Nontrivial responses of vegetation to compound disturbances: A case study of Malagasy grasslands

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Abstract

In contrast to the lush eastern rainforest, the depauperate vegetation in the Central Highlands of Madagascar has been cast as the unintended result of anthropogenic disturbances. However, recent studies have shown that many Malagasy grasslands predate Holocene human settlement, and climatic fluctuations spanning the Holocene may also have contributed to the establishment and persistence of grasslands. In order to explore the drivers of vegetation dynamics in the Central Highlands across space and time, we developed a model based on the competition-colonization trade-off that simulates change in the proportion of area occupied by the three major vegetation categories which are forest, fire-maintained grassland, and grazing-maintained grassland under four drivers: climate, fire, grazing, and deforestation. Complex dynamics emerge from the model. Most notably, deforestation could indirectly reduce the proportion of grazing-maintained grassland. Using a climatic reconstruction for the last eight thousand years, we found that accelerated drying between ~4000-3000 BP could have caused an abrupt decline in forest cover. Interestingly, fire-maintained grassland gradually increased in proportion even without human influence. This study suggests that grazing-maintained grassland, and, by induction, the now-extinct megaherbivores, might have been historically rare. Furthermore, deforestation and accelerated drying could have indirectly precipitated the demise of megaherbivores by shrinking the extent of grazing-maintained grassland. These mechanisms add to the list of factors that potentially drove the extinction of Madagascar's megaherbivores. Mechanistic approaches like the one we present here are underrepresented compared to traditional empirical and statistical (correlative) approaches in paleoecology. Although quantitative inference can be difficult, mechanistic models can bound what is theoretically possible. Combining theoretical and empirical approaches can thus creatively enhance our understanding of the vegetation history of Madagascar and paleoecology work in general.

Key words: abrupt change, coexistence, competitive hierarchy, transient dynamic, Holocene

Résumé détaillé

Contrairement à la forêt tropicale de l'Est, la végétation dépaupérisée des Hauts Plateaux de Madagascar a été considérée comme le résultat des activités anthropiques. Par contre, des études récentes ont montré que les formations herbeuses datent d'avant l'arrivée de l'Homme sur l'île. Etant donné le changement climatique durant l'Holocène, les facteurs dominants qui déterminent la dynamique spatiale et temporelle de la végétation ne sont pas résolus. Aussi, un modèle basé sur la compétition-colonisation « *trade-off* » a été développé. Il simule la proportion des surfaces occupées par les trois principales catégories de végétation dans cette région : la forêt, la formation herbeuse maintenue par le feu (FMG : « fire-maintained grassland ») et la formation herbeuse maintenue par le pâturage (GMG : « grazing-maintained grassland »), en fonction de quatre types de facteurs : la précipitation, le feu, le pâturage et la déforestation. Le modèle assume une hiérarchie à la tolérance à l'ombrage et à la capacité de capturer la lumière pour la photosynthèse. La forêt est compétitivement supérieure aux formations herbeuses (FMG et GMG) et la FMG est compétitivement supérieure à la GMG. La forêt, la FMG et la GMG sont mieux adaptées respectivement à un climat humide (>1500 mm par an), intermédiaire (850-1500 mm par an) et sec (400-850 mm par an). Dans cette étude, les objectifs sont

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de : 1) déterminer l’état d’équilibre de la végétation en fonction des quatre facteurs, 2) évaluer la dynamique transitoire par rapport à un changement brusque ou linéaire de l’un des facteurs et 3) illustrer le changement potentiel de la végétation en fonction de la précipitation des huit derniers millénaires et des scénarios de déforestations.

L’exploration des paramètres révèle qu’avec suffisamment de feu et de pâturage, les trois types de végétations peuvent facilement coexister. Par contre, le climat joue un rôle non-intuitif. Un climat sec, qui en principe est favorable à la GMG, conduit à la dominance de la FMG. En effet, ce climat sec augmente le taux de mortalité des arbres et moins d’arbres signifient moins de compétition pour la FMG. La FMG augmente et réduit la GMG qui est moins compétitive. Par un mécanisme similaire, la déforestation a un effet négatif indirect sur la GMG. Ce mécanisme est analogue à la fameuse cascade trophique que nous appelons « cascade horizontale ».

Le second résultat majeur illustre l’importance des dynamiques transitoires. La végétation ne répond pas instantanément aux changements de facteurs externes. Par exemple, un changement brusque du climat ne se traduit pas automatiquement par un changement brusque de la végétation. Par conséquent, un changement brusque ou graduel d’un facteur externe peut engendrer une trajectoire semblable de la végétation. Cette dynamique transitoire, qui peut prendre des siècles, est dû au temps que la végétation prend à s’équilibrer. Ce résultat est pertinent pour l’interprétation des séries temporelles en paléoécologie. La synchronie ou l’absence de synchronie entre les séries temporelles d’un facteur externe et de la végétation n’implique pas forcément une cause à effet ou l’absence de cause à effet.

Le dernier résultat majeur illustre le potentiel du modèle pour explorer l’effet du climat de ces huit derniers millénaires et de la déforestation sur la végétation des Hauts Plateaux. L’assèchement accéléré entre ~4000-3000 BP pourrait avoir provoqué un déclin brusque de la forêt. Par conséquent, les déforestations durant cette période n’ont probablement pas laissé de traces apparentes dans les séries temporelles paleoécologiques. Enfin, dû au climat et même sans activités anthropiques, la FMG aurait pu progressivement augmenter en proportion durant les huit derniers millénaires.

