



Dispersal limitation and fire feedbacks maintain mesic savannas in Madagascar

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Abstract. Madagascar is regarded by some as one of the most degraded landscapes on Earth, with estimates suggesting that 90% of forests have been lost to indigenous Tavy farming. However, the extent of this degradation has been challenged: paleoecological data, phylogeographic analysis, and species richness indicate that pyrogenic savannas in central Madagascar predate human arrival, even though rainfall is sufficient to allow forest expansion into central Madagascar. These observations raise a question—if savannas in Madagascar are not anthropogenic, how then are they maintained in regions where the climate can support forest? Observation reveals that the savanna–forest boundary coincides with a dispersal barrier—the escarpment of the Central Plateau. Using a stepping-stone model, we show that in a limited dispersal landscape, a stable savanna–forest boundary can form because of fire–vegetation feedbacks. This phenomenon, referred to as range pinning, could explain why eastern lowland forests have not expanded into the mesic savannas of the Central Highlands. This work challenges the view that highland savannas in Madagascar are derived by human-lit fires and, more importantly, suggests that partial dispersal barriers and strong nonlinear feedbacks can pin biogeographical boundaries over a wide range of environmental conditions, providing a temporary buffer against climate change.

Key words: range limit; deforestation; dispersal barriers; fire–vegetation feedbacks; Madagascar; range pinning; savanna–forest boundary; tropical biomes.

INTRODUCTION

Savannas—defined by codominance of grasses and trees—cover 70% of Africa (Menaut 1983), spanning a wide range of climatic conditions. Despite their ubiquity, mesic savannas are widely regarded as a climatic anomaly because they are found in regions where climate is wet enough to support forest (1,000 to ~2,000 mm Mean Annual Precipitation (MAP); Hirota et al. 2011, Lehmann et al. 2011, Staver et al. 2011a, b). The mechanism by which this mismatch between climate and biomes is maintained has been a long-standing debate in biome ecology (Bond et al. 2003, Bond et al. 2005, Staver et al. 2011b, Staal and Flores 2015) with direct implications for our conceptual understanding of which ecological processes determine tropical plant distributions and how biomes will respond to ongoing global change. In this paper, we examine this debate for savannas and forests in Madagascar, which may provide novel theoretical

insights into the spatial maintenance of global biomes, including in tropics.

Historically, biogeographers argued that biomes occur in well-defined climatic envelopes, such that the spatial limits of biomes were thought to be solely determined by climate (Holdridge 1947, Woodward 1987). Based on this view, early naturalists in Madagascar argued that because forests are widespread in eastern lowlands, climatically similar regions in Central Highlands must have been once covered by forest, concluding that overlap in the climatic ranges of savanna and forest biomes was a result of Tavy farming (de La Bâthie 1921, Humbert 1927). Some biogeographers even argued that before human arrival, ~10.6 kyr BP (Hansford et al. 2018), 90% of Madagascar was covered with forest (Humbert 1927)—much more than the 9% observed today (Table 1). Under this view, pyrogenic savannas in central Madagascar were considered to be degraded ecosystems, derived from human-lit fires. Based on this reasoning, the state of Madagascar passed antifire policies to curb fire setting by farmers and pastoralists (Kull 2000, 2004), and many international conservation organizations formulated plans to “reforest” the Central Highlands (World Resource Institute [WRI] 2014).

However, an alternative viewpoint—based on three independent lines of empirical evidence—indicates

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[Corrections were added on October 6, 2020, after first online publication: The affiliation for Julie C Aleman was updated, the subscript, “ S_s ,” in $T^*_{S_s}$ was capitalized, and grant number was included in the Acknowledgments. We apologize to the author and our readers for these errors.]

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TABLE 1. Forest cover and deforestation estimates in Madagascar.

	Historical estimates from Klein (2002)	Estimates based on satellite data from Mayaux et al. (2000)
Prehuman forest extent (<i>I</i>)	90% TLA	21% TLA
Forest extent in 2000 AD	9% TLA	9% TLA
Total forest loss (<i>II</i>)	81% TLA	12% TLA
Deforestation ($\frac{II}{I} \times 100$)	90%	57%

Note: TLA = total land area of Madagascar.

pyrogenic savannas in central Madagascar predate human arrival. First, charcoal sediments and C_4 pollen in paleocores show frequent fire activity throughout Central Highlands since the aridity peak at the Last Glacial Maxima (in Fig. 1A, we collate paleo sites from published sources; also see Table 2 and Data S1 for details on spatial chronology of fire activity in Central Highlands). In fact, the oldest record of savanna vegetation from Lake Tritrivakely in central Madagascar precedes human arrivals in Madagascar by 6.4 kyr BP (Gasse and Van Campo 1998). Second, grass and forb endemism in Madagascar is much higher than the global average for large islands (Bond et al. 2008, Vorontsova et al. 2016, Hackel et al. 2018); moreover, faunal collections reveal the coevolution of many open-habitat specialists with the surrounding pyrogenic vegetation (Bond et al. 2008). Accumulation of such diverse biota is unlikely if mesic savannas have a recent anthropogenic origin. Third, phylogeographic analysis show ancient genetic divergence (~55 kyr BP) between lemur populations dwelling in the eastern and western sides of the island (Yoder et al. 2016). Because trees are critical for lemur dispersal to maintain gene flow, the ancient divergence has been interpreted as evidence for the absence of a continuous forest habitat before human arrival. Together, these lines of evidence suggest that pyrogenic savannas in Madagascar predate human arrival and that forest cover in Madagascar before human arrival was much less than 90% of the total land area. Current estimates based on satellite imagery (Green and Sussman 1990, Mayaux et al. 2000) and historical forest maps (Humbert and Cours Darne 1965, Koechlin 1972, Bond et al. 2008) put early-20th-century forest cover around 21% of the land area of Madagascar (see Table 1 and Fig. 1A), implying that the observed overlap in the climatic ranges of mesic savannas and forests may not be an anthropogenic artifact.

