of theoretical models as well as to other measurable quantities of the real forest. Our three diagnostic variables are the mean LAI, the standard deviation or coefficient of variation of the LAI, and the mean diameter at breast height (DBH) of the top 10% of the distribution of diameters of trees located near the tran-

sect. The justification for this choice and the expected behaviour of our envisaged dynamical system is given in Section 2. To show how this concept applies to a real forest, we gathered LAI, forest canopy height, and tree diameter data from several large patches representing different stages of succession in Khao Yai National Park, Thailand.

It is worth clarifying what we mean by 'stage' and 'gap'. A stage is not a spatial unit of area, but a vegetation state describing a patch (a landscape unit usually at least several 100 m to kilometres across) characterized by a uniform age and history of disturbance. A 'gap' is the space in the canopy (up to about 50 m in length and at least 5 m wide) within a patch caused by the falling of one or a few big branches or whole trees. At a micro-scale, it starts a process of regeneration, but it is not considered to be a patch characterized by a particular successional stage. The distinction is primarily one of scale. The patch succession process begins with a catastrophic anthropogenic or natural disaster at landscape level.

The study area and the measurement techniques are described in Section 3 and the results are presented in Section 4. The final sections include a discussion of the advantages of our approach over other modelling frameworks and possible applications are suggested.

## 2 Modelling framework

For forest modelling, a significant mechanistic variable is productivity but it is difficult to measure. A more convenient quantity is the mean leaf-area index of a linear transect, $M = \text{mean}(\text{LAI})$, where the transect is located within a forest patch having an homogenous history of disturbance and development (i.e., belonging to the same stage as defined above). The LAI measures the availability of the photosynthetic tools of the ecosystem and is therefore directly linked to productivity. Structural complexity, which is the result of the turnover processes and is linked to tree lifespan, is also well reflected in the variation of LAI along a high resolution transect. We therefore consider the standard deviation of the LAI of a linear transect, $S = \sigma(\text{LAI})$. However, as $S$ is by construction limited to the maximum LAI value, we will use the normalized standard deviation (or 'coefficient of variation'), $V = S/M$, in order to have a representative measure of the structural complexity.

For a deterministic and autonomous dynamical system, trajectories in configuration space may only cross each other at a fixed point. In our low-dimensional dynamical system of diagnostic variables we wish to keep this property. This necessitates the use of a third diagnostic variable. A possible choice is $\alpha$, the biodiversity obtained from counting the number of tree species in an area equivalent to the area covered by the linear transect used for determining the mean LAI. But measuring $\alpha$ would be quite a big task. Instead we

use $D$, the mean DBH of trees above the 90th percentile of the DBH distribution for trees within 5 m of the transect. $D$ gives a good estimate of the size of the dominant trees and is thus more relevant to forest structure than $\alpha$ as well as being easier to measure.

The configuration space trajectories we have in mind are 'fuzzy' rather than sharply defined (more like tubes than lines) owing to the fact that the reduction of the original system with millions of degrees of freedom to one with just two or three will never be perfect. In other words, suppose we have the initial conditions for two different forest sites and that they have the same values of the diagnostic variables and are therefore located at the same point in our configuration space. We do not expect that the evolution of the two real sites in our configuration space will be identical since there are many variables such as the type of species involved that would influence how, for example, the LAI will change in time. Nevertheless, we expect that the time evolution of the two sites will be quite similar until stochastic factors come into play at the final stage of forest succession.

## 2.1 Expected trajectories

In favourable climates, a piece of recently uncovered land (as happens inside growing meanders of rivers in flat regions (Emmons and Dubois 2003), grassland which has been protected from fire for some time, or land previously used for farming and left to itself) will exhibit afforestation initially by pioneer tree species. We will refer to this first stage of forest succession as naturally afforesting grassland (NAG) or stage I. The afforestation can take several forms such as boundary growth (progression of the forest border into neighbouring grassland or savanna), coalescence of tree clumps (small isolated tree groups grow and end up merging), or massive afforestation (in favourable climatic conditions, and in the absence of fires, small trees will appear everywhere in the grassland or savanna, and will soon constitute an homogeneous forest) (Favier et al 2004a,b). We would expect an initially low value of $M$ which then increases with time. $S$ would also start low and increase with max(LAI) which rises as a result of scattered fast-growing trees and corresponds to what we will call very young forest (VYF) or stage II.