Cette étude établie une fondation théorique qualitative sur la dynamique de la végétation sur les Hauts Plateaux malgaches en fonctions du climat, du feu, du pâturage, et de la déforestation. Le manque de données empiriques, surtout sur le début et l’intensité des activités anthropiques, ne permet pas de faire une inférence quantitative sur la végétation durant l’Holocène. Un corollaire de cette étude est que la GMG, et par induction les mégaherbivores pourraient avoir été historiquement rares. Le fait que la déforestation puisse avoir un impact négatif sur la GMG s’ajoute à la liste des facteurs qui auraient pu causer l’extinction des mégaherbivores. L’utilisation de l’approche mécaniste est sous-représentée par rapport à l’approche empirique et statistique (corrélative) traditionnelle à Madagascar et en paléoécologie. Sachant que les inférences quantitatives sont difficiles, les modèles mécanistes peuvent montrer ce qui est possible. La combinaison d’approches théoriques et empiriques peut améliorer de manière créative notre compréhension de l’histoire de la végétation de Madagascar et des recherches en paléoécologie en général.

Mots clés : changement abrupt, coexistence, competition hiérarchique, dynamique transitoire, Holocène

Introduction

Ecological communities fluctuate in abundance and distribution due to the interplay of myriad extrinsic and intrinsic factors. Extrinsic factors are ubiquitous drivers of vegetation change (White & Pickett, 1985). These include climatic variability, such as long-term trends (e.g., the Milankovitch cycle) or seasonal variability, abiotic disturbances, such as fires and floods, and biotic disturbances, such as insect outbreaks and grazing. More recently, anthropogenic activities such as habitat destruction and overexploitation are additional extrinsic factors that shape vegetation (Millennium Ecosystem Assessment, 2005). But intrinsic processes such as competition and predation might also drive fluctuations, the lynx-hare dynamic (Krebs *et al.*, 1995) being a famous example, and should not be ignored. The relative importance of intrinsic and extrinsic factors in shaping vegetation depends on the spatial and temporal scales at which a system is studied (Levin, 1992; Leibold *et al.*, 2004). The issue of scale partially explains why the dominant driver shaping the distribution, diversity and abundance of fauna and flora of the Central Highlands of Madagascar during the Holocene remains debated (Crowley *et al.*, 2017; Li *et al.*, 2020).

The evolution of vegetation in the Central Highlands of Madagascar has been a subject of debate for nearly a century (Humbert, 1927; Koechlin *et al*., 1974; Vorontsova *et al*., 2016; Solofondranohatra *et al*., 2020; Joseph & Seymour, 2020). Unlike the lush green forest of the eastern escarpment of the island, the Central Highlands have little forest cover (13%) and are dominated by grassland (77%) (Moat & Smith, 2007). Early observers proposed that the highlands vegetation was the result of extensive deforestation by Malagasy communities (Perrier de la Bâthie, 1921; Humbert, 1927). Recent studies paint a more nuanced conclusion. The presence of charcoal in the sediments and the remains of large herbivores indicate that fire and grazing were a natural part of the system, including prior to human settlement (Burney, 1987; Burney *et al*., 2003). Furthermore, several endemic species have traits that are adapted to fire or grazing (Solofondranohatra *et al*., 2020). A modern interpretation is that the landscape of the Central Highlands of Madagascar resembles that of Africa and consists of three major vegetation categories: closed-canopy forest, fire-maintained grassland that includes grassland and tapia savanna (hereafter FMG), and grazing-maintained grassland (hereafter GMG) (Solofondranohatra *et al*., 2018, 2020, but see Joseph & Seymour, 2020). Moving beyond the binary debate concerning Madagascar's landscape pre- and post-human arrival, we address the question of how the proportions of these three vegetation types might have changed during the Holocene.

Sophisticated approaches to collect and analyze data are used to infer Quaternary patterns on Madagascar (Douglass & Zinke, 2015). Fossil records and archeological artifacts map and date the distribution of extinct species and ancient human activities (Grandidier, 1899; Simons *et al*., 1990; Crowley, 2010; Douglass *et al*., 2019). Pollen, diatoms, spores, and charcoal deposits in lake sediment cores record fluctuations in species abundance, herbivore density, and fire activity (Burney, 1987; Gasse & Van Campo, 1998, 2001; Burney *et al*., 2003). Oxygen, carbon, and nitrogen isotopes from corals, stalagmites, and fossils are increasingly used to reconstruct past climate (Zinke *et al*., 2004; Crowley *et al*., 2017; Voarintsoa *et al*., 2017; Li *et al*., 2020). The underlying drivers of vegetation patterns are generally speculated or inferred by matching these records with other synchronous independent records, such as evidence for the decline of the megafauna following human arrival on the island (Dewar, 1984). Inferring the effect of human settlement on vegetation is complicated because its chronology is still unresolved. Traces of hunting and foraging activities suggest that humans were present 2000 years before present (BP), but the precise nature and extent of potential human settlement spanning a 9000-year period remain uncertain (Douglass *et al*., 2019). Disentangling the role of humans versus non-anthropogenic processes therefore becomes challenging (Burney *et al*., 2003). Furthermore, these empirical approaches tend to focus on extrinsic factors. Yet, even the conspicuous tree collapse during the mid-Holocene in North America could have been driven by intrinsic processes and does not need abrupt and sustained changes in an extrinsic driver (Ramiadantsoa *et al*., 2019). A recent model also showed that the steep eastern escarpment might be a seed dispersal barrier and thus could prevent westward forest expansion; this mechanism potentially explains the dominance of grasslands in the Central Highlands of Madagascar (Goel *et al*., 2020). Overall, the role of humans in shaping Holocene vegetation can be difficult to infer due to gaps in settlement chronologies and the underinvestigated role of intrinsic processes in traditional empirical paleoecological approaches. However, the use of mechanistic models can provide complementary and valuable insights.