These empirical findings present a theoretical challenge: if the overlap in the climatic ranges of biomes predates human arrival, how are wet savannas maintained in central Madagascar, given that these regions are climatically suited to allow forest expansion (Fig. 1B)? Clearly, bioclimatic (one-climate–one-biome) models are insufficient in explaining savanna distribution in Madagascar (see Fig. 1A). A developing school of thought is that savanna and forest are alternative stable states

maintained by positive fire-vegetation feedbacks (Staver et al. 2011b). Based on this view, savannas in the Central Highlands could be considered as alternative biome state to forest (Staver et al. 2011a). However, recent work using one-dimensional diffusion models suggests that in a landscape with a precipitation gradient, the bistability disappears, and, like bioclimatic models, the biome boundary is solely determined by climate (see Wuyts et al. 2017, Li et al. 2019).

Diffusion models, however, too, have their own limitations. For one, these biome models assume a homogeneous flat landscape with no barrier to dispersal (Wuyts et al. 2017, Goel et al. 2020). This assumption likely fails, for example, in Madagascar, where geography and vegetation patterns are closely intertwined (Fig. 1A,C). At the large spatial scale, rainforests in Madagascar are restricted to eastern lowlands and are disjunct from highland savannas (1,200–800 m above sea level) by the eastern scarp of the Central Plateau that was formed during the Neogene period because of mantle upwelling (Wit 2003, Paul and Eakin 2017). This close association between topography and vegetation is also reflected in the Holocene paleoecological record, which shows that forests have been restricted to lowlands (Adams and Faure 1997b) despite notable climatic changes since then (Buney 1996). One explanation for this pattern could be that the plateau might limit seed dispersal by either limiting the movement of frugivores (Rakotosamimanana et al. 1999) or slowing wind dispersal (Trakhtenbrot et al. 2014), thereby arresting forest expansion.

Theoretically, this dispersal limitation hypothesis is consistent with work on stepping-stone models (discrete analog of diffusion models) in the context of range limits. Keitt et al. (2001) and Wang et al. (2019) showed that when positive feedbacks are strong (analogous to fire-vegetation feedbacks in tropical biomes) and dispersal is weak, the population ecotone (here savanna–forest boundary) may stabilize even though the climate could still permit expansion. This phenomenon, referred to as range pinning, provides a plausible theoretical mechanism that could explain how savanna and forest are maintained in Madagascar. However, these models (Wang et al. 2019, Keitt et al. 2001) consider a uniformly low dispersal landscape, whereas real landscapes have spatially varying dispersal rates (see Rapoport 1982, Gaston 2003). As a result, the dynamics of tropical biomes near and far away from the barrier may be characterized by different dynamical behavior, leading to divergent biome predictions from both low-dispersal stepping-stone models (Keitt et al. 2001) and high-dispersal diffusion models (Wuyts et al. 2017, Goel et al. 2020), respectively, especially in regions with intermediate dispersal rate.

Using a stepping-stone model that captures climate-dependent fire feedbacks with variation in landscape porosity, we analytically explore the role of topographical barriers in determining the spatial distribution of savanna–forest biomes. In particular, (1) we ask whether the escarpment of the Central Plateau could have

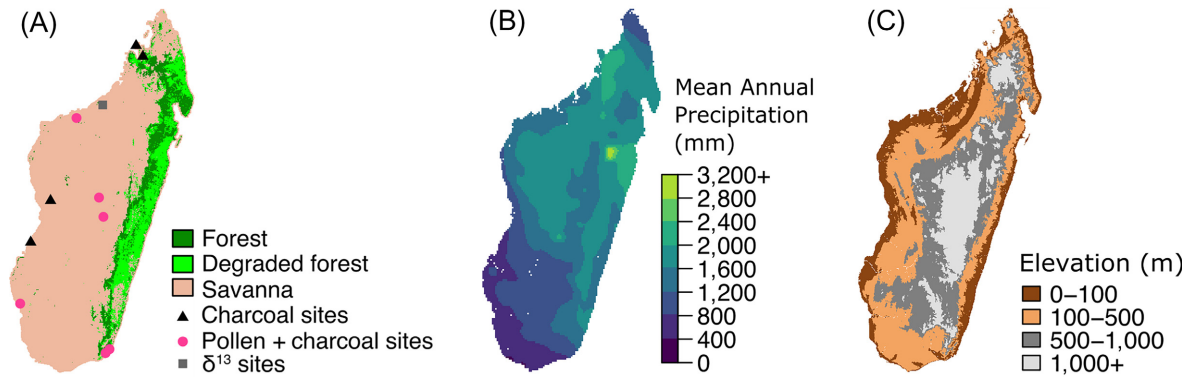


FIG. 1. (A) Remotely sensed distribution of savanna and forest biomes (Mayaux et al. 2000), (B) mean annual precipitation (Huffman and Bolvin 2013), and (C) elevation map of Madagascar (Jarvis et al. 2008). In plot (A), dots indicate the locations of paleo sites in Madagascar (see Table 2 and Appendix S1 for more details on paleoecological data). Note that the eastern edge of the Central Plateau is coincident with the savanna–forest boundary. We hypothesize that the Central Plateau could have prevented the expansion of forest into central Madagascar due to dispersal limitation, even though Central Highlands receive enough rainfall to support forest. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.com)]

maintained mesic savannas in Central Highlands by preventing forest expansion via dispersal limitation. To evaluate the robustness of our theoretical results, (2) we also simulate biome distributions using present-day rainfall (Huffman and Bolvin 2013; Tropical Rainfall Measuring Mission [TRMM]) and topography data (Jarvis et al. 2008; Shuttle Radar Topography Mission [SRTM]), with and without dispersal limitation.

Modeling framework

We model the spatial dynamics of savanna and forest in Madagascar using a stepping-stone model. In this modeling approach, space is represented as a collection of discrete patches that are arranged on a lattice. Within each patch, the vegetation dynamics are governed by local climate and fire–vegetation feedbacks. We assume adjacent patches interact via passive dispersal of seeds. Below, we first describe the local vegetation dynamics, and then the seed dispersal term.

