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Multiple modes in tropical tree cover: a multi-dimensional perspective

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Supplementary material for this article is available online

Abstract

Observations have been debated as portraying a multimodal distribution of tropical tree cover, even in regions with identical mean annual precipitation (MAP). Previous studies have discussed whether such multimodality is evidence of alternative stable states, which would indicate that tropical forests may irreversibly transition to a savanna-like state when deforestation and climate forcing reach a tipping point. However, doubts have been raised regarding this interpretation. Alternative hypotheses invoke heterogeneous environmental conditions related to soil properties, climate parameters beyond MAP, or human activity. Here, we explore the possibility that the influence of multiple environmental parameters can create multimodality in monostable systems when projected onto one dimension. We show that this situation can indeed occur, even if the system's only equilibrium state depends monotonically on the parameters, and even if the parameter values have Gaussian distributions. Such a situation would imply that tree cover may respond linearly to forcing, without any abrupt behavior, regardless of multiple peaks in the tree cover distribution. However, when considering ecologically more realistic parameterizations of tree cover, as used in process-based vegetation models, we find that multiple tree cover modes are more difficult to obtain in the absence of alternative stable states. The reason is that environmental conditions do not affect tree cover directly and independently from each other, but indirectly by affecting tree productivity and mortality. Consequently, a coexistence of forest and savanna in these models is only possible when imposing environmental parameters that are bimodal themselves. Motivated by this finding, we analyze the observed distribution of several relevant environmental parameters in South America, and find that none of them suggests a multi-modal tree cover distribution. Our results hence emphasize that possible tipping dynamics are a concern, but also call for improved estimates of tropical tree cover distribution and the role of fire-vegetation interactions.

1. Introduction

Tropical tree cover from MODIS vegetation continuous fields has been shown to display multiple modes (maxima in the frequency distribution), even for the same annual mean precipitation (MAP) (Hirota *et al* 2011, Staver *et al* 2011b). It has been widely discussed to what extent this multimodal distribution results from heterogeneous environmental conditions like climate and soil properties, or from internal non-linear dynamics in the response of vegetation to the environment. If no other environmental factors are the cause of this coexistence of modes, a compelling explanation is the existence of alternative stable states in the vegetation system (Hirota *et al* 2011). This implies that for intermediate MAP (roughly in the range of 1000–2000 mm yr^{-1}), whether a region develops a savanna or rainforest ecosystem depends on its history and is not determined by the environment alone (figure 1, red arrows). In this situation, changing climatic conditions could reach a tipping point, triggering widespread and potentially irreversible transitions of tropical forest areas—including the Amazon rainforest—toward a degraded, savanna-like state (Cox *et al* 2004, Malhi *et al* 2009, Nobre and Borma 2009, Lovejoy and Nobre 2019).

The existence of alternative stable states relies on large positive (i.e. reinforcing) feedback mechanisms, which during 'tipping' act to drive a system away from its old equilibrium state when being perturbed (Scheffer *et al* 2001, Lenton *et al* 2008). In case of tropical vegetation cover, crucial feedback mechanisms involve fire. Most importantly, vegetation fires suppress tree cover due to the faster recovery of grasses compared to tree saplings (Hanan *et al* 2008), while forest cover suppresses fires due to less fuel and moister conditions near the ground (Staver *et al* 2011a). The role of these feedbacks for the existence of alternative stable states has been investigated in a large range of models. Relatively simple, ordinary differential equation systems describing the interaction of a few vegetation types at one location typically reveal fire-induced alternative stable states (Staver and Levin 2012, van Nes *et al* 2014, Magnani *et al* 2023) or even more complex behavior (Touboul *et al* 2018). In principle, reaction-diffusion models (van de Leemput *et al* 2015) and cellular automata (Wuyts and Sieber 2023), which capture spatial interactions, support this result, though only one stable state tends to eventually dominate in the modeled domain if the environment is homogeneous and if the stability of the two states is not exactly balanced out. A number of complex dynamical global vegetation models (DGVMs) has also been shown to support alternative stable vegetation states, with fire-vegetation interactions being the crucial ingredient (Scheiter and Higgins 2009, Moncrieff *et al* 2014, Lasslop *et al* 2016, Drüke *et al* 2023). Theory and model results are also confirmed by a number of fire exclusion experiments (Swaine *et al* 1992, Louppe *et al* 1995), though doubts have been raised about the interpretation of these experiments (Veenendaal *et al* 2018, Higgins *et al* 2023). In addition to small-scale feedbacks, the continent-wide recycling of moisture evaporated by rainforest trees (Eltahir and Bras 1996) has been suggested to play a relevant role for the stability of tropical rainforests (Boers *et al* 2017, Zemp *et al* 2017, Bochow and Boers 2023).

However, other explanations for the multimodality in tropical tree cover, without invoking alternative stable states, have also been suggested. The implication is that in these scenarios, tree cover may respond perfectly linear to anthropogenic forcing, without any tipping dynamics. For instance, it has been discussed whether multimodality is an artifact resulting from the methodology used to derive tree cover from the original satellite data. The method used to generate MODIS tree cover maps has been criticized to result in a binning bias (Hanan *et al* 2014, Staver and Hansen 2015, Gerard *et al* 2017), and is not consistent with other data streams (Kumar *et al* 2019). However, other sources of data are not fully conclusive yet. For example, tree cover maps based on high-resolution nanosatellite data show large scatter in tree cover values but no obvious mode separation (Reiner *et al* 2023). In contrast, Aleman *et al* (2020) show that savanna and forest biomes have different tree species compositions, which they argue to represent alternative states. Overall, the extent of modal overlap of tree cover in climate space is not robust across previous studies, and depends not only on the observational dataset, but also on the choice of environmental drivers and statistical methods, although some overlap typically occurs at least in a few regions (Higgins *et al* 2024).

Besides such issues of data imperfections and environmental determinism, two classes of mechanisms to generate multiple tree cover modes have received widespread attention. The first class comprises hypotheses which invoke spatially heterogeneous environmental conditions other than MAP. For example, it was proposed that different soil properties may act as a sharpening switch, such that fires amplify the differences that are imposed by the soil and climate (Veenendaal *et al* 2015, 2018). Also, direct human influences on tree cover may affect the distribution (Wuyts *et al* 2017). Besides, even in case of the existence of alternative stable states, environmental heterogeneity is required for states to coexist next to each other, as shown in cellular automata models (Wuyts and Sieber 2023) and reaction-diffusion models (van de Leemput *et al* 2015, Staal *et al* 2016, Wuyts *et al* 2019), which simulate spatial interactions.