In the case of a massive afforestation, this newly afforested region might develop into a uniformly aged stand (the stem exclusion stage), with a nearly continuous canopy. $M$ will then be quite high, while $S$ will be low. Field evidence shows that in such a forest, trees often exhibit some degree of self-avoidance or anti-aggregation behaviour (see, e.g., Putz et al 1984). We will refer to this relatively homogeneous stage as a young smooth forest (YSF) or Stage III.

The YSF stage ends when the first large canopy trees die, thus opening gaps and causing a sudden drop in $M$ and increase in $S$ (and $V$). This final stage in the succession is the old growth forest (OGF) or Stage IV. At this point the dynamical system becomes more stochastic as the gaps arise randomly in time. Note that what we refer to as stages II, III, and IV correspond to the three tropical forest states described by Chazdon (2008).

Throughout the stages, $D$ slowly increases but will eventually saturate once the oldest trees have reached their maximum DBH. However, as with the other diagnostic variables, fluctuations in $D$ will arise as a result of deaths of large trees along the transect. There is no static 'climax' or equilibrium of a mature forest stand since gaps are constantly being formed as a result of tree-falls and then being filled by local succession processes. This is the 'mosaic' description of forest dynamics (Aubréville 1938; Chambers et al 2013). Each plot cycles in time within a region of configuration space corresponding to the *dynamic* climax of the mature forest and this is the attractor of the system. A typical turnover time (the time between such tree-falls at a given location) is of the order of a few decades, and a typical size for a gap along a transect ranges from a few metres to about 50 m, depending on the direction in which the tree-fall occurs.

Note that the chances of all large trees dying during the usual natural course of events in a large area is very low, and so going from stage IV (OGF) to stage II is quite unlikely. Similarly, the chances of a big perturbation leaving only trees of the same age is negligible, which rules out a jump from stage IV (OGF) to stage III (YSF). A very large (and thus very rare) disturbance, climatic or otherwise, would possibly lead to a nearly treeless grassland or savanna (stage I) in which case the OGF would only be returned to via the intermediate stages. The usual, more moderate perturbations would only pull the point in configuration space representing the patch away from the attractor centre and as a result of the resilience of the forest, the point will in time return to the attractor region if it has been moved away from it.

To illustrate the time variation of the diagnostic variables we constructed a crude cellular automaton model of a forest as detailed in Appendix A. The results of this model will be compared qualitatively with the field data describing the successional stages in Section 4.

## 3 Field study

### 3.1 Study area

Khao Yai National Park (14° 26′ N, 101° 22′ E; 700–800 m asl in the study area) lies in the Sankamphaeng mountain range around the southwestern boundary of the Khorat Plateau in Thailand and was established in 1962. It is an old growth forest ecosystem in the middle of which settlements with traditional upland farming were established by the Thai

**Fig. 1** Typical images from Khao Yai National Park, Thailand of (a) naturally afforesting grassland (NAG or stage I) (b) very young forest (VYF or stage II) (c) young smooth forest (YSF or stage III) (d) old growth forest (OGF or stage IV).

Tha Dan people at the end of the 19th or early 20th century. The forest at this elevation is seasonal evergreen with a dry season (November–April) and a wet season (May–October) and an average annual rainfall of 2100 mm.

Khao Yai National Park vegetation is a mosaic of different states of vegetation succession and contains all four stages we defined earlier (Fig. 1). Old growth forest (OGF, stage IV) does not show signs of extensive human disturbance and is well over a few hundred to a thousand years old. The OGF canopy is mostly at a height of 20–30 m with some emergent trees (often *Dipterocarpus gracilis*) reaching over 50 m (Brockelman 1998). In 1996, a long-term forest dynamics research plot (Mo Singto plot) was initiated. It now covers a 30-ha area of OGF in which every tree has been mapped, identified, measured, and permanently tagged (Brockelman et al 2011). Census of all trees $\geq$ 10 cm in diameter was completed in 2001, and a recensus in 2004–2005 included all stems $\geq$ 1 cm DBH. The plot contained 264 species of trees and shrubs $\geq$ 1 cm DBH, and about 200 species reaching $\geq$ 10 cm, in the 2005 census (Brockelman et al 2011). Young smooth forest (YSF, stage III) or the stem exclusion stage is a regrowth forest on former farmland abandoned when the park was established in 1962. Very young forest (VYF, stage II) or stand initiation is a regrowth forest on patches which were cleared and used as a military camp until 1975. Naturally afforesting grassland (NAG, stage I) occurs on a part of a former golf course allowed to regenerate since 2001. Clumps of trees are establishing