Local climate–fire–vegetation feedbacks via the mean-field approach.—In savanna and forest ecosystems, fire–vegetation feedbacks play an important role in determining local tree cover in landscape (Trapnell 1959, Swaine et al. 1992). When tree cover is low, fire spreads readily (Archibald et al. 2009, Staver and Levin 2012) and perpetually maintains the landscape in low tree cover (Higgins et al. 2000, Moreira 2000, Prior et al. 2010, Veenendaal et al. 2018). However, if tree cover increases past some threshold, the grass matrix becomes discontinuous, and fire ceases to spread (Hennenberg et al. 2006, Archibald et al. 2009, Pueyo et al. 2010, Van Nes et al. 2018). Consequently, trees form a closed canopy and exclude the remaining grass layer by shading it out (Hennenberg et al. 2006, Lloyd et al. 2008). Here, we model these fire–vegetation interactions using a mean-field approach within a patch.

For mathematical simplicity, we assume the landscape consists of only forest trees and grasses (Goel et al. 2020). In doing so, we ignore savanna trees, such that results provide intuition for the boundary between savanna/grasslands and forest, rather than tree cover within these ecosystems. We also assume that grasses colonize on much faster time scales than trees (Purata 1986). This assumption has three consequences: (1) bare ground can be ignored, because grasses quickly colonize any patch not occupied by a competitively dominant forest tree; (2) because the landscape consists of only forest trees and grasses, the sum of the local density of forest trees (T) and grasses (G) can be set to a constant (see Appendix S1: Table S1 for parameter definitions), here taken to be unity (i.e., $T + G = 1$); (3) the instantaneous dynamics of biomes can be expressed in terms of tree density alone, such that the instantaneous local grass cover is given by $G = 1 - T$.

Dynamically, we assume trees establish at a rate proportional to the product of local tree density (to approximate local seed production) and local grass density (the empty spaces for colonization), with precipitation P as the proportionality constant (see also Staver et al. 2011b, Staver and Levin 2012, Touboul et al. 2018). This proportionality constant could potentially be modified to incorporate edaphic constraints on tree establishment, although this extension is not shown here. However, results would not change qualitatively, as soils only act to change the strength of fire feedbacks (see Bowman and Perry 2017). Next, we assume that the per-capita mortality rate of forest trees in response to fire is a step function $\phi(T)$ (we provide the functional form of $\phi(T)$ in the caption of Fig. 2), which depends on the local density of grasses and, thus, trees ($G = 1 - T$; see also Staver et al. 2011b, Staver and Levin 2012). The mortality rate $\phi(T)$ is high at high grass density (such as in an open-canopy savanna/grassland, where fire spreads readily) and low at low grass density (such as in a closed-

TABLE 2. Reconstructed vegetation patterns in Madagascar since the Last Glacial Maxima (~17 kyr BP) using nonclimatic proxies—pollen, charcoal, and $\delta^{13}\text{C}$ (speleothems)—from published literature (see Fig. 1A).

No.	Sites	Latitude	Longitude	Proxy	Date for savanna biome	Date since charcoal accumulation	References
1	Anjohibe caves	-15.54	46.89	$\delta^{13}\text{C}$ (speleothems)	1060 (1040–1080) BP	–	Burns et al. (2016)
2†	Lake Andolonombay	-23.05	43.6	Pollen and charcoal	3095 (2737–3490) BP	5700 (5502–5897) BP	Burney (1993), Burney et al. (2003)
3†	Lake Mitsinjo	-16.03	45.85	Pollen and charcoal	3740 (3263–4283) BP	3740 (3263–4283) BP	Matsumotot and Burney (1994)
4†	Lake Tritrivakely	-19.78	46.92	Pollen and charcoal	17080 (16280–17760) BP	12100 (10780–13550) BP	Gasse et al. (1994)
5	Lake Kavitaha	-19.04	46.74	Pollen and charcoal	1070 (889–1263) BP	1070 (889–1263) BP	Burney (1987)
6	Lake Komango	-19.16	44.81	Charcoal	1560 (1370–1781) BP	3120 (2884–3348) BP	Burney (1999)
7	Benavony	-13.71	48.49	Charcoal	620 (524–751) BP	4400 (4152–4774) BP	Burney (1999)
8	Belo-sur-mer	-20.73	44.02	Charcoal	1680 (1462–1879) BP	2030 (1831–2293) BP	Burney (1999)
9	Amparihibe	-13.3	48.22	Charcoal	970 (779–1175) BP	1910 (1712–2142) BP	Burney (1999)
10	Mandena (matrix)	-24.93	47.01	Pollen and charcoal	1400 (1050–1480) BP & 855 (680–1230) BP	5620 (4470–6140) BP	Virah-Sawmy et al. (2009)
11†	Ste-Luce (matrix)	-24.78	47.16	Pollen and charcoal	5810 (5750–5910) BP	5810 (5750–5910) BP	Virah-Sawmy et al. (2009)

Notes: Although the time period of most proxies overlaps with human presence in Madagascar, savannas at four sites (marked by †, 2, 3, 4, and 11) predate peak in fire activity, which is interpreted as a signal of the onset of widespread human use of fire (~2.5 kyr BP; Burney 1999). Of these, the savanna record from Lake Tritrivakely (4) in central Madagascar predates human arrival by 6.4 kyr. Furthermore, additional sites, including 6, 7, and 10, show fire activity, that predates 2.5 kyr BP. The brackets show 95% confidence interval for the radiocarbon dates.

canopy forest). Combining these demographic processes yields a mean-field growth function of trees:

$$f(T, P) = \underbrace{P[1 - T]}_{\text{local birth rate}} T - \underbrace{\phi(T)T}_{\text{local death rate}}. \quad (1)$$

Phenomenologically, this mean-field model captures two important aspects of tropical biomes. First, in the intermediate precipitation range, $P_{FS} < P < P_{SF}$, fire-vegetation feedbacks are substantial. In this precipitation interval, the $f(T, P)$ has two stable roots—savanna (T_S^*) and forest (T_F^*) states (black circles in Fig. 2G)—and an unstable root, T_{unstable}^* (gray crosses in Fig. 2G). This unstable root represents the threshold tree cover below which the local grass cover becomes continuous, and fire spread readily. Second, outside the bistable region, fire feedbacks are absent, and the system equilibrates to a climatically determined equilibrium: when $P > P_{SF}$ (critical precipitation value for savanna to forest transition) forest is stable and, conversely, when $P > P_{FS}$ (critical precipitation value for forest to savanna transition) savanna is stable.