A special case of this class of explanations is suggested by Good *et al* (2016), who point out that nonlinearities in the effect of the environment on tree cover may give rise to multiple modes in the frequency distribution. They use a simple monostable logistic growth model, consisting of a single ordinary differential equation to represent tree cover dynamics, and show that such a monostable system can generate a multimodal distribution when considering spatially varying productivity β and mortality m (figure 1(a), cyan or cyan-striped arrows). However, in order to obtain a trimodal tree cover distribution (in similarity to the observed desert, savanna, and forest states), they needed to prescribe a specific distribution in parameter space (β, m), with higher mortality m at intermediate productivity, and lower m at more extreme productivity values. This relationship can be justified on grounds of the 'intermediate fire-productivity hypothesis': While very dry

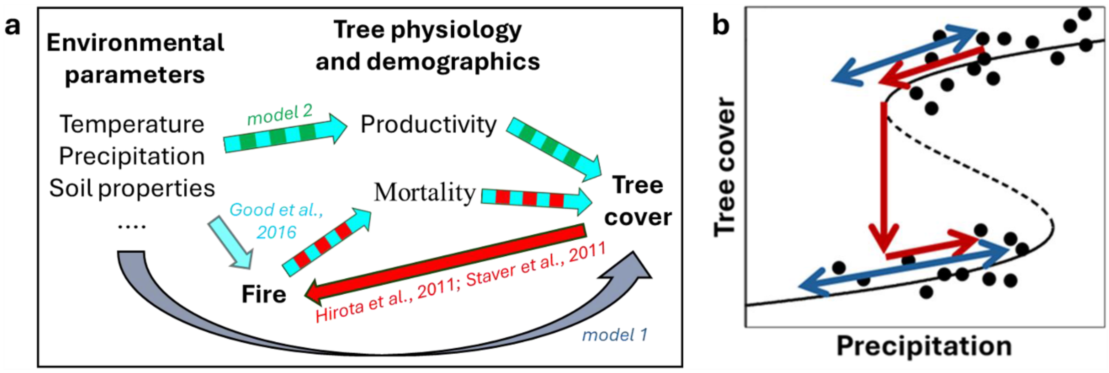

Figure 1. Conceptual illustration of different hypotheses to explain multimodal tropical tree cover. (a) Processes included in different hypotheses or models (striped arrows occur in several models). Our model 1 (dark blue arrow) directly translates environmental variables to tree cover. Model 2 (green) illustrates a more process-based approach by going through tree productivity. The model of Good *et al* (2016) (cyan) additionally involves the effect of fire on mortality. The red arrow from tree cover to fire creates a positive feedback loop potentially giving rise to alternative stable states as hypothesized in Hirota *et al* (2011) and Staver *et al* (2011b). (b) Implications for the system's response to forcing. The bistability hypothesis assumes that all data points (black dots) represent the same bistable system. Hence, reducing precipitation can lead to a tree cover collapse, with no recovery even after precipitation is increased again (red arrows). Environmental hypotheses like our model 1 also allow a linear, reversible response to forcing (blue bidirectional arrows) because each of the two data clouds results from different environmental conditions, which may not change over time. Our model 2 shows that no such multimodal tree cover distribution is possible without multimodal environmental parameters or fire. The model by Good *et al* (2016) would result in a nonlinear but reversible response to forcing (not shown).

climates have low productivity and hence low fuel for vegetation fires, and wet climates also suppress fires, intermediate climates (associated with intermediate productivity) support fires by providing sufficient dry fuel, and hence higher tree mortality. Since their suggested hypothesis relies on a range of tree productivity values in the same MAP regime, other environmental factors still have to be invoked.

The second class of hypotheses does not rely on environmental differences but instead focuses on specific features of the transient dynamics of different tree types. For example, Yin *et al* (2014) distinguish between high-growing forest trees and area-maximizing savanna trees in a conceptual model. When these tree types are assumed to have different growth rates and are stochastically affected by fires, they can also produce multiple modes in the distribution of tree cover, biomass, and leaf area index. These modes represent transient states rather than alternative stable states.

In this article, we solely focus on the first class of explanations by exploring the role of environmental conditions and nonlinear dependencies of equilibrium tree cover on these conditions. Specifically, we ask under which conditions environmental parameters can create a multimodal equilibrium tree cover distribution in a monostable, but multidimensional system. In other words, we explore a specific case of environmental determinism that may explain the observed tree cover distribution, but would not imply any abrupt dynamics. This stands in similarity to the analysis by Good *et al* (2016), but without the requirement to invoke the intermediate fire-productivity hypothesis. We apply three different models, which are all known to be monostable, i.e. they do not feature alternative stable states: 1. a simple conceptual model, which demonstrates how in principle, multiple modes can arise in a nonlinear but monostable system, for multidimensional Gaussian inputs (figure 1(a), dark blue arrow), 2. a modified version of the simple but biologically representative model by Good *et al* (2016) (figure 1(a), green-striped arrows), and 3. the comprehensive process-based vegetation model LPJmL. Building on the conclusions from these models, we investigate the observed distributions of various environmental parameters and discuss the evidence for and against the existence of alternative stable states in tropical ecosystems.

2. Methods

2.1. Model 1: conceptual model

Our first model is a very simple conceptual model. It is designed to demonstrate the mathematical possibility that multiple modes can arise from a nonlinear monotonic function with multidimensional Gaussian inputs, when the data is projected onto one dimension (here: MAP). In other words, it describes a world where multimodality in tropical tree cover would statistically emerge in a monostable system through nonlinear responses to the (perfectly Gaussian) environmental variables. We here consider tree cover Ψ as a function of two input parameters, (x_1, x_2), where Ψ can be written as a product of two separate functions $\Psi_1(x_1) \cdot \Psi_2(x_2)$. Each Ψ_i and hence the final tree cover fraction Ψ increases monotonically with each environmental variable x_i. The system is hence uniquely determined by x_1 and x_2, without having alternative solutions. We distinguish two versions of model 1, which differ in the parameters