In this study, we used a simple model to gain insight into vegetation dynamics in the Central Highlands of Madagascar during the Holocene. A

Table 1. Glossary of technical terms.

Term	Definition	References
Disturbance	Relatively discrete event in time that alters the biotic and/or abiotic components of an ecosystem.	Ratajczak *et al*. (2018)
Equilibrium	The behavior that a system will eventually exhibit and then retain indefinitely if unperturbed.	Hastings *et al.* (2018)
Coexistence	An equilibrium where each biome* attains a positive abundance.	Hardin (1960)
Transient	The behavior of a system when not at an equilibrium state.	Hastings *et al.* (2018)
Bifurcation	A qualitative change in a system's equilibrium as a parameter is varied.	Hastings *et al.* (2018)

*Coexistence generally refers to species, but we use "biome" in a broader sense throughout to emphasize the generality of the mechanisms and results. These definitions are modified from the original definitions to fit our context.

glossary of the terms used in this paper is provided in Table 1. We explored the interplay between key extrinsic factors—climate, fire, grazing, and deforestation—and intrinsic factors—life-history traits and interspecific competition—in shaping the proportion of area occupied by forest, FMG, and GMG. We developed a mechanistic model to assess 1) the range of factors allowing the three vegetation types to coexist, e.g., what range of fire and grazing regime permits the persistence of FMG and GMG yet does not lead to forest extirpation; 2) transient dynamics following a change in a driver variable, e.g., how long the system takes to equilibrate as tree mortality increases; and 3) responses to long-term climatic changes and deforestation. Questions 1 and 2 are theoretical in nature and seek to understand the behavior of the system. Reconstructed precipitation patterns are then plugged into the model to address Question 3. Our goal is not to provide an accurate reconstruction of the past but to illustrate the interplay between intrinsic and extrinsic factors and how ecological theories can be leveraged to answer paleoecological questions.

Methods

We developed and analyzed a spatially-implicit model that simulates change in the proportion of three vegetation categories: forest (closed canopy), fire-maintained vegetation (savanna and grassland, FMG), and grazing-maintained grassland (GMG). The categorization is based on a recently developed framework that distinguishes vegetation type along a gradient of fire and grazing disturbances (Archibald *et al*., 2019). For simplicity, the model assumes that FMG and GMG sit at both ends of the trait space, i.e., flammable but not palatable to grazers and palatable but not flammable, respectively. The study area can be thought of as the ~19 million hectares comprising the Central Highlands (Humbert, 1955; Figure 1A). We first provide a general description of the skeleton of the model, then describe how we add fire and grazing disturbances, and finally model the effects of climate and deforestation. The parameterizations and analyses conducted are presented at the end of this section.

In our model, the three vegetation types compete for light with hierarchical tolerance for shading. Namely, without disturbance, forest displaces FMG and GMG, and tall FMG outcompetes laterally spreading GMG (McNaughton, 1984; Mitchard *et al*., 2009; Parr *et al*., 2012; Hempson *et al*., 2015, 2019). To model the competitive hierarchy, we used the competition-colonization trade-off model as a skeleton (Hastings, 1980; Tilman,1994). A competitively inferior species can persist in the landscape by constantly colonizing empty locations due to the death of individuals before a superior competitor displaces it locally. A poorer competitor must be a better colonizer, hence the trade-off. Species coexistence is possible with a careful balance between colonization and mortality rate. In this work, we did not fine tune parameters to allow such coexistence. In fact, coexistence is expected to be maintained by fire and grazing.

Disturbances

To include fire and grazing, we added terms aimed at reducing the displacement by superior competitors. Fire prevents forest from displacing FMG. For simplicity, we used a parameter *f* (representing fire regime) from zero to one to scale the effect of fire—the proportion of FMG burned. A value of one means that no displacement by forest is possible because fire burns all FMG. We assume that fire does not burn GMG and forest. Likewise, grazing prevents forest and FMG from displacing GMG. Grazing efficiency is captured by a parameter *g,* also ranging from zero to one. Although the parameters *f* and *g* are influenced by factors such as climate (seasonality and lightning frequency), fuel, herbivore density, searching ability and handling time, and the proportion of other vegetation types, we keep them constant for simplicity.

These assumptions lead to the following set of equations

$$\begin{cases} \frac{dX}{dt} = c_X X(1 - X - f\,Y - g\,Z) - m_X X \\ \frac{dY}{dt} = c_Y Y(1 - X - Y - g\,Z) - m_Y Y - (1 - \ f) c_X X\,Y\,' \\ \frac{dZ}{dt} = c_Z Z(1 - X - Y - Z) - m_Z Z - (1 - \ g)(c_X X + c_Y Y)\,Z, \end{cases}$$

where *X*, *Y*, and *Z* denote the proportion of area occupied by forest, FMG, and GMG, respectively, and *c* and *m* represent the specific colonization and mortality rate, respectively. Note that we obtain the traditional competition-colonization trade-off model by setting *f* and *g* to zero.

Climate and anthropogenic drivers

The establishment of each vegetation type depends on precipitation (Hempson *et al*., 2015; Archibald *et al*., 2019). Forest establishment increases with precipitation, FMG prefers intermediate precipitation to benefit from a balance between sufficient productivity for fuel and low moisture for flammability, and GMG thrives in a dry environment. Although precipitation affects both colonization and mortality, in this study, we only let the mortality rate m_X, m_Y, and m_Z vary with mean annual precipitation (We also looked at the effect of precipitation on colonization parameters c but the results are qualitatively similar). However, assuming that mortality depends on precipitation allows the system to change much faster and thus maximizes variability due to climate. Finally, we model deforestation by increasing the value of m_X.