themselves in the middle of it. Elsewhere, grassland in Khao Yai Park is still maintained in some areas by fire or mowing; massive afforestation begins as soon as the patches of fields escape burning for one or two years.

## 3.2 LAI measurement

Light transmitted through the canopy was measured using a 'LAIL', a simple and inexpensive LAI meter (Cournac et al 2002). The LAIL is highly sensitive to changes in the density of the canopy and can be used to map small-scale gaps and inhomogeneities caused by individual trees. It has been successfully employed in making rapid comparative assessments of LAI in various studies (see, e.g., Vincens et al 2000; Ferment et al 2001; Emmons and Dubois 2003; Favier et al 2004b; Emmons et al 2006; Aleman et al 2012).

When taking measurements, the light sensor is held overhead at a height of about 2 m and out of direct sunlight (not always possible in forest gaps). Readings were taken only between 11:00 and 14:00 to ensure that the sun was reasonably near the zenith (Cournac et al 2002). Readings were taken at 1-m intervals along transects 200 m long: one transect in the NAG (I) part, two transects in the VYF (II) part, three in the YSF (III), and six transects in the OGF (IV) of Mo Singto. The OGF transects were measured twice (November 2005 and November 2008). The YSF transects were measured in November 2005, while the NAG and VYF were measured in November 2011.

## 3.3 Canopy height measurement

The canopy height *h* was measured using the point-intercept method of Brockelman (1998). We systematically selected 100 points spaced 10 m apart in a 1-ha grid and measured the top-of-canopy height vertically. Two 1-ha areas were measured in the 30-ha OGF (IV) by Brockelman (1998), one of which is reported again here. In addition, 100 points were measured for this study in the YSF (III) of northern Mo Singto. At each point, a Suunto clinometer was used for finding the direction of the zenith and an optical or laser rangefinder (Nikon Prostaff 550) was used to measure the height of the highest foliage over that point.

## 4 Results

Field measurements display common spatial LAI patterns at every stage of the succession but the patterns differ greatly between stages (Fig. 2). In the NAG (I) result (Fig. 2a) one can see individual trees, many gaps corresponding to grassland, and only a few tree clusters exhibiting canopy continuity over a few metres. The LAI is low on average ($M = 1.58$) but fluctuates a lot ($S = 1.13$, $V = 0.72$).
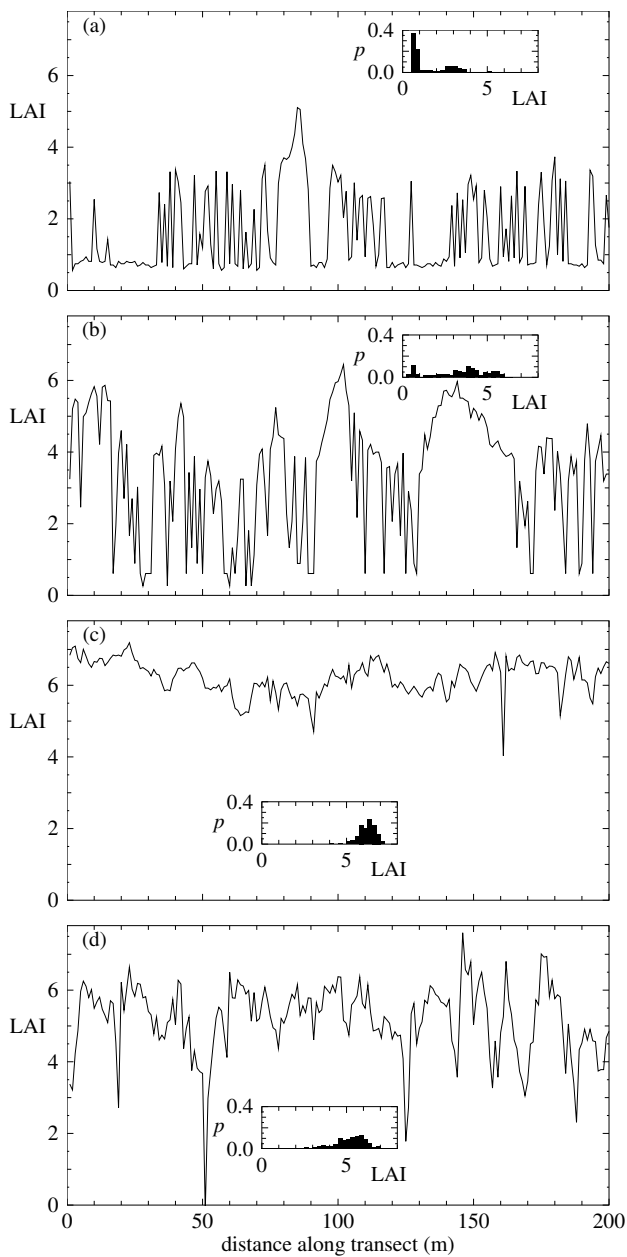
**Fig. 2** Typical LAI transects in field measurements: (a) naturally afforesting grassland (NAG or stage I) (b) very young forest (VYF or stage II) (c) young smooth forest (YSF or stage III) (d) old growth forest (OGF or stage IV). The inset plots show the distribution of LAI values: $p$ is the proportion of LAI values within each bin (bin width: 0.25).