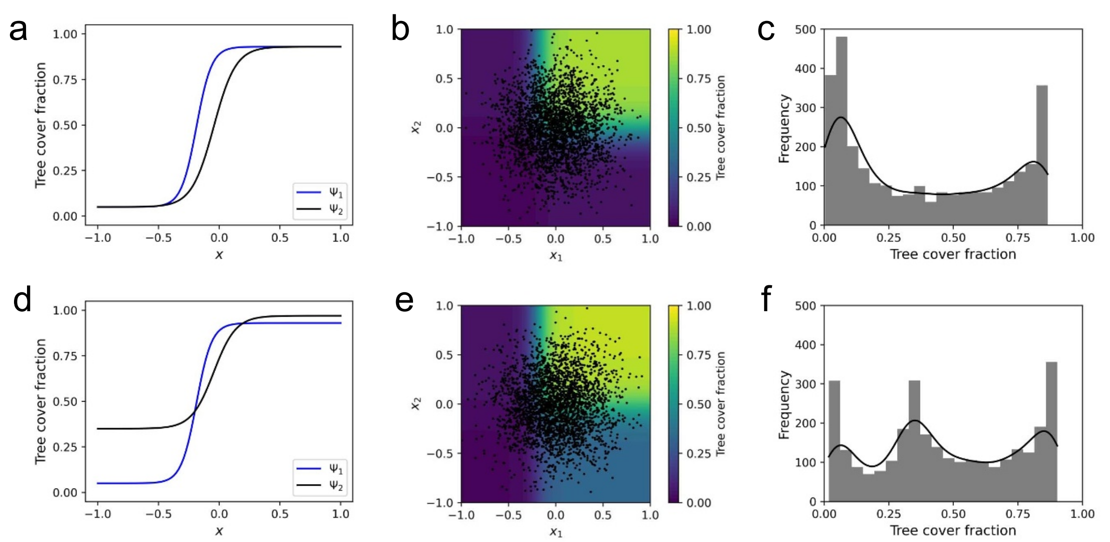

Figure 2. Dependency of tree cover distribution on two input parameters in model 1. First row (a)–(c): version 1. second row (d)–(f): version 2. first column (a), (d): response of the individual factors Ψ_i to their respective input x (equation (S2) in supplementary methods section 1.1). Middle column (b), (e): black dots mark a random sample of the two independent input variables x_1 and x_2, the colored contours show the dependency of tree cover Ψ to both input variables. Right column (c), (f): tree cover distribution resulting from the sample of input data shown in the scatter plot, with a histogram (gray bars) and a kernel density estimate (black line). While model version 1 leads to a bimodal tree cover distribution, model version 2 leads to a trimodal distribution, because baseline values for small x differ between Ψ_1 and Ψ_2 in version 2.

that determine the shapes of $\Psi_1(x_1)$ and $\Psi_2(x_2)$ (figures 2(a) and (d)). We then generate synthetic data for input variables x_1 and x_2, and obtain a distribution of Ψ values, which we analyze for multimodality. For details on the model and data generation see supplementary methods section 1.1.

2.2. Model 2: extended Good's model

Our model 2 is the model discussed in Good *et al* (2016), which is still mathematically simple, and, like model 1, features a single monotonic and nonlinear equation for tree cover depending on multiple input parameters. However, its terms are mechanistically interpretable and closer to actual vegetation dynamics in more complex Earth system models (particularly the Triffid model employed in the HadGEM model family). The model represents tree cover dynamics as a logistic function, representing a monostable system with two parameters: tree productivity β and tree mortality m. Good *et al* (2016) show that for a uniform range of productivity values β, one can only obtain a trimodal distribution of Ψ (resembling the observed states of desert, savanna, and forest) if $m(\beta)$ follows a bell-shaped curve. The intermediate fire-productivity hypothesis suggests that this shape is plausible due to the effect of fire on tree mortality (see Introduction). Here, we do not employ this relationship or any variations in m, but instead implement idealized relationships between environmental conditions and the productivity β. We thereby explore whether it is plausible that the involved nonlinearities give rise to trimodal tree cover (like in model 1), regardless of the role of fire.

We hence always set $m = 0.12$, but make β a function of three environmental input parameters: temperature, precipitation, and a nondimensional variable θ, which here stands for an arbitrary soil property, e.g. field capacity or soil fertility. We define β as the product of three functions, β_{temp}, β_{prec}, and β_θ, each of which depends on only one environmental parameter. In qualitative analogy to observed relationships, we give β_{temp} a parabolic shape, with a maximum around 28 °C (see figure 3(a)), β_{prec} a sigmoidal shape (figure 3(b)), and choose β_θ to be a simple linear function (figure 3(c)). Other physical interpretations of these input parameters are possible. The three different shapes of functions (parabolic, sigmoidal, and linear) give the model a sufficiently flexible structure to reflect typical influences of the environment on tree productivity.

As with model 1, we generate random samples of environmental parameters T, P, and θ to study the effect of this choice on the tree cover distribution.

We consider two cases:

(i) Temperature and precipitation have Gaussian distributions, while θ is set to 1 (thereby not affecting β).
(ii) As case 1, but with θ following a bimodal distribution (by overlaying two uniform distributions limited to two separate value ranges).

In each specific case, two classes of relationships are considered: one where temperature and precipitation are independent and another where

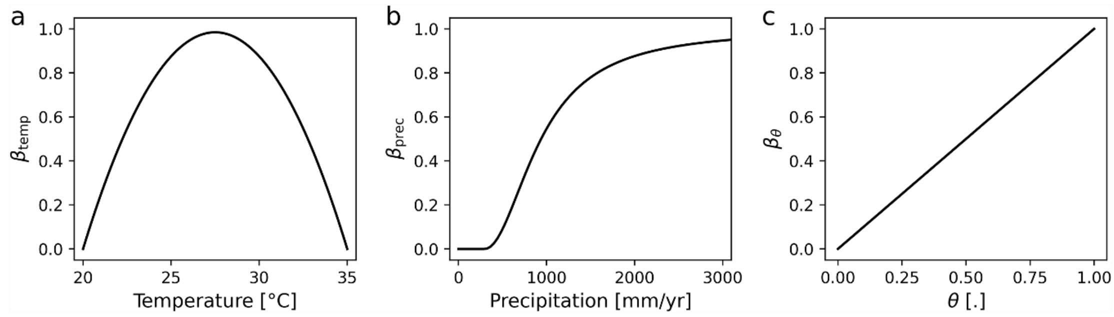

Figure 3. Productivity in model 2 as a function of considered variables: (a) temperature, (b) precipitation, and (c) a soil property θ.

Table 1. List of observational datasets used in this study.

Data	Unit	Time period	Data source/Reference
Tree cover	%	2000–2020	MODIS (DiMiceli *et al* 2015)
Precipitation	mm yr^{-1}	1979–2018	ERA5-CRU (Cucchi *et al* 2020)
Temperature	°C	1979–2018	ERA5-CRU (Cucchi *et al* 2020)
Downwelling short-wave radiation	W m^{-2}	1979–2018	ERA5-CRU (Cucchi *et al* 2020)
Downwelling long-wave radiation	W m^{-2}	1979–2018	ERA5-CRU (Cucchi *et al* 2020)
Soil depth	m	—	Pelletier *et al* (2016)
Soil type	—	1971–1981	FAO HWSD (Nachtergaele *et al* 2009)

they are linked by a linear relationship and hence linearly correlated. For details on the model and data generation see supplementary methods section 1.2.

2.3. Model 3: complex dynamic vegetation model LJPmL

As a third model, we employ the complex state-of-the-art dynamic vegetation model LPJmL (Schaphoff *et al* 2018a). It simulates the dynamics of carbon pools, plant structure, and population dynamics for eight different tree types and three grass types using process-based understanding. Tree coverage is represented by the foliage projected cover (FPC) of all woody plant types. We here use the model in its simplest form, which excludes fire, nitrogen limitation, or any kind of human activities. We employ a simulation with stationary observation-based input for the region of Meso and South America (EXP1 in Bathiany *et al* 2024). In addition, we employ a reduced version of the model for a single tree type, where we can directly provide annual biomass increments, soil moisture, and mortality as input variables to compute FPC, without running the rest of the model (for details on how the relevant equations were separated from the full model, see Bathiany *et al* 2024).