Parameterization

We assumed that without competitors, forest can cover up to 95% of the landscape and will take about a millennium to go from 10% to 95%. FMG and GMG can cover up to 98% and takes about a hundred years to fill that space (FMG and GMG have the same baseline parameter value). The values are meant to be plausible and not necessarily accurate. The baseline colonization and mortality rates were calculated from the equilibrium and the transient time which led to the parameters in Table 2.

The mean annual precipitation (hereafter, precipitation for short) considered here varies from 0 to 2500 mm per year. Following Hempson *et al*. (2015), we assumed the establishment of GMG and FMG is maximized between 400 and 850 mm per year and 850 and 1500 mm per year, respectively. To construct how establishment varies along such a gradient, we used the center of these intervals (625 and 1175) as the optimal precipitation level (i.e., minimum mortality rate which corresponds to the baseline parameter above) for the GMG and FMG. The inverse of a gaussian function was then used to scale the increase in mortality as precipitation deviates from the optimal value. For the forest, we assumed that mortality rate is a monotonic function of the precipitation and attains the background value at ~1725 mm per year; 1725 mm was chosen to ensure that the optimal values are equidistant. The change in mortality due to precipitation used throughout this manuscript is shown in Figure 1B.

We used an oxygen isotope (δ^{18}O) record derived from speleothems and covering the last eight thousand years to infer trends in past precipitation (Li *et al*., 2020). Our simulation thus only spans the period ca. 0-8,000 yr BP (years Before Present). First, we interpolated the isotopic data so they can be used in our continuous time model. Second, we performed a linear transformation to convert the δ^{18}O into mean annual precipitation. In practice, precipitation = M + V δ^{18}O, where M represents the average precipitation over the period and V is a scaling parameter to control for variability. We chose an intermediate value for M = 1175 mm (the optimal precipitation for fire-maintained vegetation). Likewise, we chose an intermediate value of V = 300; a lower V value will smooth the curve whereas a higher value can increase fluctuation and cause unrealistic extinction. The precipitation used here is shown in Figure 1C.

Model analyses

The model aims to answer three questions: 1) how do climate, fire and grazing disturbances, and deforestation influence the coexistence of the three vegetation types? 2) how long does the system take to equilibrate following a single change in baseline deforestation and precipitation? 3) how may vegetation have changed during the last 8000 years given the reconstructed precipitation and a hypothetical timing and magnitude of anthropogenic deforestation?

For question 1, we first varied fire regime (*f*) and grazing efficiency (*g*) between zero and one while assuming no deforestation and keeping precipitation constant. Second, we varied precipitation between 800 and 1600 mm per year and increased the deforestation rate from 0 to 200% of the background mortality rate while keeping fire regime and grazing efficiency constant (default values in Table 2). For each parameter combination, we ran the model until the system reached an equilibrium. For question 2, we considered two scenarios: an abrupt and sustained change vs. linear change. The magnitude of the change was the same, but the abrupt change occurred instantaneously whereas linear change spanned a thousand years. The system was set at the equilibrium before the change occurred. For question 3, we ran the model for the eight-thousand-year-period using the reconstructed precipitation and the vegetation responses (Figures 1B & 1C). First, we considered a default scenario without deforestation, and then doubled the mortality rate at three different time points: 4000, 3000, and 2000 years BP.

Given the large degree of freedom and the uncertainty of the parameters, we did not exhaustively explore the parameter space. Instead, we picked values far from bifurcations. We chose a sufficiently high value of the grazing efficiency to promote the competitively inferior GMG and a lower value of fire regime to tone down the effect of fire. Values in