Dispersal via stepping-stone approach.—We assume that dispersal (number of seeds dispersed per unit time) between adjacent patches is proportional to the density of trees in each patch, such that the proportionality rate constant is a function of the patch itself. Mathematically, we express this assumption using a stepping-stone approach in which patches i and $i + 1$ exchange seeds at a rate proportional to D_i . Intuitively, D_i is the net influx of seeds in patch i when the tree cover differs in the focal and succeeding patch by unity (henceforth referred to as dispersal rate). Similarly, patches $i - 1$ and i exchange seeds at a rate proportional to D_{i-1} . Thus, in a 1D landscape, the net dispersal flux at patch i from both directions is $\Phi_i = D_i(T_{i+1} - T_i) + D_{i-1}(T_{i-1} - T_i)$ (Humphries et al. 2011). We assume the topographical features of the landscape determine D_i : when the landscape is flat D_i takes a high value and decreases as the surface inclines. In a 2D landscape, $\Phi_{i,j} = D_{i,j}[T_{i+1,j} - 2T_{i,j} + T_{i,j+1}] + D_{i-1,j}[T_{i-1,j} - T_{i,j}] + D_{i,j-1}[T_{i,j-1} - T_{i,j}]$ (Hoffman et al. 2017). This 2D the dispersal flux term is the sum of two 1D dispersal flux terms corresponding to each spatial coordinate.

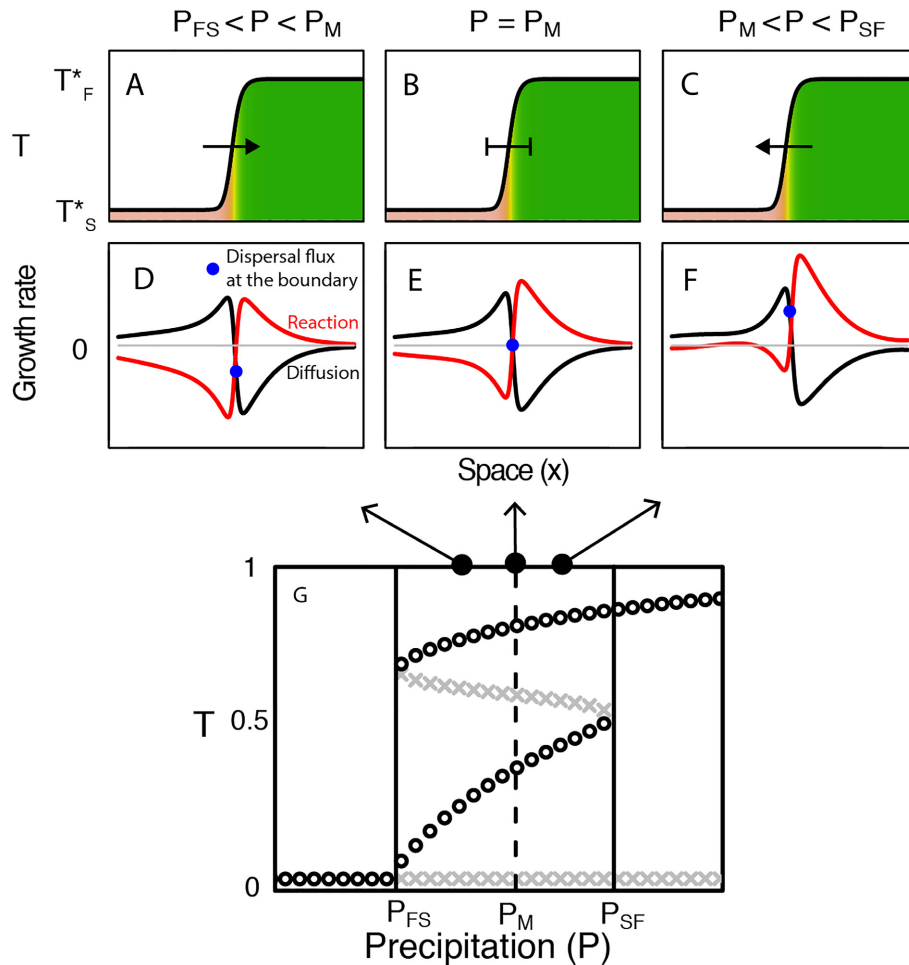


FIG. 2. Direction of boundary movement (A–C) as a function of dispersal flux (D–F) for different precipitation values in the bistable region (G). In the bistable region ($P_{FS} < P < P_{SF}$), the reaction term has two stable roots—savanna and forest (black circles)—which are separated by an unstable root (gray crosses). In the second row, the black and red lines are the reaction and diffusion terms in Eq. 3, and the blue circle represents the dispersal flux at the boundary. In the 1D diffusion model, when $P_{FS} < P < P_M$, savanna invades forest because of negative dispersal flux at the boundary (A and D). Conversely, when $P_M < P < P_{SF}$, forest invades savanna because of positive dispersal flux (C and F). A stationary savanna–forest boundary is formed only when dispersal flux is exactly zero (E). This condition is met at a unique precipitation value—Maxwell precipitation P_M (B). Thus, in a 1D landscape with precipitation gradient, the savanna–forest boundary equilibrates at P_M . We use $\phi = \phi_{T=1} + \phi_{T=0} (1 + e^{100(T-T_c)})^{-1}$ to generate the bifurcation diagram, where $\phi_{T=1} = 0.13$, $\phi_{T=0} = 0.23$, and $T_c = 0.55$ (threshold tree cover for fire spread). Plots (D–F) were generated for $P = 0.48, 0.53 (P_M),$ and 0.58 , respectively. Simulations in (D–F) were performed on a one-dimensional lattice of size 500 with $D = 50$. For these parameter values, we get $P_{FS} = 0.377, P_M = 0.53,$ and $P_{SF} = 0.668$. [Color figure can be viewed at wileyonlinelibrary.com]

Combining the local vegetation dynamics in Eq. 1 with patch-specific dispersive interactions yields a 1D heterogeneous stepping-stone model:

$$\frac{dT_i}{dt} = \underbrace{f(T_i, P)}_{\text{mean - field term}} + \underbrace{\Phi_i}_{\text{dispersal flux}}. \quad (2)$$

To obtain a 2D version of the model, we replace the subscript $[i]$ by $[i, j]$, representing x and y coordinates. Stepping-stone models in Eq. 2 are widely used ecology to describe spatial dynamics such as range limits (Keitt et al. 2001) and animal movement (Okubo 1986). Past

theoretical work suggests that Eq. 2 has a traveling-wave solution (Keitt et al. 2001, Wang et al. 2019), in which the spatial profile of the tree cover resembles a chain of falling dominos (Keitt et al. 2001, Humphries et al. 2011). In this analogy, each domino represents a vegetation patch: standing and fallen dominos represent forest and savanna patches, respectively, and the cascading front represents the savanna–forest boundary.