**Fig. 3** Distribution of canopy heights ($h$) among 100 point samples for young smooth forest (stage III: crosses) and for old growth forest (stage IV: dots).

0.49 and 0.36), thus indicating a more regular structure than the NAG.

The YSF (III) has higher mean LAI values and its canopy is nearly continuous which is why we use the term 'smooth' (Fig. 2c). In field measurements, $M = 4.72$, 5.48, and 6.22, and $S$ is low (0.52, 0.57, and 0.47; $V = 0.110$, 0.104, and 0.076). The averages for these three transects are $M = 5.47$, $S = 0.52$, and $V = 0.097$.

In the OGF (IV), the LAI oscillates over a wider range than in the case of the YSF (Fig. 2d). This indicates a less homogeneous canopy along the OGF transects. The LAI in most of the transects of the OGF occasionally drops to zero, demonstrating the presence of recent tree-falls and canopy gaps in those transects. The mean LAI value of the OGF transects is generally lower than that of the YSF transect, which is not a priori expected considering the greater biomass clearly present in the OGF ($M$ ranging from 3.81–5.74 in field measurements) but can be understood when one considers that the LAI cannot exceed 7–8 (except very locally) and that there are gaps in the OGF and not in the YSF. The variation of the LAI values in the OGF, as measured by their standard deviation $S$ (0.77–1.40 in field measurements) or coefficient of variation $V$ (0.17–0.36), is higher than that of the YSF transects.

The median height $h_{0.5}$ of the top canopy (Fig. 3) is lower in the YSF ($h_{0.5} = 21$ m) than in the OGF ($h_{0.5} = 26$ m) and $h$ is less variable in the YSF than in the OGF ($\sigma(h) = 4.1$ and 12.5, respectively). Fig. 3 shows that the canopy heights of the YSF are mainly in the range of 18–23 m, while in the OGF, they take values ranging from 0–50 m. The more homogeneous canopy height in the YSF is concordant with the more homogeneous LAI distribution described above. Canopy trees in the YSF were mostly in the 10–20 cm DBH class, with no trees > 40 cm. The main canopy trees in the OGF mostly had DBHs of 40–80 cm with a few exceeding 100 cm. The narrow range of $h$ and DBH values of trees in the YSF is another reason for describing it as 'smooth'.
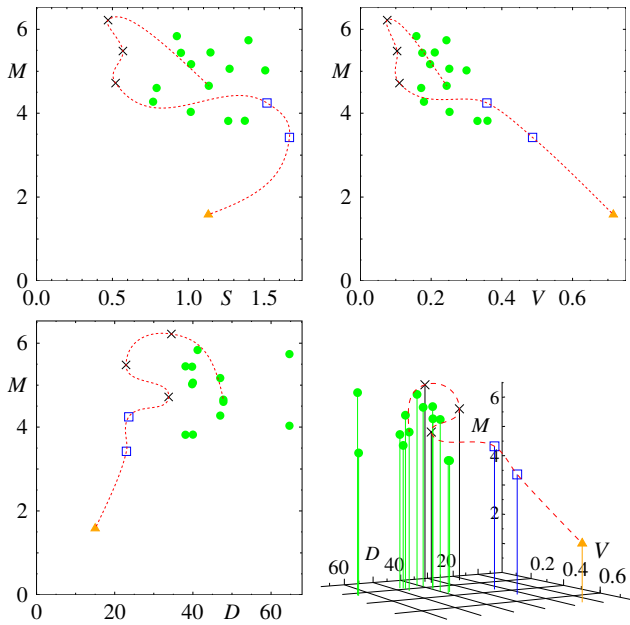
The VYF (II) shows a more continuous canopy in the sense that there are long segments where the LAI is rather high. However, there are also a very large number of small gaps, and a few more extended gaps (Fig. 2b). The mean LAI is higher than in stage I ($M = 3.42$ and 4.24 in field measurements), and while the standard deviation is higher ($S = 1.66$ and 1.52), the coefficient of variation is lower ($V =$