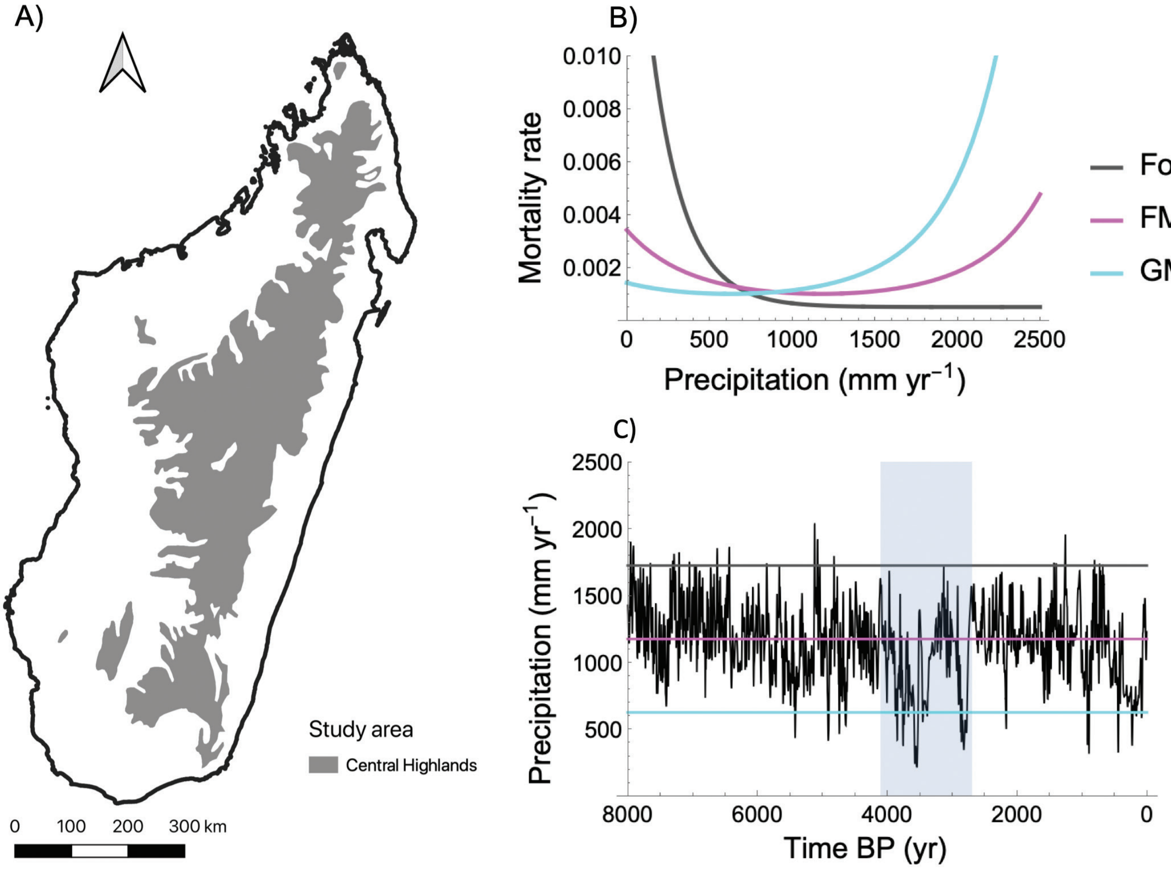

Figure 1. A) Map of Madagascar and the study area. The underlying assumptions used in the model are shown in B) as the change in mortality rate as a function of mean annual precipitation, and C) hypothetical mean annual precipitation (Data from Li *et al*., 2020, see Methods for details). The gray, magenta, and cyan horizontal lines represent the optimal precipitation (i.e., minimizes mortality rate) for forest, FMG (fire-maintained grassland), and GMG (grazing-maintained grassland), respectively. The shaded area highlights a millennium scale dry period.

Table 2 are based on retrospective analyses and picked to exhibit intermediate scenarios. All the simulations were done in Mathematica (Wolfram Research, 2019) and the code is available on the GitHub repository: (https://github.com/ramiadantsoa/grassland_holocene).

Table 2. Parameter definition and values.

Notation	Definition	Value
X	Proportion of area occupied by forest	
Y	Proportion of area occupied by FMG	
Z	Proportion of area occupied by GMG	
c	Baseline colonization rate, type-specific	{0.01, 0.05, 0.05}
m	Background mortality rate, type-specific	{0.0005, 0.001, 0.001}
f	Proportion of FMG burned (fire regime)	0.825
g	Proportion of GMG grazed (grazing)	0.975

Results

Coexistence as a function of fire, grazing, climate, and deforestation (question 1)

At high precipitation (i.e., favorable for forest), GMG did not persist regardless of the grazing efficiency (Figure 2A). FMG persisted and coexisted with forest when fire regime exceeded a threshold $f \sim 0.875$, and coexistence was lost when fire regime exceeded ~ 0.975 as forest no longer persisted (Figure 2A).

At intermediate precipitation (i.e., favorable for FMG), any scenario is possible (Figure 2B). A wide range of parameter values allowed all vegetation types to coexist. As fire regime increased, higher grazing efficiency was needed to maintain GMG. Interestingly, at low fire regime ($f < 0.82$), increase in grazing efficiency promoted the coexistence of all three categories. For instance, at $f = 0.75$, the vegetation went from forest ($g < 0.85$), to forest and GMG ($0.85 < g < 0.93$), to forest, GMG, and FMG ($g > 0.93$). With low grazing efficiency and low fire regime, forest competitively excluded the grasses and at high fire regime only FMG persisted.

At low precipitation (i.e., favorable for GMG), the coexistence of all three categories was still possible but the range of parameter values (*f* and *g*) permitting coexistence was much smaller (Figure 2C). Most notably, unlike above, the coexistence of forest and GMG without the FMG was no longer possible. At maximal grazing efficiency, GMG outcompeted the other types. Although the climate was by assumption favorable for the GMG, and all else equal, most of the parameter regions were dominated by forest and FMG.

The roles of precipitation and deforestation in shaping the proportion of each vegetation category are shown in Figure 3. Drying and deforestation decreased the proportion of forest and increased the proportion of FMG (Figures 3A & 3B). A moderate increase in deforestation barely altered the proportion of forest.

The response of GMG was not trivial (Figure 3C). Increasing deforestation also reduced the proportion of GMG. In addition, GMG responded in a non-monotonic way to drying, GMG initially increased but started to decline when precipitation fell below ~1000 mm per year. This reiterates the results above that drying does not necessarily benefit GMG.

Transient response to a driver change (question 2)

The response of the vegetation following a doubling of tree mortality or a decrease of 500 mm per year in precipitation was slow (Figure 4). As expected, an abrupt change in the driver triggered a faster response than a linear change (solid vs. dashed lines in Figure 4). However, the responses to two types of changes were qualitatively similar and differences small. Most importantly, these trajectories greatly differed from the real equilibrium even after a millennium.