METHODS AND RESULTS

In the following sections, we consider two versions of the stepping-stone model: a homogeneous dispersal

model with a constant dispersal rate to model a situation of no dispersal constraint, and a heterogeneous dispersal model in which dispersal rate is a function of the slope of the terrain that is determined by landscape features like mountains, rivers, and plateau. For each model, we (1) present a graphical approach to describe ecological conditions that yield a stable boundary and (2) simulate biome patterns in Madagascar using a parameterized model that incorporates information on both present-day rainfall and topography.

Unfortunately, neither version of the stepping-stone model can be solved analytically for the mean-field growth function in Eq. 1. Therefore, we consider a piecewise linear growth function (McKean 1970) that is structurally (i.e., dynamically) the same as the mean-field growth function in Eq. 1 and is fully analytically tractable. We present the mathematical analysis in Appendix S1 to explore the effects of dispersal barriers on the position of the boundary as a function of precipitation and dispersal constant (Appendix S1: Figs. S1, S2, and S3). Although the piecewise linear function is not biologically motivated, analytical results offer a more comprehensive insight that is otherwise challenging. We refer our readers to Humphries et al. (2011) and Marsden et al. (1993) for a detailed discussion on the analytical properties of a stepping-stone model presented in Appendix S1.

Homogeneous dispersal model

Theory.—We begin with a uniform dispersal model with isotropic dispersal rate D that does not depend on the topographical features of the landscape. This simplification allows us to express the net dispersal flux (Φ_x) as $D [T_{i+1} - 2T_i + T_{i-1}]$, which, in the high- D limit, can be further simplified to a diffusion approximation to yield a 1D reaction-diffusion model:

$$\frac{\partial T}{\partial t} = \underbrace{f(T, P)}_{\text{reaction term}} + \underbrace{\Phi_x}_{\text{diffusion term}}, \quad (3)$$

where $\Phi_x = D\partial^2 T/\partial x^2$ is the 1D Laplacian operator. By extension, for a 2D landscape, $\Phi_{x,y} = D[\partial^2 T/\partial x^2 + \partial^2 T/\partial y^2]$. The results of the diffusion model are used to establish a baseline for comparison with the heterogeneous dispersal model that is presented in the next section.

Reaction-diffusion models (Eq. 3) are an idealized representation of spatial dynamics of populations, as they ignore stochasticity in demographic rates and instead model these processes as continuous functions. This simplification is based on the idea that local stochastic processes can be approximated as continuous functions at large spatial scales (Skellam 1951, Levin 1992). This methodology can provide an intuitive understanding of boundary dynamics, including tropical

biome boundaries (Wuyts et al. 2017, Goel et al. 2020). Here, we briefly discuss the results of the diffusion model in the context of biomes in Madagascar (see Goel et al. 2020 for details).

According to Eq. 3, the dynamics at the boundary are governed by local fire–vegetation feedbacks (reaction term) and dispersal flux from adjacent patches (diffusion term). By defining the position of the boundary as T_{unstable}^* , we can neglect the contribution of fire feedbacks at the boundary because, at equilibrium, the reaction term is always zero; that is, $f(T_{\text{unstable}}^*) = 0$. However, because this equilibrium is unstable, even a small dispersal flux Φ_x at the boundary can initiate a traveling wave of one biome state invading other. When Φ_x is negative (Fig. 2D), savanna invades forest (Fig. 2A), and, conversely, when Φ_x is positive (Fig. 2F), forest invades savanna (Fig. 2C). The boundary equilibrates only when the Φ_x is exactly zero (Fig. 2E), a condition that is met at a unique precipitation value, referred to as Maxwell precipitation (P_M) (Fig. 2B). Intuitively, Maxwell precipitation is the bioclimatic limit of tropical biomes, where both savanna and forest invade each other at an equal rate. Therefore, in a landscape with a precipitation gradient, the boundary equilibrates at the spatial location that receives P_M (see Appendix S1 for analytical results). As mentioned in the introduction, the 1D diffusion model is analogous to bioclimatic models that predict the spatial limits of biomes are climatically determined.

Recent work shows that this 1D approximation is limited and that a more realistic representation of dispersal as a 2D process can qualitatively change the equilibrium position of the boundary (Goel et al. 2020). To a first approximation, the equilibrium position of the boundary is still determined by Maxwell precipitation contour (P_{Mc} ; analogous to P_M in 2D), but it may locally deviate from P_{Mc} depending on the local curvature of the P_{Mc} . These curvature effects arise because, in a 2D landscape, the dispersal flux is not only dependent on precipitation but also on the number of savanna and forest neighbors, which, in turn, is a function of the curvature of P_{Mc} . These curvature effects are a result of source–sink dynamics in which spatial subsidies from productive patches can maintain the population in suboptimal patches.