**Fig. 4** $(S,M)$, $(V,M)$, $(D,M)$, and $(D,V,M)$ plots from the measured transects. Triangle: NAG (I); squares: VYF (II); crosses YSF (III); dots: OGF (IV). The curve in each plot is a guide to the eye showing the approximate trajectory through configuration space.



**Fig. 5** Results of crude cellular automaton model giving the expected behaviour of the diagnostic variables $M$, $S$, $V$, and $D$ (in cm) as a function of time $t$ (in years). Solid lines: results from a typical run of the model; dashed lines: mean values (from 10000 runs); shaded regions show mean±SD except for the plot of $D$ in which case the upper bound is the maximum value and the lower bound is the mean−SD.

From the $(V,M)$ plot (Figs. 4) it is clear that the 'disorder' is largest in the NAG and that it decreases as the canopy closes, after which senescence-induced tree-falls push the system towards its dynamic attractor, i.e., the cloud of OGF (IV) points, and the disorder increases while the mean LAI decreases a little. In the $(S,M)$ and $(V,M)$ plots, the trajectory from the VYF (II) to the YSF (III) seems to intersect the attractor. In fact, it does not, as is apparent from the $(D,V,M)$ plot: the $D$ values for stages I–III are lower than in the OGF (IV).

The behaviour of the cellular automaton model (Figs. 5,6) predicts surprisingly well features of the successional stages measured in the field. Among these are the increase and then decline in $M$; the rapid increase, decline, and subsequent increase followed by irregular fluctuations in $S$; and the decline in $V$ followed by a slight increase. This behaviour suggests that the model is robust and captures the essential physiological and structural changes that are well known to characterize succession beginning from a massive invasion and colonization stage of grassland or bare ground. The final stage is a dynamic one displaying small-scale internal cycles of gap formation and regeneration that will persist indefinitely, until an anthropogenic or catastrophic natural disturbance of the whole forest patch sets it back to an earlier stage and results in a renewed progression to the final attractor stage.
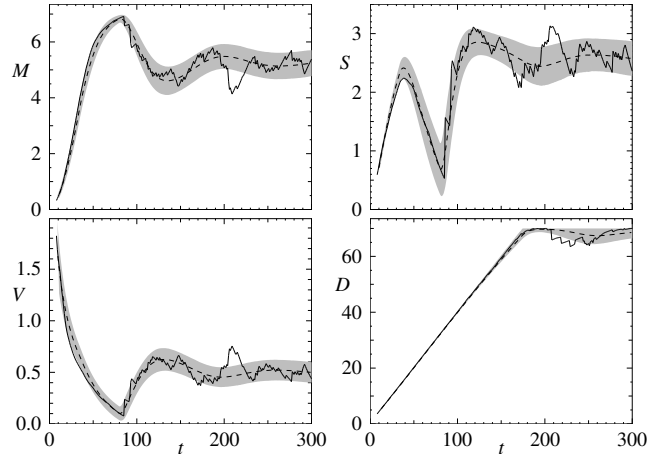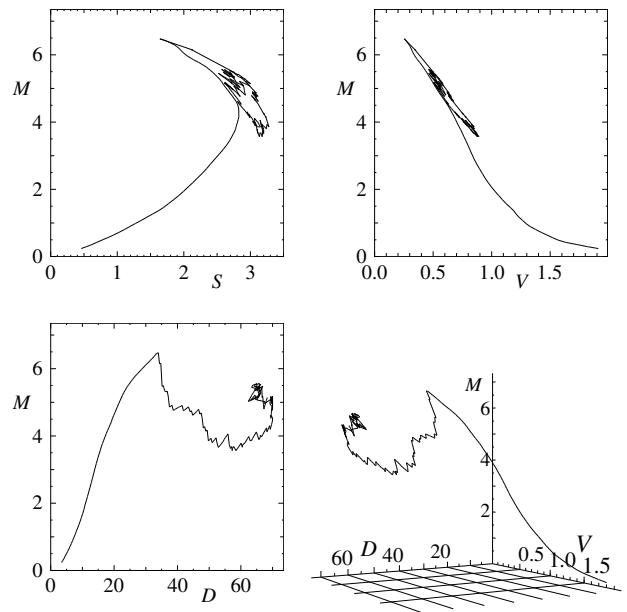