2.4. Observational datasets

We also analyze observations of selected environmental parameters to identify whether one of them could be directly responsible for a multimodal tree cover distribution. The datasets are summarized in table 1. To only focus on natural vegetation, we exclude non-vegetated areas and human-influenced areas, using the IGBP MODIS land cover dataset (Friedl and Sulla-Menashe 2015). In addition, we use the Hansen forest loss dataset (Hansen *et al* 2013) to ensure that we remove areas with potential human deforestation. The resulting masked tree cover dataset is identical to the one employed in Nian *et al* (2023). Temperature, precipitation, and both radiative fluxes are European Reanalysis (ERA5) data from the period 1979–2018, which was bias-corrected using CRU observations, and regridded to a resolution of 0.5° (Cucchi *et al* 2020). We used the daily precipitation data to also compute the Walsh–Lawler seasonality index (SI) (Walsh and Lawler 1981) (also see Smith and Boers 2023, Nian *et al* 2024). Tree cover and the four climate parameters are averaged over their entire time period. Soil properties are obtained from the harmonized world soil database (HWSD) version 1 (Nachtergaele *et al* 2009), and relationships between texture and hydraulic properties are derived following Cosby *et al* (1984). The soil types are discrete classes labeled with numbers from 1 to 12 for clay, silty clay, sandy clay, clay loam, silty clay loam, sandy clay loam, loam, silt loam, sandy loam, silt, loamy sand, and sand. Hence, a higher number tends to indicate lighter soils.

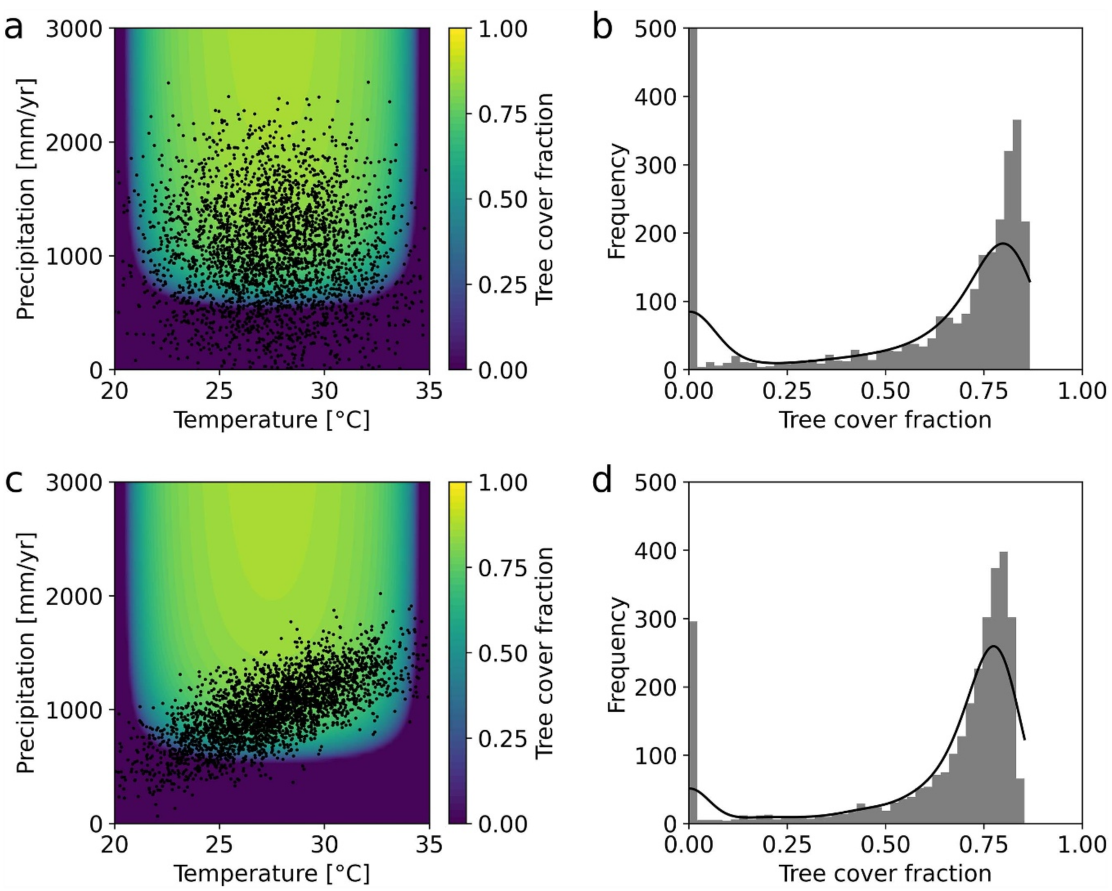

Figure 4. Dependency of tree cover distribution on input parameters in model 2, case 1, involving two variables with unimodal input. The left column (a), (c) displays the data points of inputs (black dots) on a contour plot of tree cover, while the right column (b), (d) presents the resulting tree cover distribution as a histogram (gray bars) and a kernel density estimate (black line). Temperature and precipitation are independent in (a)–(b) and correlated ($r = 0.72$) in (c)–(d).

3. Results

3.1. Model results

3.1.1. Model 1: trimodal tree cover from Gaussian inputs

We first use model 1 by prescribing parameters x_1 and x_2 (figure 2). By generating samples of uncorrelated Gaussian distributions for x_1 and x_2 as described in the methods section above, we obtain distributions of tree cover Ψ (figures 2(c) and (f)). Under the condition that the minimum and maximum saturation values of Ψ_i are similar between the two functions (as in version 1 of this model, figures 2(a)–(c)), the tree cover distribution only features the desert and forest state, but no 'savanna' peak in between. In version 2 of the model (figures 2(d)–(f)), tree cover values for the two functions are substantially different for small values of x. This leads to three distinct modes in the frequency distribution: a 'desert' mode resulting from data regimes with small x_1, a 'savanna' mode dominated by points with small x_2 and large x_1, and a 'forest' mode resulting from values with large x_1 and x_2.

We conclude that in this idealized model, multimodal tree cover can indeed emerge statistically in a monostable system exposed to multiple environmental parameters. If this model described reality, one would not require the intermediate fire-productivity hypothesis, or the existence of alternative stable states. Tipping points may then be less of a concern. The question arises, however, if a more process-based vegetation model could behave in a similar way. In the following, we therefore perform a similar analysis with model 2.