Large-scale simulations.—To establish a baseline prediction, we simulate vegetation in Madagascar using a calibrated homogeneous 2D diffusion model with $P_M = 1538$ mm MAP (see Appendix S1). This estimate of P_M was obtained from the analysis of vegetation patterns in mainland Africa (Goel et al. 2020 found P_M lies within $1,508 \pm 84$ mm MAP, with 1,538 mm MAP as the most probable value), where the diffusion model provides more accurate distribution of biomes and is consistent with other recent empirical (Staal et al. 2016) and theoretical studies (Wuyts et al. 2017). We initialize our simulation with historical estimates of biome distributions in Madagascar in Fig. 1A (our best estimate of

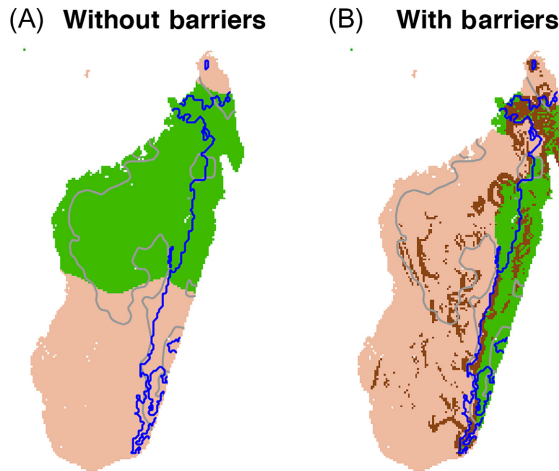


Fig. 3. Simulated distribution of savanna and forest without (A) and with (B) dispersal barriers. The blue and gray lines indicate the forest extent from Mayaux et al. (2000) and Maxwell precipitation contour ($P_M = 1538$ mm Mean Annual Precipitation), respectively. The brown pixels in the plot (B) indicate dispersal-limited patches. The uniform dispersal model (2D diffusion model) produces extensive forest cover in central Madagascar (A). However, when topography is included in the simulation, the savanna–forest boundary is pinned at the escarpment of the Central Plateau (B). The heterogeneous dispersal model in (B) reproduces biome patterns with 92% accuracy, which is much higher than 54% accuracy from the uniform dispersal model in (A) (see Appendix S1, Fig. S6, and Data S2). Thus, boundary pinning may explain how mesic savannas are ecologically maintained in central Madagascar. [Color figure can be viewed at wileyonlinelibrary.com]

“initial conditions” on the island). This initial condition roughly matches reconstructed biome patterns from Last Glacial Maxima and Holocene that show forest in Madagascar were restricted to the eastern lowlands (see Boney 1996, Adams and Faure 1997a).

We find that this basic diffusion model overpredicts forest cover (Fig. 3A) and cannot explain how mesic savannas are maintained in central Madagascar. Note that the biome boundary is not coincident with P_M because of the source–sink dynamics described above.

Heterogeneous dispersal model

Theory.—In the above model, we assumed a homogeneous landscape with a high dispersal rate. This assumption allowed us to approximate dispersal as a continuous diffusion process. However, the diffusion approximation fails when the dispersal rate is low, as it is when the savanna–forest boundary approaches a dispersal barrier. In this section, we show that in a stepping-stone model with a low dispersal rate, a stable biome boundary can arise because of fire–vegetation feedback despite the availability of environmentally suitable patches ahead. This property of bistable traveling waves is referred to as range pinning in range limit theory (Keitt et al. 2001).

To examine how range pinning affects the boundary propagation near a dispersal barrier, we make two simplifying assumptions. First, we only consider biome dynamics in a 1D landscape. Although previous work shows that this assumption is not ideal (Goel et al. 2020), we think that it may be reasonable in Madagascar, based on the observation that both the savanna–forest boundary and the eastern slope of the Central Plateau run linearly along the eastern coast of Madagascar. This symmetrical arrangement suggests that we may be able to ignore the second dimension, but a full analytical treatment of the 2D stepping-stone model can be found in Hoffman et al. (2017; note that we also provide supporting 2D simulations after offering analytical intuition for 1D case). Second, we consider a constant dispersal rate between adjacent patches, except between patches k and $k + 1$, corresponding to the location of the dispersal barrier. We incorporate the barrier in our model using a binary dispersal scheme in Eq. 2: $D_k = d$ and $D_{i \neq k} = D$ such that $D \gg d$.

This dispersal scheme has the advantage that when the boundary is far from the barrier, the biome dynamics can be described using the diffusion approximation; that is, the equilibrium position of the boundary is uniquely determined by P_M . However, if the boundary encounters a barrier during propagation, the diffusion approximation breaks down. As a result, the boundary may become pinned at the barrier before reaching its bioclimatic limit P_M . To build intuition for how this mechanism could have stabilized the biome boundary at the edge of the Central Plateau, we investigate the dynamics of forest invading savanna at the dispersal barrier when $P > P_M$.

Consider a 1D traveling wave with savanna in patches k and below, and forest in patches $k + 1$ and above. Because the dispersal rate at the barrier is low, the boundary savanna (patch k) and forest (patch $k + 1$) patches can be considered to be near their equilibrium densities. This simplification allows us to approximate dispersal flux in Eq. 2 at patch k as $d(T_F^* - T_S^*)$. Next, using this approximation, we examine the conditions on d for which forest fails to invade savanna.

At patch k , the biome dynamics can be expressed as

$$\frac{dT}{dt} \approx \left[P(1 - T) - \phi + d \left(\frac{T_F^*}{T_S^*} - 1 \right) \right] T \quad (4)$$

(for convenience we lose the subscript k). In the bistable region, the system has at most four roots (see bifurcation diagram in Fig. 2G). Because $T = 0$ is a trivial root, we direct our attention to the other three roots, which can be obtained by setting the square bracket term to zero. Graphically, finding the roots is equivalent to identifying points where growth function intersects the zero growth line. When $d \approx 0$, $d(T_F^*/T_S^* - 1)$ is negligible, and the dynamics at patch k are solely governed by the $P(1 - T) - \phi$, which intersects the zero growth line at two