**Fig. 6** $(S,M)$, $(V,M)$, $(D,M)$, and $(D,V,M)$ plots for the cellular automaton model output shown in Fig. 5.

## 5 Discussion

The behaviour of the diagnostic variables taken from field measurements from the four stages is in agreement with our predictions in Section 2.1 based on simple considerations and a crude cellular automaton model. Thus our low-dimensional dynamical system view of forest succession has the potential to capture how the canopy builds up throughout secondary succession following large-scale disturbances as well as the dynamics of canopy structure in old-growth forests.

In our low-dimensional framework, forest which is recovering from a major disturbance (or even appearing where grassland existed before) starts from somewhere in configuration space and follows a trajectory which eventually leads to a 'dynamic attractor' which is stochastically explored as a result of the occurrence of gaps and subsequent local canopy closure in the OGF. Although this attractor is likely to be a mixed stage between mostly old and some new sites regenerated from gaps, its nature clearly differs from that of the YSF stage which precedes it in the succession. This mixed or 'mosaic' stage is well known in the literature, and is the basis of many mature forest models using gap creation and closure (see, e.g., Shugart 1998).

The concept of a dynamic attractor sheds a new light on the old 'climax' concept in OGF in which the climax is taken as a static forest structure (see, e.g., Selleck 1960; Ghazoul and Sheil 2010). It is now well understood that the climax is not a static equilibrium, but it still can be a useful idea if it is instead considered as the centroid of the attractor.

Note that the extent of the attractor envelope enclosing all the OGF will depend on the sample size (i.e., transect length). In fact, if we increase the sample size it will reduce the size of variations in the structural complexity and average LAI, and hence the attractor size would shrink.

The modelling framework used here deliberately ignores anthropic interaction and significant ecological characteristics, such as the change in functional types of species implied in succession and the temporal variation of the biodiversity, which are generally the core of studies concerned with secondary succession (Guariguata and Ostertag 2001; Chazdon 2003; Chazdon et al 2007; Lebrija-Trejos et al 2010). When compared to other low-dimensional models such as those of Enquist et al (1999), Enquist et al (2009), and West et al (2009), our modelling framework has the following advantages. First, it can easily be fitted to capture the spatial heterogeneity resulting from non-competitive sources such as those from external disturbances. Second, large trees are a cause of deviation in the allometric-based model (West et al 2009), but in our case, as $D$ is one of the three variables, the inclusion of the largest trees in the modelling framework is essential. Including large trees in any model is desirable as they are the most important source of seeds and microclimate. Finally, the LAI provides more information about the forest structure and productivity (Clark et al 2008) than the tree size distribution.

Our simple three-variables cellular automaton model does not give such a detailed picture of tropical forest evolution as many-variables models can do (Pacala et al 1993; Dislich et al 2010). Its interest resides in the robustness with which it describes the trajectory through the successive stages towards the 'climax' attractor.