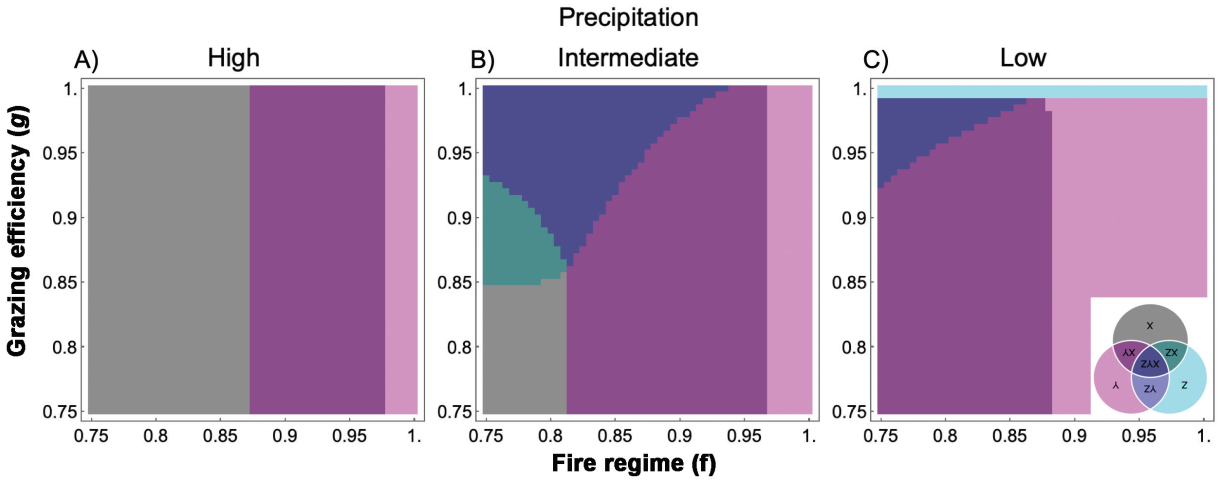

Figure 2. Stable coexistence of the three vegetation categories as a function of fire regime (x-axis) and grazing efficiency (y-axis). The precipitation levels are chosen so that mortality is minimal for each vegetation category (see Figures 1B& 1C). The Venn diagram codes which categories coexist. X, Y, Z denotes forest, FMG, and GMG, respectively. Precipitation does not vary within each panel. Other parameters are indicated in Table 2.

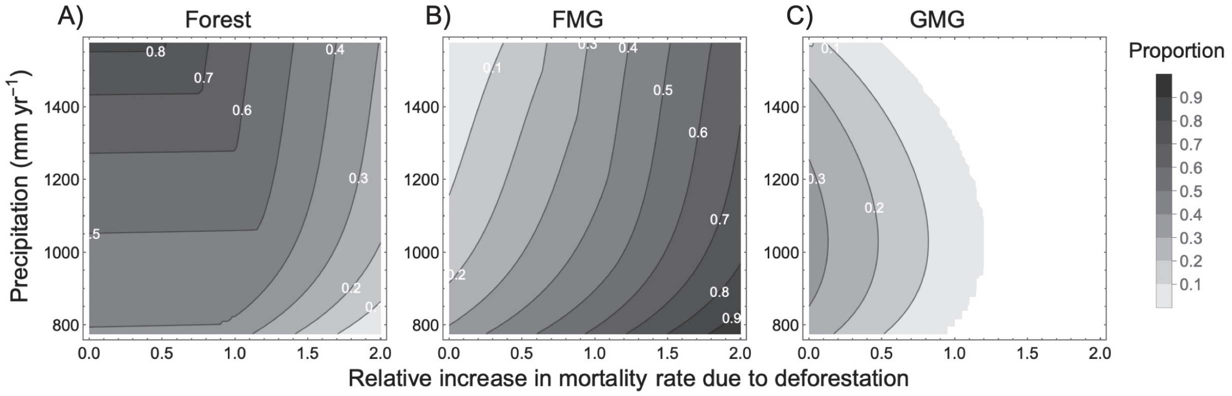

Figure 3. Relative abundance of each vegetation category at equilibrium as a function of the deforestation rate (x-axis) and change in mean annual precipitation (y-axis). The white area means that the vegetation type cannot persist. Left, center, and right panels denote forest, FMG (fire-maintained grassland), and GMG (grazing-maintained grassland), respectively. Other parameters are indicated in Table 2.

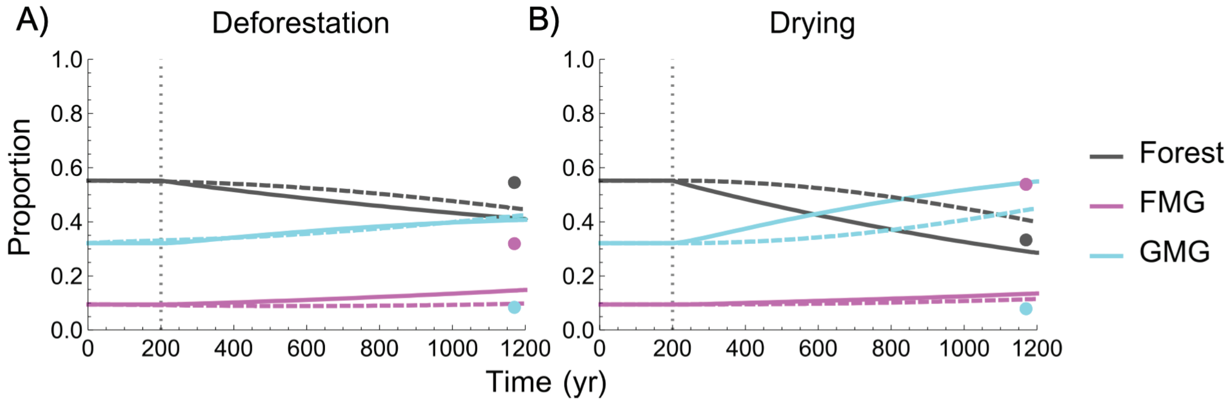

Figure 4. Examples of transient dynamics following changes in the drivers. The system is at equilibrium before the change occurs at t = 200 (dotted vertical line). Continuous and dashed lines show the change in proportion due to abrupt and gradual change in the parameters, respectively. The gradual change is set such that the parameter values are the same at t = 1200. The dots show the equilibrium state of each category. Left panel represents an increase of 80% in background mortality due to deforestation. Right panel represents a reduction of 525 mm of mean annual precipitation (default 1175 mm per year). FMG: fire-maintained grassland, GMG: grazing-maintained grassland. Other parameters are indicated in Table 2.