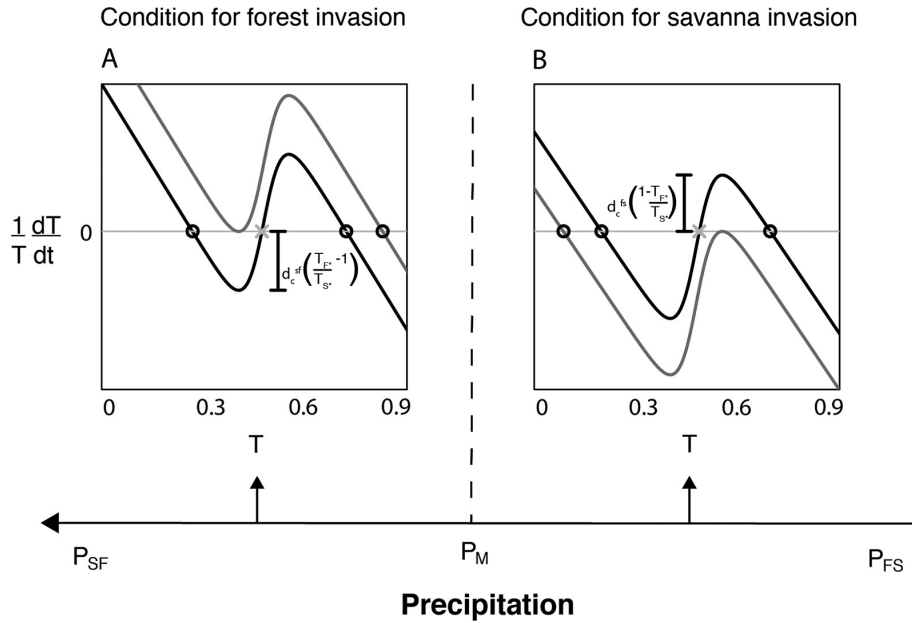


FIG. 4. Critical threshold value of dispersal below which the savanna–forest boundary ceases to move despite climatically suitable patches ahead. The black and gray curves in each plot represent the per-capita growth rate (square bracket term in Eqs. 4 and 5) at the barrier when dispersal constant is zero and d_c^{fs} (d_c^{sf}), respectively. The length of I-shaped arrow represents the magnitude of per capita dispersal flux above which forest fails to invade savanna (A) and vice versa (B). In particular, when dispersal is below d_c^{fs} , forest fails to invade savanna even though climate favors forest (i.e., $P < P_M$) (A). Similarly, when dispersal is below d_c^{sf} , savanna fails to invade forest even though climate favors savanna (i.e., $P < P_M$) (B). Thus, in a 1D landscape with a precipitation gradient, the savanna–forest boundary may stabilize at the dispersal barrier due to fire–vegetation feedback even though it may not have realized its bioclimatic limit P_M . This ecological mechanism—referred to as range pinning—can potentially explain how mesic savannas are maintained in central Madagascar.

stable equilibrium points—savanna and forest—and at an unstable equilibrium $T_{unstable}^*$ (black curve in Fig. 4 A). Because the patch is initially in the savanna state, fire feedbacks maintain the patch in the savanna attractor and, consequently, forest invasion fails.

Next, we increase d , which graphically corresponds to raising $P(1 - T) - \phi$ by $d \left(\frac{T_F}{T_S} - 1 \right)$. For a low value of d , the resulting curve given inside the square brackets again has two stable roots. But if d increases past a threshold value, d_c^{sf} , the savanna and unstable roots collide and disappear, and the tree cover jumps to the forest equilibrium (gray curve in Fig. 4A). Thus, for any value of $d < d_c^{sf}$, forest fails to invade savanna, that is, the boundary ceases to move when it encounters the barrier. Intuitively, forest invasion fails because, in a limited dispersal landscape, fire feedbacks at the boundary savanna patch prevents trees from closing the canopy.

Note that the above graphical argument only provides sufficient conditions on d for range pinning. In fact, pinning occurs even when d is slightly greater d_c^{sf} (see Appendix S1). In Appendix S1: Fig. S4, we numerically simulate Eq. 4 to obtain necessary and sufficient conditions on d for which forest fails to invade savanna, supporting the intuition developed herein. These simulations also reveal that the likelihood of pinning, or the pinning range, increases near P_M .

An analogous argument can be constructed to find sufficient conditions on d for which savanna fails to invade patch $k + 1$ when $P < P_M$. At this patch

$$\frac{dT}{dt} \approx \left[P(1 - T) - \phi + d \left(\frac{T_S}{T_F} - 1 \right) \right] T. \quad (5)$$

Here again, we lose the subscript $k + 1$ for convenience. As d increases, $P(1 - T) - \phi$ drops by $d(1 - T_S^*/T_F^*)$. The bracketed term in Eq. 5 has one unstable and two stable roots until a threshold value of d , d_c^{fs} , above which the forest and unstable roots collide and disappears, and the tree cover jumps to the savanna equilibrium (Fig. 4B). Thus, in a 1D landscape with precipitation gradient, the boundary can pin at the dispersal barrier, which otherwise would continue until it reaches P_M .

The model elaborated above makes four key assumptions that may be violated in Madagascar. First, the model assumes a landscape with one barrier; in reality, landscapes often have multiple barriers. Humphries et al. (2011) showed that multiple barriers have no or little effect on the conditions under which pinning is expected, but may determine where the boundary is pinned. For example, in a landscape with multiple barriers, the boundary will equilibrate at the one that it

encounters first, provided all the barriers meet the pinning requirements. Second, we present pinning conditions at the barrier. It is possible that the boundary may instead pin before reaching the barrier, because of long-range dispersal effects. Using a piecewise linear growth function, we present analytical conditions for pinning for all locations. We find that the boundary may pin at multiple locations near the barrier, but the pinning interval is widest at the dispersal barrier (see Appendix S1 and Fig. S2). Third, a linear barrier in a 2D landscape may have holes (e.g., mountain passes) that may allow the climatically favorable biome state to escape. Using simulations, we show that, if the width of the pass is small, the boundary may still stabilize at the edges because of edge effects and curvature dynamics described above (see Appendix S1: Fig. S5). Fourth, in our model, we assume local dispersal dynamics even though it is well known that plants can disperse over long distances (Kot et al. 1996, Clark et al. 1998), which may allow forest to establish beyond the barrier and expand thereafter. However, we are justified in ignoring it; our previous work has shown that long-distance dispersal has no effect on biome dynamics when they are governed by strong fire–vegetation feedbacks (see Aleman and Staver 2018, Goel et al. 2020). Because of this property of bistable systems (Elmer and Van Vleck 1999, Bates et al. 2003), occasional long-distance dispersal of forest seeds into highlands savanna patches will not flip the system to forest state. Therefore, all four scenarios produce results that are qualitatively consistent with our intuition from the 1D stepping-stone model presented above.