3.1.2. Model 2: trimodal tree cover requires bimodal inputs

Model 2 takes one more step toward biophysical realism: the environmental parameters first determine tree productivity β, which then determines tree cover. In case 1, we prescribe temperature (T in °C) and precipitation (P in mm yr^{-1}), either independent or correlated, while case 2 includes an additional variable θ with bimodal input. Results for case 1 are shown in figure 4. Colored heat maps (panels (a) and (c)) again show how tree cover depends on the two input parameters. In panels (a) and (b), temperature and precipitation distributions (black dots in figure 4(a)) are independent. As a result, two peaks (treeless and forest) appear in the tree cover distribution (figure 4(b)). In reality however, environmental

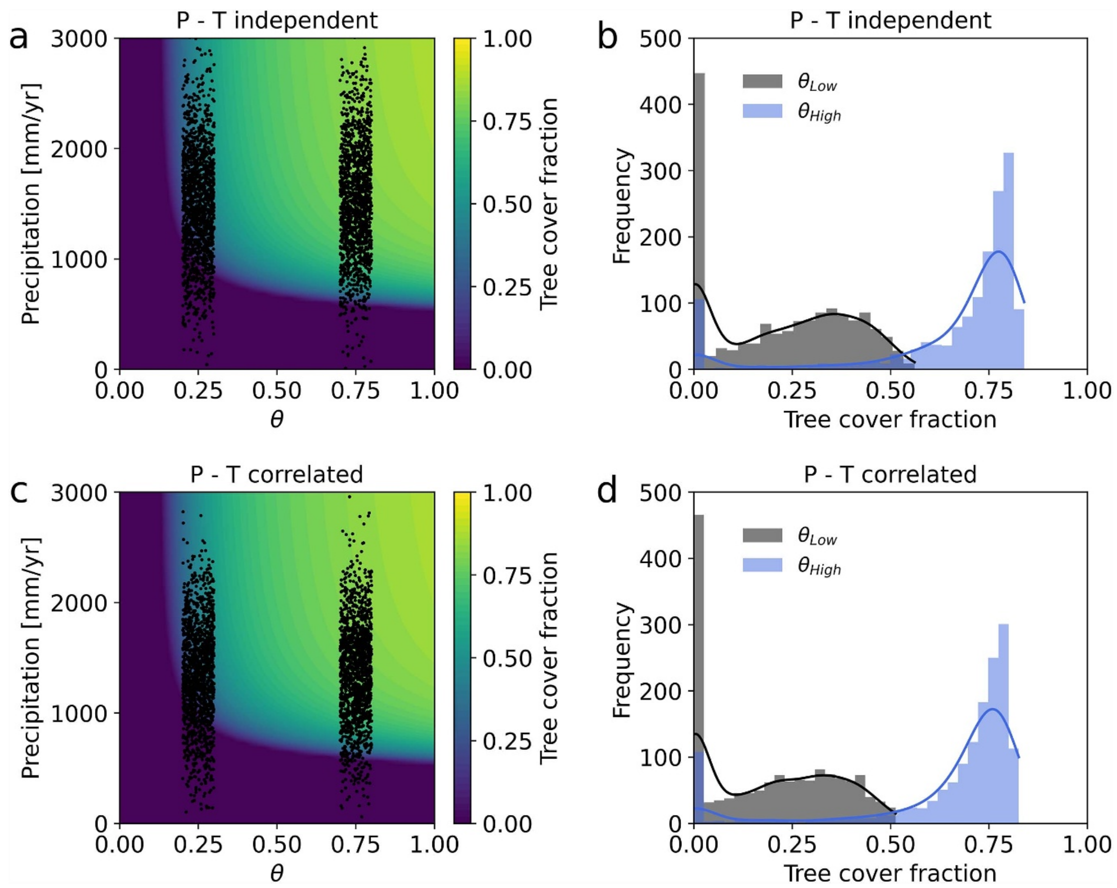

Figure 5. Dependency of tree cover distribution on input parameters in model 2, case 2, involving two variables with unimodal input and one variable with bimodal input in a monostable dynamical system. The left column displays a visualization of low and high range data points of θ, while the right column presents the resulting tree cover distribution as a histogram (gray and blue bars) and a kernel density estimate (black and blue line), distinguishing low (black) and high (blue) θ. Temperature and precipitation are independent in (a)–(b), and correlated ($r = 0.73$) in (c)–(d) (see methods).

parameters are correlated, which may lead to a different distribution of tree cover. We therefore also analyze a scenario with correlated T and P (see methods), but again obtain a bimodal tree cover distribution (figure 4(d)).

The data shown in figure 4 relies on a fixed, prescribed mean and standard deviation of the two input variables, and a certain correlation between them (arising from the choice of coupling parameter a in table S1, supplementary methods section 1.2). In principle, the result can depend on these choices. We therefore also systematically explore how these assumptions affect the number of peaks in the resulting tree cover distribution. Specifically, we repeat the analysis for all combinations of mean temperature T between 20 °C–35 °C (in steps of 2.5 °C) and mean precipitation P between 1000 and 3000 mm yr^{-1} (in steps of 500 mm yr^{-1}), and for three different standard deviations in T (2, 3, and 4 °C) and in P (300, 500, and 1000 mm yr^{-1}). The number of peaks in the tree cover distribution are assessed automatically (see section 'Code and data availability'), and verified visually. Some of the experiments result in one, and some in two peaks, but none showed more than two peaks (figure S1). In other words, the trimodality we obtained in model 1 fails to emerge.

We now turn to case 2, where the input value of θ comes from one of two narrow uniform distributions (see supplementary methods section 1.2). We again distinguish the case of independent temperature and precipitation and the case of correlated T and P (for statistical models and parameters, see methods). Figure 5 shows the results for both independent (top) and correlated input (bottom). Figures 5(a) and (c) show parameter θ instead of temperature, with its bimodal distribution. In these graphs, temperature is not shown, but can be imagined to lie on a third axis, perpendicular to the plane spanned by the graph. The lower range of θ leads to a peak at intermediate values in the tree cover distribution (gray peaks in figures 5(b) and (d)), while the higher range of θ corresponds to high forest cover (blue peaks).

Hence, for each class of θ values (low and high values), the distribution is bimodal, as demonstrated for case 1: where precipitation is very low, tree cover is also low (desert state); where precipitation is high, the tree cover is close to its saturation value for the given θ. This is due to the sigmoidal dependency