Vegetation scenarios with reconstructed climate and deforestation (question 3)

The vegetation dynamic was much smoother compared to the variability of the precipitation (Figure 5A vs. Figure 1C). Episodes of extremely low and high precipitation were barely noticeable in the vegetation time series. However, the extensive drying, both in magnitude and duration, between ~4000-2700 years BP was identified in the vegetation time series. That millennial period triggered a noticeable change in the vegetation: a rapid collapse of forest and an expansion of GMG. After that period, forest increased again, and GMG declined. Interestingly, even without anthropogenic activities, FMG gradually increased, possibly tracking the overall decline in precipitation during the last 8000 years (Figure 5A).

Without knowledge of the baseline scenario (Figure 5A), the effect of deforestation was not conspicuous. Deforestation starting around 4000 years BP would roughly coincide with the rapid drying (Figure 5B). Deforestation starting during the dry period ~3000 years BP was barely noticeable (Figure 5C). Finally, deforestation starting 2000 years BP almost had no signal. The conspicuous difference among the scenarios was however reflected in the present proportion, the earlier the onset of deforestation, the lower the proportion of forest at present time.

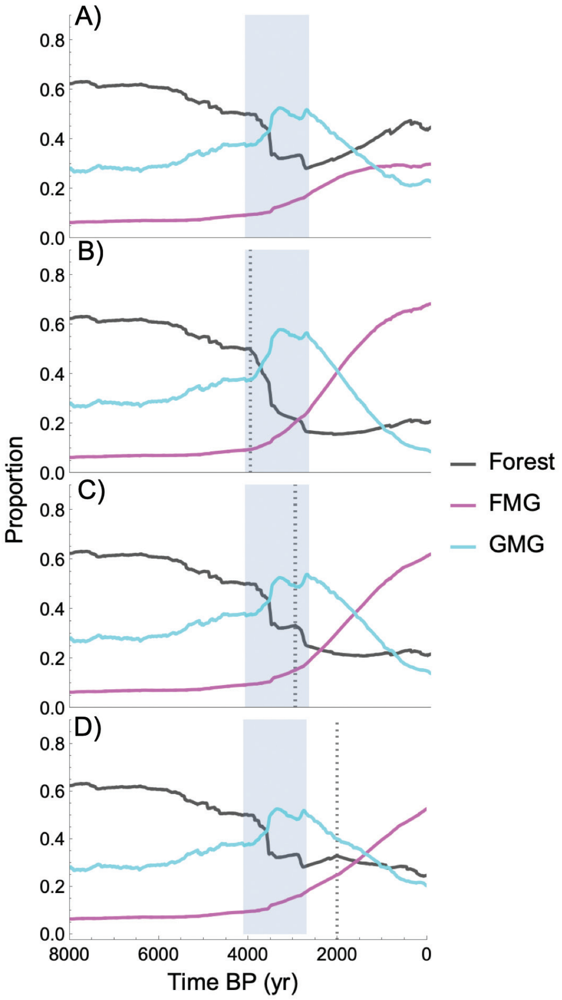

Figure 5. Change in the vegetation given climate scenario in Figure 1C and three timings of deforestation (dashed vertical lines). A) Top panel shows a baseline scenario without deforestation. B-D) panels depict scenarios where additional mortality (an increase by 100% compared to the baseline) was due to deforestation at 4000, 3000, and 2000 years BP, respectively. The shaded area highlights a millennium scale dry period. FMG: fire-maintained grassland, GMG: grazing-maintained grassland. Parameters are indicated in Table 2.

Discussion

In this work, we developed a mechanistic model to explore how the vegetation in the Central Highlands of Madagascar might have changed during the last eight thousand years. Our goal was not to reconstruct the vegetation *per se* but to illustrate the interplay between extrinsic and intrinsic factors. We found that by considering interspecific competition, deforestation may cause an indirect decline in the extent of grazing-maintained grassland, and drying does not necessarily favor grazing-maintained grassland. More work is needed to assess how pervasive these phenomena are, but our results underscore the importance of mechanistic models for revealing unintuitive phenomena. In addition, long transient dynamics caused a mismatch between the shifting variable (e.g., climate or deforestation) and the observed vegetation. Transient dynamics created a lag and could mask the effect of an abrupt change in a driver variable. For instance, the system has not yet stabilized after a thousand years (Figure 4). As a corollary, interpreting synchronous changes in extrinsic variables as causes of vegetation changes can be misleading.

Numerous models have investigated the role of fire-vegetation feedbacks to understand the coexistence of forest-savanna-grassland (Higgins *et al*., 2000; Staver *et al*., 2011; Ratajczak *et al*., 2017). Here, we introduced a mechanistic model to explore the relative importance of fire and grazing in maintaining three vegetation types. Forest, fire-maintained grassland, and grazing-maintained grassland stably coexisted as long as disturbance regimes were sufficiently high, and grazer efficiency (g) had to be higher than fire regime (f) to maintain the grazing-maintained grassland. Essentially, the disturbance regimes act as equalizing mechanisms reducing competitive exclusion due to asymmetric competitive ability (Chesson, 2000). A novel result is that higher grazing efficiency could benefit fire-maintained grassland and promote the coexistence of all vegetation types. Increasing grazing efficiency increased the proportion of area occupied by grazing-maintained grassland and thus decreased that of forest. But a decrease in forest also benefited its most immediate competitor: fire-maintained grassland. When the proportion of forest was sufficiently reduced, fire-maintained grassland eventually persisted. The same mechanism explains why deforestation and drying, i.e., elevating the mortality of forest, might disadvantage grazing-maintained grassland. Although these results seem paradoxical, similar indirect effects have been shown before when species interactions are strong. For example, the "enemy of my enemy" hypothesis allows the weaker competitors (savanna and grasses) to team up and prevent exclusion by forest (Ratajczak *et al*., 2017). Trophic cascades, where change at one trophic level ripples through other trophic levels, is another classic example (Pace *et al*., 1999). Whether the "horizontal cascade" simulated here occurs in reality remains to be tested.