The framework we have proposed suggests the need for further investigations of the structural self-organization of forests and its relationship with ecological forcing. First, one needs to improve the description of the structural characteristics of stage III; specifically, the strong homogeneity in canopy height, which can be understood to be a result of the competition for light, and the role of self-thinning due to competition for light and soil nutrients. A second important point will be to understand how old-growth forest explores the attractor and to relate turnover time to disturbance characteristics.

It should be mentioned that this work, which has used a simple ground-based LAI measurement method, could be reproduced using air-borne high resolution lidar measurements: increasing numbers of studies use this method, and more and more data is available (see, e.g., Kellner et al 2009; Tang et al 2012).

# 6 Conclusions

The recent vegetative history of Khao Yai National Park has given us the opportunity to confirm that when grassland is left unperturbed (in favourable climatic and pedologic conditions), the transition to forest follows what was expected for the chosen diagnostic variables of mean LAI, standard deviation or coefficient of variation of the LAI, and the mean DBH above the 90% percentile of the DBH distribution along a transect. The study also showed that the concept of the mature forest stage as an attractor of a three-dimensional dynamical system is a valid one.

Our study also suggests that it is possible to build mechanistic models that can explain succession in tropical forests. We think that such models require three separate regimes: (1) a description of the transition of savanna or grassland to VYF (Favier et al 2004a) (where the dominant factors are climate, fires, and human impact), (2) a description of the formation of a continuous canopy (where competition for light determines self-thinning of trees), and (3) a description of the dynamical climax of the mature forest (where the dominant process is the gap dynamics).

A possible practical application of our approach would be to make high-resolution LAI transects in mature forests which are to be selectively logged; the comparison of measurements before and after harvest would enable quantification of the regeneration rate of a mature forest and help to define sustainable management policies. In a similar way, such measurements could also be used as a guide for managing forest restoration projects in tropical regions.

# A Cellular automaton model

The model is an $n_x \times n_y$ cellular automaton with periodic boundary conditions. Each cell represents a 5 m × 5 m quadrat and has values of LAI and DBH. The DBH corresponds to the DBH of the largest tree in

the quadrat. Each time step (representing 1 year) is composed of two sub-steps: tree-falls followed by tree growth.

In the tree-falls sub-step, each cell with a DBH larger than $d_o$ has a probability $p_d$ of dying. Such a tree is assumed to be 50 m in height and falls in a random direction, killing trees where it falls (by setting those cells to zero LAI and DBH) with probability $p_{dtf}$.

In the tree growth sub-step, if the DBH is nonzero it is incremented by $\Delta d$ up to a maximum of $d_{max}$ at the next time step. If the LAI is nonzero, it is incremented by $\Delta L$ up to a maximum of $L_{max}$. If the LAI (and therefore also the DBH) of a cell is zero and is surrounded by $k$ cells with an LAI greater than $L_s$ (using a 4-cell neighbourhood and so $k = 0, 1, \ldots, 4$), the probability that the LAI becomes $\Delta L$ at the next time step is $p_{wa} + k p_f$. The parameters $p_{wa}$ and $p_f$ (both much less than 1) correspond to the probability of germination of seeds dispersed by, respectively, wind or animals, and falling from a neighbouring tree.

Initially all cells have zero LAI and DBH. Values of $M$, $S$, and $V$ are found from the values of LAI along a line of $n_x$ cells in the $x$-direction. $D$ is found from the values of DBH in these cells and the row of cells of the same length alongside.

Values of parameters used: $n_x = 40$, $n_y = 21$, $d_o = 32$ cm, $\Delta d = 0.4$ cm, $d_{max} = 70$ cm, $\Delta L = 0.2$, $L_{max} = 7$, $L_s = 2$, $p_d = 0.01$, $p_{dtf} = 0.2$, $p_{wa} = 0.04$, $p_f = 0.01$. With the exception of the last three, which are difficult to estimate from the data available to us, the parameter values were chosen to be in line with field data. $p_{dtf}$ clearly only has an effect once trees start dying; increasing its value results in larger fluctuations in the OGF stage. In the model, $p_{wa}$ and $p_f$ are assumed to be small. Increasing $p_{wa}$ results in a more uniform YSF stage. The effects of changing $p_f$ are more complex and are coupled to other parameter values. But overall, the qualitative features of the model output do not depend on the precise choice of parameter values.

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