Large-scale simulations.—To check if range pinning is consistent with vegetation patterns in Madagascar, we simulate biome patterns using the 2D calibrated model presented in the previous section. Simulation methods are similar to those described in Goel et al. (2020), but this time, we also include information on the topography. Again, we use a binary dispersal scheme: using the topography map of Madagascar, we code all the patches along the steep slopes (that is, elevation angle above 3.5×10^{-3} rad) of the Central Plateau as dispersal limited (brown patches in Fig. 3B) with d equal to 0.1% of D . For all the other patches, we used the dispersal rate for the homogeneous stepping-stone model in the previous section (see Appendix S1: Fig. S6).

The simulation predicts drastically different biome patterns in Madagascar (Fig. 3B) when compared to the 2D diffusion model (Fig. 3A). We find dispersal limitation at the escarpment of the Central Plateau not only maintains mesic savannas in Central Highlands by preventing forest expansion but also maintains rainforests in southeastern Madagascar by preventing savanna expansion. Thus, simulation suggests range pinning provides a plausible theoretical explanation for how savannas could have been naturally maintained in mesic regions of Central Highlands.

DISCUSSION

Here, we develop a stepping-stone model to examine the potential role of dispersal barriers in the maintenance of tropical biomes in Madagascar. Contrary to the predictions of the bioclimatic models (Wuyts et al. 2017), the heterogeneous dispersal model suggests that the savanna–forest boundary in Madagascar is not set by climate (Fig. 3). Instead, topography, in interaction with fire feedbacks, exerts an overriding control in determining the location of the biome boundary. Specifically, the model predicts that the boundary can stabilize at a dispersal barrier despite being far from its bioclimatic limit (Fig. 4). This phenomenon, referred to as range pinning (Keitt et al. 2001), is consistent with reconstructed biome patterns from paleodata (see Fig. 1A, Table 2, and Appendix S1) and also explains why forests have not expanded into highland savannas, even though these regions are climatically suited to support forest. This mechanism for the maintenance of biomes suggests that savannas in central Madagascar may not be a product of deforestation.

During the French colonial era, environmentalists in Madagascar perceived fire as a destructive agent that had consumed 90% of the island's forests (de La Bâthie 1921, Humbert 1927). Postindependence, these views were reinforced by international organizations (Klein 2002), that contributed millions of dollars to fund conservation projects for planting trees and suppressing fires (Scales 2014). In support, the state of Madagascar introduced legislation to discourage burning practices, leading to conflicts between forestry departments and Malagasy farmers who have traditionally relied on fire for pastoral activities (Kull 2000, 2004). Similar misinterpretation of the role of fire in maintaining mesic savannas and domestic conflicts are widespread in tropical regions, including India (Joshi et al. 2018), Brazil (Durigan and Ratter 2016), and West Africa (Fairhead and Leach 1996). These notions have misdirected global conservation efforts in wet savannas that are under threat not only from land-use change (Aleman et al. 2016) but also from “reforestation” projects—such as the Bonn Challenge (WRI 2014)—that are aimed at sequestering carbon to slow global warming (Bastin et al. 2019) and restore “lost” forests that were never forests to begin with (Veldman et al. 2019). However, a growing theoretical, as well as empirical, literature on tropical plant distributions emphasizes that fire, in combination with other ecological processes, such as dispersal, may play a key role in maintaining overlapping rainfall ranges over which savanna and forest occur.

Broadly, two analytical approaches are used to explain the mismatch between climate and biomes. The mean-field models that ignore dispersal suggest that the climatic mismatch is maintained by fire feedbacks (Beckage et al. 2009, Staver and Levin 2012), which stabilizes initial biome states into local basins of attraction (e.g., in small isolated island ecosystems with no dispersal

influx or outflux). Meanwhile, 2D diffusion models that incorporate dispersive interactions at the savanna–forest ecotone posit that the climatic mismatch is instead maintained by source–sink dynamics, which is mediated by the geometrical shape of rainfall contours (see Goel et al. 2020 and homogeneous dispersal model above). Most landscapes, however, are dissected by dispersal barriers, such as rivers, plateaus, mountain ranges, and human settlements, to yield partially disjoint landscapes (Rapoport 1982). The stepping-stone model, presented here, describes the dynamics of biomes in such a landscape. When the landscape has a high dispersal rate, the width of the pinning interval approached zero around the Maxwell precipitation, and the stepping-stone model behaves like the diffusion model (see Appendix S1). But as dispersal becomes limited, the pinning region widens, and as a result, fire feedbacks may locally stabilize the boundary depending on the patch specific dispersal rate and the climatic conditions. Thus, spatial heterogeneity and local fire feedbacks can maintain savanna in regions where the climate can support forest and vice versa.

These dynamical properties of the stepping-stone model also present a very different view of how biomes will respond to climate change. For starters, range pinning at dispersal barriers may buffer against climate change and introduce spatial lags between bioclimatic and observed spatial limits of biomes (e.g., Rupp et al. 2001). Although experimental demonstration of spatial lags is often limited by the time scales of ecological change, paleoecological records corroborate this claim in Madagascar, where the current biome boundary (see Mayaux et al. 2000 and Fig. 1A) is remarkably consistent with Holocene distributions (Adams and Faure 1997b) even though the climate has changed substantially over this time (Buney 1996). There is an important caveat to this prediction, however. If climate change exceeds the pinning threshold (Fig. 4), we should expect to see rapid irreversible biome expansions over large spatial scales. These catastrophic shifts can also incur, for instance, as a result of ill-conceived afforestation plans in Central Highlands (WRI 2014). If the afforested patches increase beyond a critical size, the forest will rapidly expand to realize its bioclimatic limit (Goel et al. 2020), resulting in loss of both human livelihood and savanna biodiversity.

Conceptually, the maintenance of savanna and forest biomes in Madagascar by range pinning challenges the hierarchical view of distribution in biogeography (Pearson and Dawson 2003). Bioclimatic models often assume that at the continental scales, the climate is the dominant factor that determines the distribution of biota, whilst the importance of topography (amongst other factors) increases only at more local scales. However, our analysis suggests that synergetic effects of dispersal constraints and nonlinear feedbacks can equal or even sometimes outweigh the contribution of the climate in explaining tropical plant distributions. More broadly, because negative growth rate at low abundance is

ubiquitous in plant and animal populations (Allee 1927, Allee et al. 1949), even partially porous barriers can, in effect, become absolute barriers and stabilize geographical ranges over wide climatic conditions.

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