Although equilibrium is a fundamental concept, an ecological system might never be at equilibrium (Hastings *et al*., 2018). Instead, most systems track fluctuating environmental conditions (e.g., climate). The mismatch between the equilibrium state and the current state is due to transient dynamics. This mainly happens when the rate at which a system approaches an equilibrium is much slower than the rate at which the driver variable is changing. With vegetation types with long life-spans, long transient dynamic could be the rule rather than the exception. Transient dynamic is a well-known phenomenon called disequilibrium state in paleoecology (Davis, 1984; Svenning & Sandel, 2013). We illustrated here how observed system states can be far from the real equilibrium quantitatively and qualitatively (Figure 4). For instance, in the right panel of Figure 4, grazing-maintained grassland became the dominant vegetation type after a drying phase, yet if conditions remain the same, grazing-maintained grassland would be the rarest vegetation (cyan dot in the same panel). Furthermore, forest-grassland models have been shown to exhibit cyclic dynamics caused by intrinsic processes (Staver & Levin, 2012) and these fluctuations mean that an observed state does not necessarily reflect the environmental conditions that generated it. A final consequence of the transient dynamic is that abrupt change in a driver does not necessarily manifest itself as an abrupt change in the response. Overall, these results caution against interpreting synchronous patterns or lack thereof in driver and response variables as evidence or absence of causal effects (Ratajczak *et al*., 2018).

A few theoretical insights and expectations arise from this study. First, the millennial drought between 4000-2700 years BP most likely triggered a rapid change in vegetation, which should be clearly detectable in paleoecological records. The rapid drying should have caused extensive and rapid tree death. Teasing apart the role of natural death and deforestation in causing a decline in flux or proportion of pollen during that period might be challenging, as land use practices of human communities that may have been on Madagascar at this time remain unknown (Douglass *et al*., 2019).

Second, in our simulation the proportion of fire-maintained grassland gradually increased for the past eight thousand years even without widespread evidence of human activities. In our model, this increase is driven by forest contraction tracking a long term and gradual decrease in mean annual precipitation. Although flammability is contingent on favorable climatic conditions such as extended seasonal drought and lightning strikes, as a first order approximation, the expansion of fire-maintained grassland most likely favored non-anthropogenic fires. This result suggests that separating anthropogenic and natural burning might also be difficult just by looking at reconstructed time series especially during the last two thousand years. The non-anthropogenic increase in fire-maintained grassland, and thus fire, could partially explain the difficulty other researchers have encountered in teasing apart anthropogenic and non-anthropogenic burning (Burney *et al*., 2003).

Finally, the competitively inferior grazing-maintained grassland might have been naturally rare (it currently covers less than 5% of the vegetation, Solofondranohatra *et al*., 2020). This implies that independent of the impact of human pressures, megaherbivores might have been less abundant on Madagascar prior to their decline than we might otherwise assume. Their habitat could have further shrunk from gradual drying and deforestation making them even more vulnerable to novel human pressures. With small initial population sizes, hunting and the introduction of domesticates (Burney *et al*., 2004; Rakotozafy, 2012; Hixon *et al*., 2021), along with drying and deforestation (herein), the deck was most likely stacked against the survival of endemic megaherbivores.

This work purposefully avoided inferring past vegetation of Madagascar or comparing the results with empirical patterns. Our simple four-parameter model cannot capture the entire complexity of a system. Instead, the results illustrate general concepts such as coexistence and transient dynamics. Unlike traditional disturbance models (Staver & Levin, 2012), the model did not exhibit alternative stable states. That choice was made to simplify the model and its analyses. Additional nonlinearity could have been added (e.g., feedback between vegetation abundance, fire regime and grazing efficiency) but that would increase the number of stable equilibria. Alternative stable states imply that the dynamic would also depend on the initial proportion of each vegetation type, yet that is one of the main unresolved questions. Our mean-field model is spatially homogeneous, yet dispersal and spatial variability also matter. A recent study for instance showed that topographic features could have limited forest expansion from the eastern escarpment of Madagascar and sustained the dominance of grassland in the Central Highlands (Goel *et al*., 2020). Finally, we did not separate anthropogenic and non-anthropogenic fire and grazing, in order to simplify the analyses, but also due to large uncertainties about these values. Instead, we focused on climate and hypothetical deforestation as an example of how anthropogenic activities might affect vegetation dynamics. Adding realism to the model and actual inference of past vegetation is beyond the scope of this study but will be the subject of future studies. While acknowledging the limitations of our study and also the multitude of assumptions that can be added, we posit that simple mechanistic models such as the one we have presented can reveal interesting system behavior and should be more widely used in paleoecology.

Conclusion

We used a simple model to simulate changes in the proportion of three major vegetation categories, namely, forest, fire-maintained grassland, and grazing-maintained vegetation under four types of drivers: climate, fire, grazing, and deforestation. The model provided qualitative insights into the coexistence of the vegetation types and their responses to changes in extrinsic processes. Refining the model, e.g., empirical estimates of the parameter values, can generate quantitative hypotheses on how human settlements might have transformed the fauna and flora of the Central Highlands of Madagascar. In contrast to empirical approaches commonly used in paleoecology and archaeology, where uncertainties are present at each step of the process (from deposition to lab analyses), the approach taken here is deliberately simplified. Combining empirical and modeling approaches can be a powerful way to advance our understanding of the evolution of vegetation on Madagascar and in paleoecology in general.

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