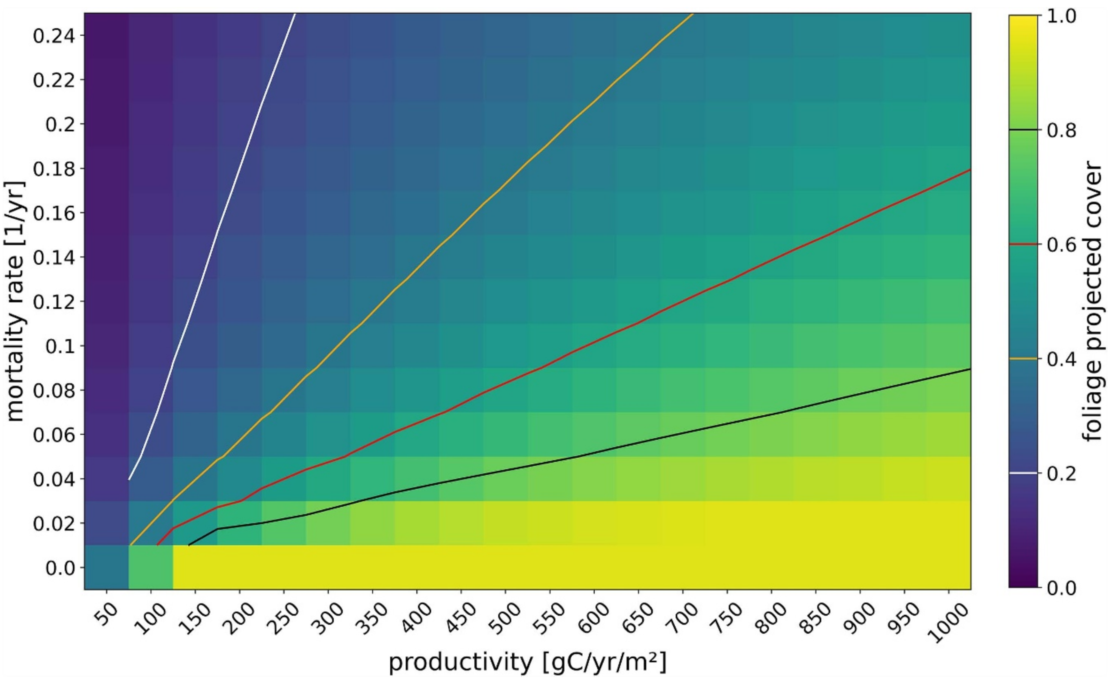

Figure 6. Dependency of FPC of tropical broadleaved evergreen trees as a single tree type, depending on prescribed allocated biomass per year and tree mortality, in the complex dynamic vegetation model LPJmL. The four colored lines are contours denoting values of 0.2 (white), 0.4 (orange), 0.6 (red), and 0.8 (black).

of tree cover on precipitation. When Gaussian input for θ is used, without considering high and low values, as was done for T and P, the resulting distribution is bimodal (not shown). The additional effect of temperature on tree cover, and the correlation between temperature and precipitation do not affect this main result, as shown previously. Only when considering high and low θ together, three tree cover modes emerge. Also, for a given range of precipitation (such as 1300–1700 mm yr^{-1}), one obtains two modes which correspond to the two samples with different θ values (not shown). As in case 1, we also systematically vary the statistical parameters (mean and variance) of the uncorrelated distributions for T and P. In many cases, we find three peaks in the tree cover distribution, but never more than three (figure S2). Obviously, the bimodal input variable θ plays the crucial role in generating an additional peak in the tree cover distribution in both independent and correlated scenarios of temperature and precipitation. We hence require a multimodal environmental variable. Without it, trimodal tree cover cannot emerge unless there are additional mechanisms (like fire) or even feedback at play, which are not part of our model.

3.2. Model 3: confirmation of results with a complex dynamical vegetation model

Since model 2 is still a very simple and conceptualized representation of tropical vegetation, we compare key results to the state-of-the-art dynamic vegetation model LPJmL (Schaphoff *et al* 2018a). We first employ a reduced part of the full model (Bathiany *et al* 2024) that simulates the area coverage of a specific woody tree type (here: tropical broadleaved evergreen trees), depending on productivity (biomass increment per year available for allocation) and a prescribed mortality rate. All model equations are identical to the full LPJmL model; the reduced version however allows us to prescribe productivity and mortality (which are interactive variables in the original version), just like in the model of Good *et al* (2016). Although their model is also based on a dynamic vegetation model used in the context of Earth system models (the Triffid vegetation model), the approach in both models differs substantially (Lotka–Volterra approach in Triffid versus population-dynamics of individual trees with an area coverage determined from biomass and empirical allometric constraints). Nonetheless, the result obtained with LPJmL is very similar: The equilibrium woody tree coverage depends monotonically and rather linearly on productivity and mortality, creating tilted straight isolines in a diagram spanned by both parameters (figure 6). This very closely resembles model 2 (see figure 3 in Good *et al* 2016), and agrees with the stable solution to their logistic equation (equation (S3) in supplementary methods, section 1.2). In this context, the fact that our version of LPJmL does not include fire, or different plant cohorts and the interactions between them, is not a limitation: if heterogeneous environmental parameters alone could lead to multiple tree cover modes, without any fire-vegetation interactions (as demonstrated by model 1), this should also be possible in

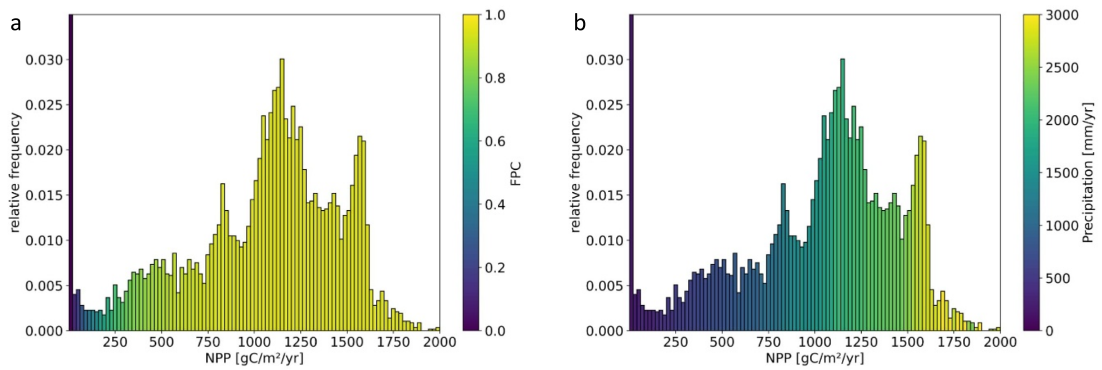

Figure 7. Frequency distribution of woody NPP (net primary production) in LPJmL in tropical South America, forced by observed daily atmospheric data. Each bin is color-coded by (a) the mean foliage projected cover (FPC), and (b) mean annual precipitation (MAP), conditioned on those grid cells that contribute to the bin. Obviously, multiple peaks in NPP do occur in the model, but only in the regime where tree cover is not affected, and only because precipitation substantially differs for each peak.

LPJmL. The absence of such multiple modes suggests that the qualitative relationship between β, m, and tree cover Ψ in model 2 are realistic. Three tree cover modes (or two modes for the same MAP regime) are then only possible if β and m co-vary in a specific non-linear way (according to the hypothesis discussed in Good *et al* 2016), or if β and/or m show distinct multiple modes themselves, as we discussed above.

We therefore investigate the frequency distribution of tree productivity in LPJmL, and of the variables that are affected by it (most importantly, FPC). To this end, we pick a simulation for the domain of Meso and South America described in detail in Bathiany *et al* (2024), which is forced by observations, and includes eight natural tree types that differ in their bioclimatic limits and phenology. We here use all land cells in the domain enclosed by 84.75 W–34.5 W and 35.25 S–15.5 N, which includes tropical rainforests (mainly the Amazon forest), savannas, deserts, and mountain ecosystems (the Andes).

In the chosen domain, tree cover, simulated as the sum of FPC over all woody plant types, only has a desert mode and a forest mode (not shown). In contrast to observations, the savanna mode is missing, which is a common limitation of DGVMs (Baudena *et al* 2015). At the same time, some values of woody NPP (net primary productivity of woody plant types) are more common than others, leading to a distribution with more than two modes. These modes, however, do not lead to different amounts of tree cover because FPC has already saturated at NPP values above 500 gC m^{-2} yr^{-1} (figure 7(a)). Provided that LPJmL roughly represents the geographical distribution of NPP and FPC realistically (Schaphoff *et al* 2018b), it does not appear plausible that the model is biased in a way that would shift the relationship between FPC and NPP sufficiently to create multiple tree cover modes. Moreover, we find that each peak in the NPP distribution occurs under a different precipitation regime (figure 7(b)). Consequently, these modes also appear in the frequency distribution of MAP over the domain (figure S4). In contrast, multiple tree cover modes in observations occur even for the same precipitation regime (Hirota *et al* 2011).

The results obtained with model 3 hence resembles those obtained with model 2: multiple tree cover modes for the same MAP can only occur for multimodal input in both models. Also, LPJmL suggests that such multimodal input does not occur in South America. Consequently, this suggests that the observed tree cover distribution in the real world can only be explained by processes or environmental factors that are not (or not realistically) represented in LPJmL, such as fire mortality (Good *et al* 2016) or the existence of alternative stable states (Hirota *et al* 2011).

3.3. Observed distributions show no evidence for environmental determinism

The results of model 1 on the one hand, and models 2 and 3 on the other hand, differ fundamentally: while multiple Gaussian environmental parameters are sufficient in model 1 to generate three tree cover modes, the more process-based models require a multimodal environmental parameter in order to generate a third tree cover mode. The structure of the model (i.e. the way how the input variables translate into tree cover values) seems crucial: in model 1, the environmental variables independently scale tree cover via individual nonlinear functions, which need to differ from each other. In models 2 and 3, the environmental variables are all arguments to parameter β (and potentially m), which only then translates into tree cover. The agreement between models 2 and 3, and the fact that they are motivated by actual biological processes, documents that this structure is mechanistically more plausible than the mere mathematical possibility displayed by model 1.

This result suggests that trimodal tree cover (or bimodal tree cover for a given precipitation value), if totally determined by the environmental conditions, requires either of the following three conditions

(i) a bimodal distribution of an input variable like θ in model 2, case 2, above, or
(ii) a highly nonlinear relationship between several (unimodal) input variables, which goes beyond the linear correlations employed above, and which leads to multiple maxima in the distribution of tree productivity β (which then translates into tree cover), or
(iii) a very specific relationship between β and m as shown in Good *et al* (2016) and supported by the intermediate fire-productivity hypothesis

In the remaining part of this study, we analyze a number of observed parameters representing climate and soil properties, to assess whether there is evidence in support of conditions 1 or 2 above. To do so, we analyze the distribution of these parameters, and how these are associated with the observed tree cover distribution. We use the identical domain as used in the LPJmL simulations above (now masking out all grid cells with substantial human land use) and analyze observed annual mean temperature, precipitation seasonality, downwelling long-wave radiation, downwelling short-wave radiation, soil depth, and soil type (see methods). Our aim is to find parameters that explain the bimodal tree cover when conditioning on mean annual precipitation (MAP). Therefore, we condition our analysis only on grid cells where MAP is between 1600–2200 mm yr^{-1}, i.e. the regime where observations show multimodal tree cover.

Figure S3 shows the geographical distribution of tree cover, MAP, and the six additional parameters we considered. The most notable indication for multiple tree cover states is the difference between the dense Amazon rainforest and the savanna regions in the South East of the domain (Southern Brazil and Uruguay). All six additional environmental parameters, whether related to temperature, radiation, hydrology or soils, show substantial spatial variations. The full frequency distributions for our domain (figure S4) show two distinct peaks for tree cover (forest and savanna-like state), several modes for MAP, two highly dissimilar modes for soil depth (most soils are either just up to 1 m deep, or almost 50 m deep, resembling our idealized parameter θ from model 2), and a number of distinct soil types (involving loam, clay, and sandy soils). None of the parameters resembles a Gaussian distribution.

Given the non-Gaussian and sometimes multimodal distribution of parameters, and the fact that they are nonlinearly correlated due to physical relationships, it is conceivable that this situation might lead to multiple modes of tree productivity (and mortality) and hence tree cover. Our main interest here is to assess whether one of the parameters (other than MAP) can explain the alternative tree cover modes. We therefore analyze the distributions of tree cover and each parameter for the intermediate range of precipitation between 1600–2200 mm yr^{-1}. Even when limited to this range, tree cover still shows a bimodal distribution, similarly to when no conditions are applied (not shown). At MAP values below 1600 mm yr^{-1}, the savanna state is dominant, while the forest state is dominant at values above 2200 mm yr^{-1}. Figure 8 shows the distribution of each of the six environmental parameters next to a scatter plot spanning the parameter value versus tree cover. The individual distributions, here conditioned on the intermediate MAP regime, do not show significantly different features compared to when the entire precipitation range was considered (not shown). Both temperature and downwelling long-wave radiation show a highly asymmetric or even bimodal distribution (by construction, the choice of binning somewhat affects the number of peaks, but not the overall shape). Also, soil depth is still bimodal and different types of soils are represented by a similar amount in the conditioned data. If one of these parameters caused the bimodal tree cover distribution, we would expect a clear correlation between the value of the explanatory parameter and tree cover. Ideally, this would show as a monotonic relationship in the scatter plots in figure 8.

However, none of the scatter plots shows such behavior. Instead, both savanna and forest states involve a substantial number of grid cells with high temperature and lower temperature, high and low seasonality, large and small soil depth, and a combination of soil types. Arguably, the most striking relationship occurs for downwelling short wave radiation SW_{down}, with a preference for lower tree cover where SW_{down} is high. However, there is still a very large overlap such that most values of SW_{down} are equally likely to occur in forests or savannas. Furthermore, the relationship most likely does not reflect a direct effect of shortwave radiation on tree cover, but can be explained by the fact that the moist, high tree cover regions tend to have higher cloud cover. Consequently, we conclude that in the six observed parameters considered, we cannot identify a parameter that fulfills the role of θ in model 2, i.e. a property which is bimodal (or close to bimodal) and which affects tree cover in a substantial way that would explain the observed tree cover modes. Based on this data, it appears that environmental drivers cannot explain the multimodality observed in MODIS tree cover. Hence, other mechanisms like fire or even positive feedbacks may be involved, which supports the idea that tropical forests could exhibit tipping dynamics.

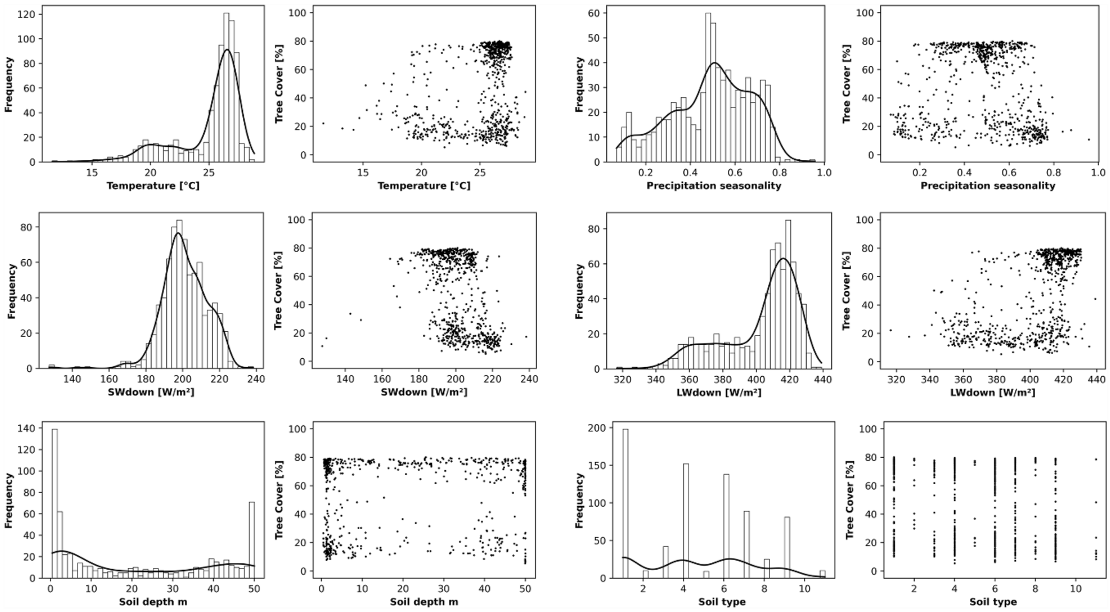

Figure 8. Distribution of observed parameters and tree cover conditioned on a range of mean annual precipitation (MAP) between 1600 mm yr^{-1} and 2200 mm yr^{-1}. Each histogram shows the distribution of temperature, precipitation seasonality, downwelling short-wave radiation, downwelling long-wave radiation, soil depth, and soil type, respectively, for grid cells where MAP is within this intermediate range. Tree cover is bimodal in this regime. Scatter plots show each parameter versus tree cover for the same data, revealing that there is no monotonic relationship between tree cover and any single parameter we considered, and that hence, bimodal tree cover cannot be explained by bimodal or unevenly distributed environmental conditions.

4. Discussion and conclusions

The main goal of this study was to assess whether multimodality is possible in a monostable system, and whether this can lead to a multimodality in tropical tree cover. Such a scenario would suggest that critical thresholds ('tipping points') may be less of a concern in tropical ecosystems than previously suggested. Our results confirm that this hypothesis is plausible in idealized cases. This is most clearly demonstrated by our model 1, which shows a multimodal distribution for a monostable system, even for Gaussian input data, by using a multiplication of sigmoidal functions. In contrast, generating a trimodal distribution as seen in observations was challenging in the model by Good *et al* (2016) (model 2). The model readily produced a bimodal distribution with treeless and forest peaks, whereas generating the savanna state was only possible by prescribing a bimodal input variable. Apparently, the mathematical formulation of tree cover dynamics and its dependency on environmental parameters is crucial. Results obtained with the complex process-based model LPJmL (model 3) resemble the ones from model 2, and hence confirm the requirement of multimodal background conditions.

However, we also find that among six environmental parameters considered, no suitable candidate emerged that can explain the observed coexistence of savanna and forest biomes. This leaves room for several possible explanations for the existence of multiple tree cover modes:

(i) The multiple modes result from a specific relationship between tree productivity and mortality as shown in Good *et al* (2016), where mortality peaks at intermediate productivity values.
(ii) They result from dynamical features of vegetation dynamics that are not sufficiently realistic even in state-of-the-art DGVMs. An example for this possibility is the hypothesis that a large fraction of observed tree cover states are not in equilibrium but transient states (Yin *et al* 2014).
(iii) They originate from the inherent multistability of tropical terrestrial ecosystems, most likely due to feedbacks between fire and tree cover (the hypothesis discussed in Hirota *et al* 2011).
(iv) They result from spatial differences in environmental conditions (the hypothesis of this study), but the six parameters we picked were not the most crucial ones.

We consider the forth point as possible in principle, given the limited number of parameters we considered. For example, other indicators of seasonality than the SI may better capture the relevant hydrology as savannas are known to thrive with highly seasonal rainfall (Mayer and Khalyani 2011). Interestingly, TRMM precipitation data from 1998–2010 and MSI SI used by Wuyts *et al* (2017) did separate modes of MODIS tree cover in South America. Also, orography can play a role for moisture availability, in particular on smaller scales than we considered (Zwaan *et al* 2024). More scrutiny would hence be needed to reveal what the effect of different datasets, time periods, resolutions, and climate indices is, also with regard to potential uncertainties in precipitation records. A particular problem is also that observed tree cover statistics are still not robust, revealing either a large or only a tiny precipitation regime with multiple tree cover modes at least in Africa (Higgins *et al* 2024). Other soil properties as considered here have also been suggested to play a role, with fire acting as a sharpening switch between regimes (Veenendaal *et al* 2018). It is also conceivable that in reality, no single background parameter can explain the observed distribution, but only a nonlinear combination of parameters can, where parameters may be statistically associated in a specific way that generates multiple tree cover modes (like the phytoclimatic transform used in Higgins *et al* 2023). Ways forward may involve data-driven approaches in order to reveal possible and mechanistically meaningful explanatory features. However, the environmental parameters we considered in this study are known to be among the most relevant factors for vegetation, which is why they are typically used to drive offline vegetation models like LPJmL. These models can represent tree cover relatively well and some models can also simulate multimodal behavior when fire dynamics are included (Lasslop *et al* 2016, Drüke *et al* 2023). We therefore conclude that the evidence of our model analysis rather points against the hypothesis of environmental determinism. Consequently, once moisture availability in tropical forests drops below a threshold, these forests may not recover, even if human forcing were to return to previous levels.

Data availability statement

No new data were created or analyzed in this study.

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Code and data availability

All observational datasets we used (tree cover, precipitation, temperature, radiation, soil type, and soil depth) and their references are listed in table 1. The Python code used for simulating models 1 and 2, and for the analysis of LPJmL (model 3) and the observational datasets is available on Github (https://github.com/ejkim25/TropicalTreecover).

The sensitivity analysis utilized the Python library and functions 'scipy.stats.gaus-sian_kde' and 'scipy.signal.find_peaks'. The 'scipy.stats.gaussian_kde' function, with 'kde' standing for 'kernel density estimation', was used to estimate the probability density function, and the 'scipy.signal.find_peaks' function was employed to identify peaks (local maxima) within a given density (Virtanen *et al* 2020).

Author contributions

EJ K performed the analysis, wrote the code, generated most of the figures, and wrote the first draft of sections 2, 3.1 and 3.3. SB conceived and designed the research, supported writing the results section, and wrote the final draft of this study. NB conceived and designed the research, guided the analysis, and supported writing the final draft.

Conflict of interest

The authors declare no conflicts of interest.

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